SZENT ISTVÁN UNIVERSITY

ANALYSIS OF OBSERVATION AND HUNTING BAG DATA OF EURASIAN WOODCOCK (*Scolopax rusticola* LINNAEUS, 1758) IN HUNGARY BETWEEN 2009-2018

Thesis of PhD Dissertation

Gergely Tibor Schally

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Doctoral school

Name: Doctoral School of Animal Science

Field of science: Animal Science

Head: Dr. Miklós Mézes
Professor, CMHAS
Szent István University
Faculty of Agricultural and Environmental Sciences

Supervisor: Dr. László Szemethy
Professor, PhD
University of Pécs
Faculty of Cultural Sciences, Education and Regional Development

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Approval of the head of the doctoral school	Approval of the supervisor

1. Introduction and objectives

1.1. Background

Eurasian Woodcock (*Scolopax rusticola*) is a species specialized in a cryptic way of life. Due to their camouflage and behaviour, the detectability of the individuals is very low. Thus, it is not surprising that the amount and the quality of information about the population size and trend are generally low. Not only their limited observability but also their migration in spring and autumn makes data collection and evaluation difficult. Hunting for Woodcock is allowed in most countries of Europe, so the majority of information available of the species is also from- or connected to hunting. However, in order to ensure the sustainable management of the species, it is essential to collect data on the population with reliable methods on a regular basis.

Regulation of Woodcock hunting in Hungary has changed several times until now. From 1970, the method of hunting was limited to posting, and the season was limited to spring. The two main reasons for this regulation were that this hunting method is most likely to have the least adverse effect on the population and that this season has no overlap and therefore no conflict with big game hunting. However, according to the European Union Council Directive 79/409/EEC on the conservation of wild birds, hunting in spring is prohibited, because it is the season when breeding and the migration to breeding grounds takes place. Although both regulations aim to protect the species, they formally contradict each other. The possible effects and risks caused by the derogation from the EU legislation can only be evaluated properly when scientific research and data are available. To preserve the traditional spring hunting in Hungary, a monitoring program started in spring 2009 with the coordination of the Hungarian Hunters' National Association. The primary goal of the program was to estimate the size of the migrating population associated with the country based on synchronized census data and to track its long term changes. The continuous and regular data collection makes it possible to evaluate the sustainability of hunting in the Hungarian context and its possible effects on the population. In addition to the basic information, the monitoring program also provided an opportunity to carry out further research through samples collected by hunting, to better understand the structure of the population and the biological background of the behavior of the birds.

1.2. Aims

Since the beginning of the monitoring program in 2009, I have been continuously involved in the collection and processing of data. The aim of my thesis was to analyse the occurrence and the population structure of the Eurasian Woodcock in Hungary between 2009–2018, based on the data of the monitoring program. Furthermore, I have evaluated the possible changes and trends in the given period. I processed the spring and autumn observation data, as well as spring hunting bag data of the National Woodcock Monitoring Program, and I evaluated them on the basis of uniform criteria, taking into account their temporal and spatial trends. I was looking for answers to the following questions:

1. How can the trend of the temporal and spatial occurrence of Eurasian Woodcocks be characterized during spring and autumn in Hungary?
2. Is there a difference between spring and autumn detections in terms of their frequency, the number of birds seen, and the proportions of birds heard relative to total detections?
3. How large was the population occurring in Hungary in spring between 2009–2018, and how did it change during that period?
4. Is there a relationship between the size of the population in spring and the measure of the hunting bag, as well as its sex and age ratios?
5. How did the sex and age ratios of the hunting bag change between 2015–2018, and was there a trend in them depending on the time of taking (month-day)?
6. Can any subpopulations be identified in the population sampled in Hungary, and can a spatiotemporal pattern be found in terms of genetic distances between individuals?

2. Material and Methods

2.1. Data collection

For this study, I used the observation and hunting bag data of the Hungarian Woodcock Monitoring Program. As the operation of the program would not be possible without the cooperation of many participants and a large amount of invested work, I consider it very important to clearly indicate the processes in which I actually participated actively. These processes were the following: design of observation and hunting bag data forms, design and operation of an electronic data upload system, collection, verification, storage and processing of electronic and paper-based data, acquisition and delivery of equipment for hunting bag sample collection, processing and evaluation of samples, taking part in annual county briefings for observers and publishing the results.

2.1.1. Collection of observation data

The program was maintained with national coverage, and it was based on synchronized roding survey counts performed weekly, 12 times during each spring and autumn. By comparing the census data from time to time, it is possible to detect the spatial and temporal changes that occur in it. The locations of the observation points were chosen by the observers and they carried out the observations every Saturday night in spring (Table 1) and every Tuesday night in autumn (Table 2). As the dates of the observations fell on different calendar days in each year, I determined their sequence numbers based on the sequence numbers of the calendar weeks (weeks 6–18 in spring and weeks 37–50 in autumn). There was a difference between the numbers of the starting week between among some years, so I was finally able to split the data into 13 observation dates in the case of spring, and 14 in the case of autumn. The data recorded on the standard paper forms were the identification number of the observation point, its geographical coordinates, the number of birds detected (seen and heard), the estimated size of the observed area, the exact duration of the observation, the weather characteristics and the land cover of the area. Coordinates of observation points were also available, making it possible to perform spatial analyses. In the period between 2009–2018, I collected and processed data from 101 710 spring (7 140–12 563 per year) and 47 467 autumn (7 755–10 364 per year) observation forms. Autumn observations were performed only in the period 2009–2013.

Table 1: Dates of the observations in spring (mm-dd) between 2009–2018

	Calendar week	Year									
Number	**number**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**
1	6		02-13	02-12	02-11				02-13		
2	7		02-20	02-19	02-18	02-16	02-15	02-14	02-20	02-18	02-17
3	8		02-27	02-26	02-25	02-23	02-22	02-21	02-27	02-25	02-24
4	9	02-28	03-06	03-05	03-03	03-02	03-01	02-28	03-05	03-04	03-03
5	10	03-07	03-13	03-12	03-10	03-09	03-08	03-07	03-12	03-11	03-10
6	11	03-14	03-20	03-19	03-17	03-16	03-15	03-14	03-19	03-18	03-17
7	12	03-21	03-27	03-26	03-24	03-23	03-22	03-21	03-26	03-25	03-24
8	13	03-28	04-03	04-02	03-31	03-30	03-29	03-28	04-02	04-01	03-31
9	14	04-04	04-10	04-09	04-07	04-06	04-05	04-04	04-09	04-08	04-07
10	15	04-11	04-17	04-16	04-14	04-13	04-12	04-11	04-16	04-15	04-14
11	16	04-18	04-24	04-23	04-21	04-20	04-19	04-18	04-23	04-22	04-21
12	17	04-25	05-01	04-30	04-28	04-27	04-26	04-25	04-30	04-29	04-28
13	18	05-02				05-04	05-03	05-02		05-06	05-05

Table 2: Dates of the observations in autumn (mm-dd) between 2009–2013

	Calendar week	Year				
Number	**number**	**2009**	**2010**	**2011**	**2012**	**2013**
1	37	-	09-14	-	-	-
2	38	09-15	09-21	09-20	09-18	09-17
3	39	09-22	09-28	09-27	09-25	09-24
4	40	09-29	10-05	10-04	10-02	10-01
5	41	10-06	10-12	10-11	10-09	10-08
6	42	10-13	10-19	10-18	10-16	10-15
7	43	10-20	10-26	10-25	10-23	10-22
8	44	10-27	11-02	11-01	10-30	10-29
9	45	11-03	11-09	11-08	11-06	11-05
10	46	11-10	11-16	11-15	11-13	11-12
11	47	11-17	11-23	11-22	11-20	11-19
12	48	11-24	11-30	11-29	11-27	11-26
13	49	12-01	12-07	12-06	12-04	12-03
14	50	-	12-14	-	-	-

2.1.2. Collection of hunting bag samples

Hunting of Woodcock between 2010–2018 was only allowed for the participants of the monitoring program with strict regulation and obligatory sample collection from each bird. The main purpose of sample collection was to assess the sex- and age structure of the population, but it also allowed us to examine factors that affect the observations and also the genetic relationships among the birds. Only the official participants of the monitoring program were allowed to hunt for Woodcock, they have got the necessary permits from the hunting authority only for the purpose of collecting samples. Samples from birds between 2010–2014 were processed by the University of Sopron, and from 2015, they had to be sent to the Szent István University, Institute for Wildlife Conservation (IWC). The sample collection was conducted at national level between 2015–2018, in my dissertation I examined the data derived from that period. The data of the taken birds (place, time with year-month-day-hour-minute accuracy, body length, body weight, sex of the individual) were registered by the hunters on standardized paper forms. In addition, wing samples had to be sent with each paper form, which was needed to estimate the age ratio of the population. Based on the moult stages of the wing feathers, it can be determined whether the given Woodcock was a first-year bird or an adult one.

Between 2015–2017, muscle tissue samples were also collected from each individual for population genetic studies. The result can be used to assess whether the Woodcocks migrating through Hungary at different times and in different places originate from the same or different breeding grounds. The containers for collecting the samples (2 ml "Micro test tube" half-filled with 70% ethyl alcohol), paper forms and envelopes were packed together and they were sent to the participants of the monitoring program with the help of the county coordinators according to quotas established annually. The samples collected by the hunters were forwarded to the IWC with the help of the county coordinators. We recorded the data of the samples in a database and we also created a photo archive of the wings. In total, I processed the data of 11 073 individual spring hunting bag samples (2 021–3 609 per year) in the period between 2015–2018.

2.1.3. Assessment of the areas characterized by the observation points

It can be assumed, that the size of the visible area during observation influences the probability of detection. However, the size of the visible area is not necessarily suitable for characterizing the density of Woodcock in a given area, at most if the individuals are evenly distributed in space. As the spatial distribution of individuals is much more likely to be uneven, the density calculated from the visible area can be a significant overestimation. It would be very difficult to determine for each point, exactly how large an area they characterize, but a general approximate value is definitely worth determining. Based on the reported distances covered by the birds during habitat-changes (DURIEZ *et al.* 2005; HOODLESS & HIRONS 2007; GUZMÁN *et al.* 2017) and the radius of the area used during roding flights (HIRONS 1980), I chose 1 km^2 as the size of the area characterized by the observation points. With GIS software, I covered the entire country with a 1 km^2 cell-size grid (93 832 in total). Based on their location, I assigned the observation points with properly identifiable coordinates (2 160 – 79,7% of the total data set) to the cells encompassing them. Further data processing based on observation numbers (calculation of weighted spatial means and population size estimation) was performed using the data projected on the 1 km^2 grid. The number of cells covered by the observation points varied between 809–966 in the case of spring and between 713–848 in the case of autumn data. While there was no significant variation in the number of cells covered over the years, there was large variability in their locations. I was able to link the hunting bag data to 539–750 cells per year.

2.2. Data analysis

Data management and graphical representation were performed with Microsoft Excel 2016. Statistical evaluations were performed with PAST (v3.24) and R (v3.6.0) software. I performed spatial analyses, database connections, and data mapping with QGIS (v2.18.24).

2.2.1. Analyses of observation data

The analyses of the observation data for the spring and autumn periods were performed according to uniform criteria, and I compared their results with each other.

- I prepared a descriptive characterization of the time spent with single observations, and the size of the visible areas reported by the observers (minimum, maximum, median, mean, standard deviation) for the spring and autumn observation data grouped by years. I also examined the possible differences of both variables within and between years using a one-way ANOVA method. The effect of the size of the areas and the length of time for the observations influencing the number of detections was tested by Spearman rank correlation analysis.
- I prepared a descriptive characterization of the number of Woodcocks detected (seen / observation point / observation date) (minimum, maximum, median, mean, standard deviation) for spring and autumn observation data grouped by years, and plotted their frequency distributions with boxplot diagrams grouped by year and observation date.
- I calculated the ratio of Woodcocks heard compared to all detections (seen + heard) for each observation (at one observation point and one

date) and plotted their mean and standard deviation at the time of observation. Ratios were aggregated on an annual basis (total heard / total detected in a given year) and compared by Welch t-test between spring and autumn periods.

- Detection rates (the ratio of successful observations to total observations) were calculated to eliminate discrepancies from multiple observations for each observation time point. To determine the proportions, I used only the number of Woodcocks seen, but the number of birds heard was not taken into account during this process due to their presumably high periodic variability. I plotted the temporal variation of the detection rates within a year and calculated a correlation between the data series of each year by pairing the detection rates of the same observation times. I also calculated the annual variability of the results for each observation date (coefficient of variation – CV), which I compared between the seasons with a two-sample t-test. Detection rates were also calculated on an annual basis (total number of successful observations / total number of observations) and compared between seasons with a two-sample t-test for the period 2009–2013. I compared the annual averages of the birds observed (total number of sightings / observations in a given year) between the seasons with Welch t-test.
- To characterize the spatiotemporal aspects of the detections, I connected the data to the cells of the 1 km^2 cell-size grid using GIS software. The number of points in each cell was not uniform, despite the recommendation of a distance of 1,5 km between them, so only the point with the maximum detection value was included in each cell. Spatial mean points weighted by the number of Woodcocks seen were calculated for each observation date (separately per year). I plotted the development of the X and Y coordinates of the spatial mean points (in meters) per observation date on a map and diagram. The temporal trend of the spatial means was examined using a general linear regression model.

2.2.2. Analyses of hunting bag sample data

- I prepared the descriptive characterization of the number of birds taken at one point and one event (mean, standard deviation, minimum, maximum). I calculated the total number of takings at one point in a year, and the summary was also performed with the cells of the 1 km^2 cell-size grid.
- I plotted the changes in the number of takings within a year (the number of birds taken per day and in total per week) on a scatterplot, and similarly to the observation data, I evaluated the relationship between the changes in the annual data series using Spearman rank correlation analysis.
- To characterize the spatiotemporal changes of the takings, I connected the hunting bag data to the cells of the 1 km^2 cell-size grid with GIS. Each cell contains the weekly sum of the number of takings for each point within. To ensure comparability with observation data and the proper sample sizes required for spatial processing, I summarized the numbers of birds taken on a weekly basis according to the schedules of observation dates. Spatial mean points weighted by the number of takings were calculated for each (observation) date. I plotted the changes in the mean points over time on a map and a diagram, and I examined the temporal trend of the spatial means of each year with a general linear regression model.
- I examined the relationship between the weekly spring detection rates and the weekly taking trends (using Spearman rank correlation) within each year for the 2015–2018 period. For comparability, I also used the 1 km^2 grid and the weekly aggregation of the hunting bag data.
- I characterized the development of sex and age composition within a year. I only took into account the data of the takings for which the time of the taking and the age and / or sex of the given birds were properly available. I examined the differences between the sex and age composition between the years with χ^2 test and Cramér's V-test, the trend of their development within the years with a linear regression model, and their possible correlation with the size of the hunting bag with Pearson correlation test.
- The within-year changes in the total number of males and females per week were compared using the Pearson correlation test, and the comparison was also made for the age groups.

2.2.3. Assessment of the population size

- I calculated the basic land cover composition ("forests", "agriculture" and "other" combined categories) of the cells covered by observation points by intersecting the 1 km^2 cell-size grid with the current latest (2018) national land cover map of the CLC (© Copernicus Program; created with the support of the European Union). Based on the result, I determined the criteria for the selection of cells potentially suitable for Woodcocks. The main consideration in defining the criteria was the presence of forested areas, the proportion of which exceeded 10% in 95% of the examined cells, and the proportion of agricultural areas could not exceed 90%. Based on the criteria, I categorized each cell in the whole country into “suitable” (the proportion of forested areas is at least 10% and the proportion of agriculture is at most 90%) and “unsuitable” groups. I did not classify cells that did not cover entirely the territory of the country.
- I determined the maximum values of the detection numbers of the points in each cell for each observation date in each year in order to avoid errors due to multiple counting. Thus, only the detection data of one point in a cell was calculated.
- The distributions of the detections in the cells were extrapolated to all the 36,600 cells classified as suitable at each time point. For example, if 50% of the cells contained 0 detections, 1 bird was detected at a further 40%, and 2 were detected at 10%, then the total number of individuals at that time was calculated as:
  N = (0,5 × 0 × 36 600) + (0,4 × 1 × 36 600) + (0,1 × 2 × 36 600).
- According to previous studies, the proportion of females is influenced by the method of sample collection and observation (FARAGÓ & LÁSZLÓ 2013), thus I corrected the population sizes calculated for the given dates with the sex ratio. The assumed sex ratio differs from the proportions previously registered in hunting bags. The proportion of males is higher than that of females in the spring hunting bag (~ 80% males), so presumably their proportion may be similar during observation – in fact, it may be even higher if males are more likely to be repeatedly observed. However, in wintering areas, during hunting with pointing dogs, this proportion was different (~ 40% males) (FARAGÓ & LÁSZLÓ 2013). During that type of hunting in wintering grounds, the sex ratio of the hunting bag is likely to be much closer to the true sex ratio. Therefore, I have applied the following correction: I calculated 80% of the estimated number of birds (number of males) and then divided it by their proportion registered during hunting with pointing dogs (0,4)($\mathbf{N \times 0{,}8 = N_{corr} \times 0{,}4}$; or simply $\mathbf{N_{corr} = N \times 2}$).

- I summarized the numbers of individuals for each observation date and calculated their maximum value for each year for the entire spring period. The maximum value shows the maximum number of Woodcocks occurring in Hungary at one time (“detection peak” or “migration peak”) during a given period, thus eliminating the possibility of taking into account individuals multiple times because they are staying in the same place for several weeks in a given period. The sum of the numbers of individuals from each observation date takes into account all individuals seen, so the results are likely to be affected by multiple counts. In order to reduce the uncertainty, I used both the maximum value of each date and the total number of individuals for the whole period to characterize the population of the given year, and the strength of the relationship between the results of the two methods was examined by Pearson correlation analysis.
- I examined the trend of the spring population size determined with this method in the period between 2009–2018 using a general linear regression model.
- I examined the relationship between the estimated population sizes and the hunting bags for each year with Pearson correlation analysis, and I checked whether there could be a connection between the estimated population size of the given year and the hunting bag size of the previous year. I did not only take into account the hunting bag data from the period 2015–2018 because the game management statistics collected regularly at the national level (CSÁNYI et al. 2018) allowed me to use also the data of the period 2010–2014 for the comparison.

2.2.4. Methods of the population genetic study

The population genetic studies were carried out with the coordinated work of a well-organized team, a significant part of which – the laboratory tests and the analysis of the data derived from them – were performed by the staff of the National Agricultural Research and Innovation Centre. As a member of the team, I was involved in the design of the studies, the sample collection, the selection of the subsample actually tested, and the evaluation and publication of the results. Therefore, in view of the overlapping work processes, I describe the methods and results of the research in plural form.

In our study, we analyzed the variability of eight microsatellite markers and characterized the genetic diversity of Eurasian Woodcocks occurring in Hungary in the spring period and the possible structuring of the population. We examined whether any subpopulations could be distinguished in our sample and examined whether individuals that were closer to each other in space and time were genetically closer to each other than to other individuals. We performed analyses of 240 Woodcock muscle tissue samples preserved in 70% ethyl alcohol collected in the spring period of the National Woodcock Monitoring Program. During the selection of the subsample, we aimed to maximize representativity in terms of space and time, as well as sex and age. When determining the spatial parameters, we divided the country geometrically into 4 approximately equal parts. When establishing the time parameters, the duration of the 2015 spring season was divided into 3 nearly equal parts: February 15–March 7, March 8–April 5, April 6–May 2. An equal number of individual samples were randomly selected from the groups we formed. Sex and age groups were also selected in equal proportions if sufficient numbers were available. The sex of the birds was determined by dissection, and their age was determined by the molting stages of their feathers. For five birds, it was not possible to determine the age. The groups served only to ensure the representativeness of the sample, but due to their low number of items, they were not used as variables in further analyses.

Muscle tissue samples were stored in ethyl alcohol at –20 °C. Whole genomic DNA was isolated from the samples using the Genomic DNA Mini Kit (Geneaid Biotech Ltd, Taiwan) and the High Pure PCR Template Preparation Kit (Roche Diagnostics AG, Switzerland) according to the instructions of the manufacturers. The quality and amount of isolated DNA were checked with an ND-1000 spectrophotometer (NanoDrop Technologies, Inc., USA) and DNA integrity was determined by 1% agarose gel electrophoresis. DNA samples were diluted to a concentration of 15 ng/µl for PCR examinations; DNA products below 15 ng/µl were used undiluted for further analysis. After isolation, genomic DNA was stored at −20 °C until further processing. For genotyping of the samples, we used STR primers (Sru1-24b, Sru1-24c, Sru54b, Sru74a, Sru79d, Sru87b, Sru113a, Sru128b) isolated and tested previously by CARDIA *et al*. (2007), and then we optimized the strength of the obtained signals under multiplex conditions (comparing several markers in one reaction space). PCR multiplexes were compared in a final volume of 25 µl using the QIAGEN Multiplex PCR Kit (QIAGEN GmbH, Germany) in a LifeECO instrument (Hangzhou Bioer Technology Co., Ltd, China). PCR products obtained with fluorescently marked primers were separated by capillary electrophoresis at BIOMI Ltd. using an ABI 3100 Genetic Analyzer (Applied Biosystems Group, USA). Allele sizes were determined using Peak Scanner (v1.0) software (Applied Biosystems Group, USA), and the resulting allele sizes were recorded in an MS Excel spreadsheet. The filtering of null alleles and scoring errors was performed with Microchecker software (v2.2.3). To avoid the re-sampling of individuals, we performed the "Identity Analysis" function of the CERVUS software (v3.0.6). The number of alleles per locus (Na), the expected (HE) and observed values (HO) of heterozygosity, the deviation from Hardy-Weinberg equilibrium (HWE), and the degree of genetic diversity for each locus and averaged for all loci were calculated with CERVUS and GenAlEx (v6.501) software.

Several different approaches were used to assess population differentiation in the study area. The Bayesian clustering method and Markov Chain Monte Carlo (MCMC) simulation implemented in STRUCTURE (v.2.3.4) were used to infer the most probable number of genetic clusters without a priori definition of populations. The analyses were run using an admixture model and correlated allele frequencies with a burn-in period of 250 000 replicates and a sampling period of 750 000 replicates for the number of clusters (K) from 1 to 10 with ten independent runs for each K. To determine the number of genetic clusters, we used the method of EVANNO *et al*. (2005) with the program Structure Harvester (v.0.6.94). The second approach was a discriminant analysis of principal components (DAPC), a multivariate method implemented in the adegenet package with R (v.3.3.1) that identifies clusters of individuals without using any population genetic model. We used the "find.clusters" function for the identification of the optimal number of clusters (K) with the "choose.n.clust" option and the Bayesian Information Criterion (BIC). After that, DAPC was employed to assign individuals into populations, retaining all the principal components. Additionally, to detect possible spatiotemporal patterns of population structuring, we performed a general linear model with the genetic distance between samples as the dependent variable, the temporal (days) and the geographical (meters) distances and the interactions of these factors as independent variables. Genetic distance values were calculated with GenAlEx, and the model was fitted using the function "lm" with R (v.3.3.1).

3. Results

3.1. Observation data

Observers spent an average of 1,1 hours ($s = 0,3$ hours) with observation during in spring. The duration of the observations also varied between the years ($F_9 = 26,64$; $p < 0,001$) and the dates ($F_{12} = 9,153$; $p < 0,001$), but the differences were presumably only due to the relatively large number of data and can be considered methodologically insignificant. During the spring observations, the observers registered an average of 0,9 ha ($s = 2,3$ ha) as visible area. The sizes of the visible areas also varied between the years ($F_9 = 1524,2$; $p < 0,001$) and the dates ($F_{12} = 16,16$; $p < 0,001$), but the differences were presumably due to the relatively large number of data, which can be considered methodologically insignificant. It is important to highlight the mean and standard deviation of the starting year, 2009, which differed significantly from the following years. The main reason for this is that observers initially did not specify the size of the area within which they can surely detect Woodcocks, but the distance within which their actual visibility reaches. To eliminate this problem, the correct way to enter the distance was subsequently indicated on the observation form.

The number of sightings (Woodcocks seen) registered by observers during spring observations ranged from 0 to 28 ($\bar{x} = 0,8$; $s = 1,5$). It is important to highlight the average and standard deviation of the starting year, 2009, which differed significantly from the following years. The lower quartile and mean of the number of birds seen were also the highest at the 7^{th} observation date. In 65,9% of all observations (67 073 / 101 710) no Woodcock was seen. There was a significant but very weak correlation between the size of the visible area and the number of Woodcocks seen (Spearman $r = -0,069$; $p < 0,001$). I also found a significant but very weak correlation between the duration of the observations and the number of Woodcocks seen (Spearman $r = -0,008$; $p = 0,008$).

Observers spent an average of 1,2 hours ($s = 0,4$ hours) with observations in autumn. The duration of observations varied between years ($F_4 = 117,31$; $p < 0,001$), but not between dates ($F_{13} = 0,972$; NS). The differences were presumably detected due to the relatively large number of data and can be considered methodologically insignificant. During the autumn observations, the observers occasionally registered an average of 0,8 ha ($s = 1,2$ ha) as the size of the visible area. The size of the visible areas differed between the years ($F_4 = 89,657$; $p < 0,001$), but not between the dates ($F_{13} = 0,859$; NS). The number of sightings (Woodcocks seen) occasionally recorded by the observers in autumn ranged from 0 to 12 ($\bar{x} = 0,4$; $s = 0,9$). The mean number of Woodcocks seen at each observation date was 0. In 72,4% of all observations (34 355 / 47 465) no Woodcock was seen. The annually aggregated detection rates did not differ significantly between spring ($\bar{x}$ = 0,4; s = 0,1) and autumn ($\bar{x}$ = 0,3; s = 0,01) (Welch t_4 = 2,408; NS), but the annual averages of the number of Woodcocks seen (spring: $\bar{x}$ = 0,9; s = 0,3; autumn: $\bar{x}$ = 0,4; s = 0,03) differed between the two periods (Welch t_4 = 3,395; p < 0,05). No correlation was found between the duration of the observations and the number of Woodcocks seen (Spearman r = 0,006; NS). I found a significant, but very weak correlation between the size of the visible area and the number of Woodcocks seen (Spearman r = 0,016; p < 0,001). I found a difference in the annual proportions of heard birds relative to total sightings between spring and autumn (t_8 = 18,288; p < 0,001). Autumn values were only a fraction of those registered in spring.

I found strong (r > 0,58) and statistically significant (p < 0,05) correlations among the majority (34 / 45 data series pairs – 75,6%) of the annual spring detection rate curves. The curve for 2017 differed from the curves of several other years, but despite the minor differences, this outstanding year was the same as the other years in terms of its basic characteristics. The temporal dynamics of detection rates can be characterized by a single-peak bell curve in each year. The ratios of 0% between 10 to 28 February rose steadily to 70–90% until 20 March, after which they fell to around 0% by 15 April. At the peak, 8,7%–11,4% of all detections (seen) occurred in each year. In the period before the peak, the degree of variance was higher between the years, in the period after the peak it was much smaller. Variability was lowest at the peak.

In the case of the autumn data, I found a strong (r > 0,70), statistically significant (p < 0,05) correlation among the majority (7 / 10 data series pairs – 70%) of the annual curves of the individual detection rates. The temporal dynamics of detection rates, like in spring, could be characterized by a single-peak bell curve in each year. A significant difference was that the values recorded at the autumn peak were much lower than in the spring. They rose steadily from around 0% from 15 September to around 50% until 31 October, before falling back to around 0% until 30 November. In 2010, the observation period was unusually two weeks longer (14^{th} date), in which case a further decrease in detection rates to around 0% was observed. The variability was a fraction of the spring values in the case of autumn, but the two periods were similar in that the degree of differences between the years was the smallest at the peak.

There was a spatiotemporal shift in the weighted spatial means of the spring detections, toward both North and East. Within a given year, the direction was not clear in all cases, but the aggregate data confirmed the increasing trend. The mean values for both X and Y coordinates showed a continuously increasing trend (X: r^2 = 0,30; t = 7,043; p < 0,001; Y: r^2 = 0,48; t = 10,323; p < 0,001), the standard deviations of the X coordinate (W–E) were notable in the first three and last two dates, while in the case of the Y coordinate (S–N), the first and last two dates were notable. In the case of the hunting bag data, a trend with a similar direction and slope were observed in spring, the strength of the linear relationship was also similar (X: $r^2 = 0,26$; $t = 3,549$; $p < 0,01$; Y: $r^2 = 0,59$; $t = 7,084$; $p < 0,001$). The weighted spatial means of the autumn observations, although to a lesser extent, also showed a spatial shift (X: $r^2 = 0,02$; $t = –1,015$; NS; Y: $r^2 = 0,16$; $t = –3,302$; $p < 0,01$), in the opposite direction as in spring, in compliance with the previous hunting experience and presumption.

3.2. Hunting bag sample data

During the spring periods, data forms of 1–6 birds taken ($\bar{x} = 1,2$ specimens; $s = 0,5$ specimens) were received from each point. The total number of takings at the level of 1 km^2 size cells also ranged from 1 to 6 ($\bar{x} = 1,2$ specimens; $s = 0,5$ specimens) at each date. The number of Woodcocks taken in one year at one observation point varied between 1–30 specimens ($\bar{x} = 3,6$ specimens; $s = 3,2$ specimens). Annual takings at the level of 1 km^2 cells also ranged from 1 to 30 specimens ($\bar{x} = 3,9$ specimens; $s = 3,4$ specimens).

Without exception, I found statistically significant ($p < 0,01$), moderately strong correlation ($r > 0,46$) between the daily changes of the takings of each year. The low taking values recorded during periods, which are otherwise characterized by high numbers, are the results of takings registered on Saturdays. The majority of the participants in the monitoring program only performed observations on Saturdays and did not hunt that day, especially in the evening. The exception was mainly the data of the takings registered at dawn, which I did not use in the comparison of the daily developments in order to avoid distortions. I found a strong correlation between the spring detection rates and the total number of takings on a weekly basis within each year with the Spearman rank correlation analysis (2015: $r = 0,94$; $p < 0,001$; 2016: $r = 0,93$; $p < 0,001$; 2017: $r = 0,91$; $p < 0,001$; 2018: $r = 0,91$; $p < 0,001$). In the case of the spring hunting bag data, a spatiotemporal trend with a similar direction and slope to the observation data was observed.

Between 2015–2018, the proportion of males was several times higher than that of females, and the proportion of females ranged between 15,3–24,9%. Among the years, the χ^2-test indicated a significant difference in the proportions of the sexes ($\chi^2_3 = 80,566$; $p < 0,001$), but the χ^2-test is sensitive to large sample sizes, therefore I used Cramér's V value, which highlighted that the degree of association between columns (sex) and the rows (years) was extremely low (Cramér's V = 0,086). The proportion of females in the total annual hunting bag did not show a trend-like change over the years ($r^2 = 0,46$; $t = 1,300$; NS). There was no correlation between the annual sizes of the hunting bag and the proportions of females within them (Pearson r = –

0,91; NS). The proportion of females did not follow a clear temporal trend in each year ($r^2 = 0,03$; $t = 1,078$; NS), but narrowed down to the observation dates with the appropriate number of data (3–9), the proportions can be characterized by a moderate linear trend ($r^2 = 0,56$; $t = 5,712$; $p < 0,001$). Despite the differences in the ratios from time to time, I found a strong correlation between the changes in the total number of taken males and females per week within the years (2015: Pearson $r = 0,95$; $p < 0,001$; 2016: Pearson $r = 0,92$; $p < 0,01$; 2017: Pearson $r = 0,97$, $p < 0,001$; 2018: Pearson $r = 0,99$; $p < 0,001$).

Between 2015–2018, the proportion of first-year birds in the annual hunting bag ranged between 48,3–57,6%, and in the examined period it decreased continuously ($r^2 = 0,92$; $t = –4,648$; $p = 0,043$). There was no correlation between the annual size of the hunting bag and the proportion of first-year birds (Pearson $r = 0,73$; NS). The change in the proportion of first-year birds by date could not be characterized by a clear trend in each year ($r^2 = 0,006$; $t = –0,481$; NS), nor narrowed down to the observation dates with the corresponding number of elements (3–9) ($r^2 = 0,01$; $t = –0,589$; NS). I found a strong correlation between the within-year changes in the number of first-year and adult Woodcocks in each year (2015: Pearson $r = 0,99$, $p < 0,001$; 2016: Pearson $r = 0,98$; $p < 0,001$; 2017: Pearson $r = 0,96$; $p < 0,001$; 2018: Pearson $r = 0,997$; $p < 0,001$). I did not find any difference in the proportion of sexes between the different age groups (Cramér's $V = 0,060$).

3.3. Assessment of the population size

According to the calculation method I developed, the size of the spring population in the period 2009–2018 for the entire observation period was 418 122–915 996 individuals per year ($\bar{x}$ = 650 858 individuals; s = 159 548 individuals). In the case of data narrowed down to the observation peaks, it ranged between 125 286–257 624 individuals ($\bar{x}$ = 178 014 individuals; s = 47 971 individuals). Within each year, I found a strong relationship (Pearson $r = 0,87$; $p = 0,001$) between the two population sizes determined. The size of the population was characterized by a slightly decreasing trend in the examined 10 years, in the case of the aggregated data for the whole observation period ($r^2 = 0,46$; $t = –2,606$; $p < 0,05$) and also in the case of the data narrowed to the peaks of detection ($r^2 = 0,58$; $t = –3,344$; $p < 0,05$). However, if we do not take into account the data of the starting and outlying year of 2009, the decreasing trend could not be justified either for the whole observation period ($r^2 = 0,29$; $t = –1,690$; NS) or for the data narrowed to the peaks of detection ($r^2 = 0,44$; $t = –2,340$; NS). The ratio of the hunting bag compared to the population size in the given years was between 0,3–0,6% for the aggregated data ($\bar{x}$ = 0,5%; s = 0,1%), and between 1–2,2% ($\bar{x}$ = 1,7%; s = 0,3%) for the data limited to the peak of detection in the period 2010–2018. I found a significant correlation between the sizes of the hunting bags and the population sizes of the given year (for the whole period in total) (Pearson $r = 0,74$; $p < 0,05$). However, I did not find a correlation between the hunting bags of a given year and the estimated population size of the following year (Pearson $r = -0,27$; NS).

3.4. Genetic diversity and population structure

The degree of genetic variability was found to be relatively high, with an average allele number of 8,625 and ranging from 4 to 15 per locus. The mean heterozygosity observed was 0,585, while the expected heterozygosity was 0,654. For two of the eight loci, we found a significant difference from the Hardy-Weinberg ratios; the differences were caused by a heterozygous deficit, presumably due to the high proportions of null alleles. Polymorphic Information Content (PIC) ranged from 0,309 to 0,838 ($\bar{x} = 0,614$) and the Shannon Information Index ranged from 0,674 to 2,142 ($\bar{x} = 1,395$). Both indicators point to a relatively high degree of genetic diversity.

Both STRUCTURE and DAPC studies have indicated genetic structuring. STRUCTURE assigned the highest mean probability points to a single genetic unit (K = 1) for the entire data set. Although the five-cluster (K = 5) model also received a high probability value, individuals could be assigned to the groups with the same probability. The “find.clusters” function of the DAPC study also detected genetic subunits. The lowest BIC values were obtained for an eight-cluster model, but these values were very similar for clusters 6–8. The general linear model showed a significant but very weak relationship between genetic distances and temporal and spatial distance values. ($r^2 = 0,002$; $F_{3,28} = 21,48$; $p < 0,001$).

3.5. New scientific results

1. Based on the large number of spatially and temporally representative observational data collected within the framework of a country-wide monitoring program which was developed with my participation and which was successfully operated for 10 years, I confirmed that there was a clear spatiotemporal shift in the concentration of the detections in Hungary. The shift occurred in a southwest-northeast direction in spring, and in the opposite direction, from northeast to southwest in autumn. The results confirmed the previous assumption that the evolution of the observations over time is related to the evolution of the migration of the birds and that reflects its course.
2. Based on the spatial and temporal changes of the spring hunting bag data of Eurasian Woodcock, I obtained the same result as with the spatial and temporal changes of the spring observations. The results confirmed the previous assumption that the spatial changes of the takings over time are related to the spatiotemporal changes of the migration and that reflects its course.
3. I confirmed that observers recorded significantly more detections of Woodcocks in spring than in autumn with the same methodology. Although there was no detectable difference between the two seasons in the annually aggregated detection rates, the lower number of birds detected and the significantly lower proportion of birds heard suggest that individuals behave differently in autumn and consequently have poorer observability.
4. Using the observation data of the monitoring program, I developed a possible calculation method for determining the size of the Hungarian Woodcock population in Hungary, which is suitable for characterizing the annual trend of the migrating Eurasian Woodcock population in spring.
5. I evaluated the trend of the spring population of Woodcock in Hungary in the period between 2009–2018. I found a remarkable fluctuation in the annual population sizes but based on my results, no clear increasing or decreasing linear trend could be identified.
6. I confirmed that there was a correlation between the estimated population size of the Eurasian Woodcock and the size of the hunting bag. Based on the result, the hunting bag – under persistent hunting conditions – may be suitable for monitoring changes in the size of the population.

7. On the basis of a large and representative sample, I confirmed that in the period between 2015–2018, the sex ratio of the hunting bag of Woodcock changed depending on the date. The proportion of females in the periods with the appropriate number of samples – between the beginning of March and the beginning of April – was characterized by a slightly increasing trend. Despite the within-year differences in the sex ratios, I found a strong correlation between the changes in the total number of males and females per week for each year examined.
8. On the basis of a large and representative sample, I confirmed that in the period between 2015 and 2018, first-year and adult Eurasian Woodcock were present in approximately equal proportions in the hunting bag, the variation in the ratios within a year could not be characterized by a clear temporal trend. I proved with a statistical method that the proportion of first-year birds in the hunting bag decreased continuously between 2015 and 2018. This decline may indicate a deterioration in their survival, but it may also indicate that breeding success has declined in recent years.
9. I confirmed that the genetic diversity of the Eurasian Woodcock population occurring in spring in Hungary was high, subpopulations that could be related to different breeding sites could not be clearly distinguished in the studied sample. Spatial and temporal patterns in the extent of genetic distances between individuals could not be detected.

4. Discussion

4.1. Observation data

I did not find an evaluable correlation between the time spent with observations and the number of recorded detections either for the spring or autumn periods, from which I conclude that the probability of observations peaks in a relatively short period of 0,5–1 hour. Observation for a shorter period of time is likely to reduce the probability of detection, but a longer period of time does not substantially increase it. Based on the results, in order to clarify and standardize the monitoring method based on the observation of roding Woodcocks, I propose that the observations should start uniformly half an hour before sunset and should last over a period of one hour. The size of the visible area may affect the probability of detection, however, this correlation has not been confirmed by the data. Similar to the time spent on observations, the size of the visible area on the observation forms was used to ensure the possibility of corrections with the factors influencing the results of the observations. In view of the results, I do not consider it necessary to indicate the size of the visible area on the monitoring data forms. In order to determine the size of the areas characterized by the observation points more precisely, I propose to carry out short-term, high-precision telemetry examinations based on the data of male Woodcocks caught with curtain nets during roding in spring.

During the spring periods, the majority of successful observations were occasionally limited to 1–5 detections, regardless of the year. The proportion of detections exceeding 5 did not exceed 10% in each year, the largest differences between the years can be explained by such outstanding values. In the case of high detection numbers, the multiple detections of some individuals presumably also played an important role. The numbers of detections clearly differed between spring and autumn observations. This is mainly due to the fact that the rate of successful observations was much lower in autumn, and the number of detections also proved to be higher in spring. There are two possible explanations for this. On one hand, there may not be as many Woodcocks present in Hungary in autumn as in spring, because they choose different migration routes. On the other hand, it is much more likely that in autumn, the behavior of the birds is different in some aspects than that in spring, which makes them much less likely to be detected during evening flights, resulting in a smaller number. This explanation is confirmed by the significant difference in the detections based on hearing between the two periods. Sounds affect the probability of detection since based on their sound, the presence of given birds can be detected from a larger distance, often before they are seen. Sounding, like communication between individuals, was of course also experienced in autumn, so in itself, it is not clearly related to reproduction, however its intensity proved to be much lower.

The spring detection rate curves can be characterized by the same main characteristics in each year, but in addition to the similarities of the main characteristics, the detection rates also showed remarkable variability at some observation dates, with the largest differences before the detection peak in the second third of March. The high variability of early spring observations is most likely due to weather conditions. Although the weather plays an important role in the accessibility of earthworms as a primary food source and in the conditions required for migration, there were no such differences found in the autumn observation data. The variability in autumn was a fraction of the results in spring, which can also be explained by the fact that the weather factors affecting the migration (temperature, precipitation and wind) also significantly influence the phenomenon of roding, which is typically connected to spring. Despite the differences, the seasons were similar in that the variability was also the lowest at the detection peak in autumn (early November). The detection rate curves did not reach 0% in autumn during the entire observation period, but in the one year in which the observation period lasted two weeks longer than in the others (2010), they fell lower than before. Based on this, it can be assumed that the autumn migration lasts longer than in spring.

The changes in the spatial concentration of the detections confirmed the previous assumption that there is a difference between the southwestern and northeastern corners of the country in the time of the appearance of the Woodcock. The spatial progress presumably does not reflect the spatial progress of the appearance of roding as a behavioral pattern within a population, but it actually reflects the displacement of the population in space. This assumption was mostly confirmed by the spatial progression of autumn detections, which occurred in the opposite direction compared to the spring data. The spatial shift reflects the progress of the majority of the migrating population. There may be several explanations for the larger variations in the early (before the 4^{th}) and in the late (after the 11^{th}) observation dates. They indicate, on the one hand, the great individual variability in terms of migration time and rate of progression, i.e., that individuals decide and choose their migration strategy based on environmental conditions, body condition, and genetic background. On the other hand, they may indicate that in the initial period, the majority of the detections result from birds wintering in Hungary, while the later ones result from the birds that are breeding in the country.

4.2. Hunting bag sample data

The maximum values of individuals taken at one point in an evening were in line with previous hunting experience and the observation data. It is important to note that while detections were recorded above 10 (in some cases even above 20) in several cases, the number of takings did not exceed them. In addition, the takings were, of course, limited to only 1–2 specimens in the majority of the cases. This can be explained on one hand by the fact, that shooting is a challenge for hunters, and they cannot shoot all birds. However, it may also confirm that repeated observations of individuals are usually common during observations. Assuming that the maximum values of the takings were derived from cases in which the hunters were able to shoot all roding individuals, these can be considered as the maximum registered densities in a given area. I found a strong relationship between the temporal progression of the hunting bag data and the temporal progression of the detection data in each of the studied years. The strong relationship confirms that the two data sets characterize changes in the same background variable (presumably the actual number of individuals). The spatiotemporal progression of the hunting bag data in a direction and slope similar to that of the observation data also confirms this, and the larger variations at the early and late dates were also noticeable.

One of the most important questions about the composition of the hunting bag is why it comprises mostly of males. According to the most obvious and generally accepted explanation, during spring roding, males are searching for females, so they fly more and can be shot more often. However, this behavior may make sense if mating can occur, which requires mature gametes. The results of previous histological examinations confirmed that the males may already have active sperm in the spring period (STRONACH 1983; MACHADO *et al*. 2006; ELBLINGER *et al*. 2008). The genitals of females, on the other hand, suggest a much less advanced state based on the results published by STRONACH (1983). However, the degree of sexual activity of females, at least in terms of follicle size, does not necessarily limit the success of mating. In birds, some degree of the capability of storing sperm is essential, because it takes 24 hours or more for mature oocytes to detach, but fertilization occurs less than an hour after ovulation (BIRKHEAD & MØLLER 1992b). Without the ability to store sperm, synchronization of mating, ovulation, and fertilization would be very difficult. Although such data on Woodcock are not yet known, based on documented data about bird species of similar body size and clutch sizes, such as the Japanese quail (*Coturnix japonica*), the Rock pigeon (*Columba livia*), or the American kestrel (*Falco spaverius*) time between mating and fertilization can take even about 8–10 days (BIRKHEAD & MØLLER 1992a). During that time, female Woodcocks can travel up to 1 300–1 700 km after mating, based on the results of satellite telemetry studies (ARIZAGA *et al.*

2015), and can begin nesting somewhere within that distance. Another explanation for the lower proportion of females may be that they may migrate at different times. The assumption that males may have some advantage from reaching the breeding grounds faster may be a logical explanation. Based on the within-year changes in the proportion of females in the hunting bag, it can be concluded that there is a difference between the sexes in terms of the start of migration, as the proportion of hens in the hunting area increased continuously during the spring period. However, even at the end of the spring period, the proportion of males was still higher, when the number of birds taken / detected had already been reduced to a minimum. On the other hand, the progression of the total number of takings per week for each sex was very similar each year. Another explanation can be that the females may be migrating at other times of the day. The Woodcock can usually be successfully observed in two relatively short periods during the day: at dawn and at sunset, at dusk. It is more likely, that during this period we observe Woodcocks that spend a few days resting and preparing to continue a long-distance flight than those who are just moving on; they may be at higher altitudes during the migration anyway. However, if, the latter were to exist for whatever reason, there would be no reason to seek a difference between the two sexes either. Migration-related relocation is an activity that puts a heavy strain on the birds and involves a number of risks; therefore, it is essential to do that under the best environmental conditions. Since there is no significant difference in body dimensions between the two sexes, it can be assumed that there is no difference in the optimal conditions for them either.

There are two possible explanations for the nearly 50% proportion of first-year birds in the hunting bag. One explanation is that first-year birds are more likely to be shot during spring hunts than adult ones because older individuals are more experienced. In this case, the proportion of first-year birds in the hunting bag was higher than their actual proportion within the population. Based on the ringing data, the proportion of birds aged as first-year was slightly lower (41%) (SCHALLY 2017), however, that was not a remarkable difference between the results of the two methods. The other explanation is that the probability of Woodcocks being shot or detected during roding is independent of their age. In this case, their proportion in the hunting bag shows their actual proportion within the population. This assumption is also confirmed by the result that I did not find a clear temporal trend in the proportions of the age groups within each year, they varied on a very wide scale, seemingly completely random, regardless of the time. The role of individual variability in the progression of the migration and in the detections is presumably much greater among age groups than in the case of sexes. The decreasing trend in the proportion of first-year birds in Hungary between 2015–2018 may indicate that their survival has deteriorated, but it may also indicate that the success of breeding itself has declined in recent years. However, as I have only examined a short period of time, I consider it very important to continue examining age ratios in the future in order to accurately assess and monitor the process.

4.3. Population size and trend

The size of the total European population of Woodcock has been determined in a wide range (13 800 000–17 400 000 individuals) (BIRDLIFE INTERNATIONAL 2016). The part of the population migrating through Hungary is probably only a fraction of this, given the location and size of the country. The population in Hungary in the spring period, calculated on the basis of observation data, has also ranged within wide limits in the last ten years, but in terms of its size it has fitted well with the available information on the European population. The final result of the calculation, of course, depends on many influencing factors, the greatest uncertainty of which is undoubtedly caused by the high degree of individual variability in the time, speed of the migration, and length of time spent at stopover sites. In order to reduce the uncertainty, I used both the maximum value of the dates and the total number of individuals for the whole period to characterize the population of the given year. In addition, I found a strong relationship between the values obtained by the two methods. The result of the calculation is also greatly influenced by the determination of the size of the area characterized by the observations. Therefore, it is possible that the population determined by the method I developed was significantly smaller than a previously published population size (1 483 000–6 890 000 individuals at the peak of detection and 5 924 000–28 317 000 individuals for the entire period), obtained with a different calculation method (SZEMETHY *et al*. 2014). The main reason for such a difference was that the previous method for the estimation of the density was based on the size of the visible areas reported by the observers. Since the size of the visible area did not affect the results of the observations, contrary to the previous assumption, it is presumably not suitable for characterizing the density of Woodcocks of a given area either. In addition, in many cases it results in density values that were many times larger than the densities calculated on the basis of the registered takings. For example, in the case of a 100 × 100 m reported visible area, 1 Woodcock detection results in a density of 100 individuals / 1 km^2, whereas the maximum value of simultaneous takings registered within 1 km^2 was only 6 based on the data collected in the monitoring program.

Absolute population estimation, with the influencing factors known so far, can only be done with very high uncertainty, and certain critical points, such as the size of the areas considered potentially suitable for the birds, do largely determine its outcome. Instead of an absolute population estimate, I consider it to be more reliable to use relative indices such as the "detection rate" and the "rate of high-density sites" to characterize the trend of the population. However, it would be essential to improve the spatial representativeness of data collection for this purpose. For this reason, and in order to better understand the habitat selection of Woodcock, I propose considering the partial or even full integration of the spatial sampling methodology used in France (FERRAND *et al*. 2008) or the United Kingdom (HOODLESS *et al.* 2009) in the Hungarian monitoring program. The essence of the method is that the territory of the country is divided into regions, and the squares (cells) of the same size with forest cover, which act as the location of the observations, are randomly selected in the same proportion in each region every year.

I found a remarkable fluctuation in the annual population sizes but based on my results, no clear increasing or decreasing linear trend could be identified. A decreasing trend was justified only in the case when I also took into account the data of the starting year of 2009, which can be considered outlying in many respects. However, as several data in that year – including the number of birds seen – differed significantly from the others, it can be considered as a preliminary survey, a methodological experience, and its comparison with the results of later years can be misleading. There were significant differences between the sizes of the population determined on an annual basis, and the trend can be characterized as fluctuating. This also makes it more difficult to clearly identify long-term changes.

Based on the available data, the size of the hunting bag was very low compared to the size of the population and it did not significantly affect the trend of the population size. The hunting bag of a given year depended greatly on how many Woodcocks could have occurred in the country in a given spring. Based on the result, the hunting bag – under unchanged hunting conditions – may be suitable for monitoring the changes in the size of the population. However, hunting-based migration research is not only a professional issue, thus for the appropriate assessment, policy and social perspectives must also be considered. The size of the population in the given year was completely independent of the previous year's hunting bag, the hunting in Hungary in its current form presumably does not affect the trend of the population.

Monitoring must be continued so that a given condition can always be assessed on the basis of up-to-date data and can be better understood by supplementing it with the results of further studies. To this end, I propose: (1) monitoring the trend of the population according to the previously developed methodology, with a possible increase in spatial representativeness (2) continuous collection of data on the age distribution of the hunting bag; (3) a specific and regular survey of the breeding and wintering population in Hungary; (4) a more precise understanding of the potential breeding areas of Woodcocks present in Hungary during spring with the help of modern technological tools, such as satellite telemetry and hydrogen isotope analysis.

4.4. Population genetic study

Relatively high genetic diversity was found in our sample of the population using microsatellites. According to the weak differentiation found in our samples, grouping all of them in one cluster seems more appropriate, suggesting an extensive admixture between populations of different breeding sites. Although some degree of structuring can be assumed, the clusters formed were largely overlapping and could not be clearly separated. Various demographic and historical factors may contribute to the lack of population structure. A high level of dispersal would be enough to prevent genetic structuring. There is no direct information about philopatry and the extent of natal dispersal in the species, but ringing data indicate that some individuals may breed away from their natal site (HOODLESS & COULSON 1994, SCHALLY 2017). Birds from different breeding areas can assemble in the wintering areas, and they can also cross each other's routes during the later spring migration. If mating of Woodcock is not limited to the breeding sites but occurs also during migration, this could affect population structuring like dispersal. Male and female Woodcock originating from different natal sites, regardless of their philopatry, could mate on migration and parent offsprings together. The low level of structuring can also be explained by the continuous nature of European breeding populations and the lack of barriers. If any population structuring does occur, it is not more likely to represent gradual differentiation over very large distances, and perhaps, this cannot be observed in a small snapshot of birds, like the ones that pass through the Hungarian flyway. Our results did not support the assumption that Woodcocks occurring in different places at different times in Hungary would belong to different breeding populations. The reason for a lack of spatial or temporal patterns in genetic differences is clear if there are no subpopulations to be distinguished. According to the European breeding population estimates (BIRDLIFE INTERNATIONAL 2015), and also to the European hunting bag estimates (FERRAND & GOSSMANN 2001) it is possible that a population in the scale of millions of individuals may traverse through the central European region during spring. Population genetic studies of such big populations would also require very large sample sizes in order to be able to identify differences clearly. For further studies about migration connectivity, it would be essential to compare our samples to populations of a broad range of breeding areas.

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