Thesis of the Ph.D. dissertation

IMPACT OF THE EUROPEAN EXPANSION OF THE EURASIAN COLLARED DOVE (*STREPTOPELIA DECAOCTO*) ON THE GENETIC DIVERSITY OF THE SPECIES

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Debrecen, 2018

1. Background and goals of the thesis

From being an occasional visitor, the Eurasian Collared Dove (*Streptopelia decaocto*) has become one of the most common bird species in Hungary over a relatively short time (30-40 years). It expanded similarly to the major regions of Europe and the expansion continues towards the African, Asian and American continents as well (SNOW et al., 1998; CROOKS et al., 1999; ROCHA-CAMERERO and HIDALGO DE TRUCIOS, 2002; ERAUD et al., 2007). This phenomenon is not uncommon however. Today, even though in a slower rate, masses of species colonize new territories to an extent that raises much concern as non-native species strongly impact biological diversity (HULME et al., 2009; BUTCHART et al., 2010; GALLARDO et al., 2017). The decline of diversity represents one of the major, increasingly important reasons for species extinction. The sudden appearance of invasive species in a new environment can upset the biological balance of the give territory (IUCN, 1999; BELLARD et al., 2016). They are successful competitors in the race for resources and often carriers of new diseases and parasites (BERNDT et al., 2014). In this situation, researches focusing on invasive species gains significance.

From its original range in Asia Minor, the Eurasian Collared Dove spread rapidly to European territories (GLUTZ és BAUER, 1980; CRAMP, 1985; FUJISAKI et al., 2010). For this reason and because its expansion in Europe is well-documented with several studies about the effect of their settlement, they make an excellent model animal of rapidly expanding species (HUDSON, 1972; COOMBS et al., 1981; HENGEVELD, 1988; ROBERTSON, 1990; KASPAREK, 1996; ROMAGOSA és LABISKY, 2000; ERAUD et al., 2007). Previous results also highlighted the need for genetic studies on such species (LEE, 2002, TSUTSUI et al., 2003) but the related knowledge is still incomplete in terms of the Eurasian Collared Dove. Genetic studies that focus only on this species haven't been performed yet. It is still unknown to what degree the European populations genetically correspond to the populations living in today's genetic center and it also remains unclear wheatear there are populations in Europe that became genetically isolated after the expansion. If there are such populations, it raises the question if they exhibit significant genetic variance or have to be considered a uniformed super-population.

A so-called non-invasive procedure – the collection of moulted feathers – was chosen as a sample collecting method, although during application the identification of the feathers

was uncertain in some cases. Distinguishing the moulted feathers of the European Collared Dove and those of the Feral Pigeon proved to be difficult even for professionals in some cases because of their similarities both in size and color. It was especially common when only a few pieces of feather were available from an individual.

Since in the sample collecting areas (predominantly urban areas) Feral Pigeons visit the same sites (parks, suburban areas) that are visited by the Eurasian Collared Dove there is a high chance for their feathers to mingle. Since using falsely identified feathers in the study would have lead to wasting of the available resources and gaining incorrect results it was necessary to limit the risks as much as possible. As no suitable method was found in the reference literature, we decided to use a method that is easy, quickly applicable and inexpensive. An exact method was developed allowing the identification based on moulted feather, and the method was used in genetic studies as well. Initially, more methodical approaches were used; finally morphological data sampling proved to be the most efficient solution for providing the best results and the one that meets the above criteria. The second part of the thesis examines this method development.

During the research the following goals were set:

- The identification of the haplotype of the Eurasian Collared Dove (*Streptopelia decaocto*) sequences that stem from Europe and other regions of the world was done with the 658 bp fragment of citochrome-oxydaze (COI) domain inside the mitochondrial gonenome (fragment 3651-4309 of sequence KX372273).

- Detection of the degree of genetic diversity between populations of the species living in different areas

- Morphometrical characterization of the Eurasian Collared Dove and Feral Pigeon (*Columba livia domestica*) feathers that are the most suitable for Deoxyribonucleic acid (DNA) isolation, data bank construction

- Method development applicable in genetic studies for the identification and species-level differentiation of the moulted feathers of the Eurasian Collared Dove

2. Material and method

2.1. Genetic examination

Samples (n=134) were collected from 14 countries altogether between 2013 and 2015 (Belarus 1, Bosnia and Herzegovina 1, Cuba 1, Cyprus 1, Czech Republic 6, France 11+10 (Guadeloupe), Great Britain 12, Hungary, 62, Italy 1, Netherlands 4, Poland 2, Romania 8, Spain 10, Turkey 4). Primarily moulted feathers were collected (HORVÁTH et al., 2005; VILI et al., 2007; VILI et al., 2009) but muscle tissue, blood and eggshells were also applied. Sample taking took place near nesting and sleeping sites where birds are the most likely to shed feathers. Shed feathers on the ground strongly degrade after a relatively short time (a few months) for this reason intact or less damaged feathers were used in the examination that were left by the doves a few weeks before collection (VILI et al., 2009). Feathers were stored at room temperature in dark, dry place between the times of arrivaland isolation (1-4 weeks). Delivery of the moulted feathers was done via post (VILI et al., 2009). During sample taking primary and secondary feathers were preferred since due to their size the Eurasian Collared Dove feathers do not contain enough blood necessary for the isolation method used in the study. Muscle tissue samples were taken from individuals shot during hunting in Hungary or from individuals hit by cars on roadsides. Muscle tissues were stored in Eppendorf Tubes filled with 96% ethanol at –20 °C (SEUTIN et al., 1991). Storing eggshells was provided in Eppendorf Tubes as well in the way described above. Blood samples were stored at –20 °C. Additional 18 sequences were available from NCBI data bank and involved in the examination during analysis, thus enabling us to have access to samples from areas that otherwise would not have been accessible for us.

The method by VILI et al. (2009) was used. Firstly the classification and identification of the feathers was done. During classification we removed fathers that were too damaged or polluted and therefore unsuitable for further work. Identification equaled the selection and removal of feathers stemming from other species. It was done based on size and color features of this species. After this in order to isolate genomial DNA (gDNA) the fraction at the upper umbilicus was removed with a blade. There is a thrombus here that is perceptible to the eye, the reaming of the withdrawn connective tissue during egg formation, because the nursing artery joins the calamus at this point. Nucleated red blood cells forming in this closed region usually (in case of larger feathers) contain DNA of suitable quality for the examination (HORVÁTH et al., 2005). In order

to maximize the amount of extractable DNA tissues found in the calamus were also applied and the tip of the calamus when it was necessary (blood was available) For gDNA extraction GeneJET Genomic DNA Purification Kit (Thermo Scientific, USA) was used. This Kit is suitable for DNA isolation in various animal tissues; bacterial cells and blood. Therefore DNA isolation from muscle tissue, blood and eggshell was performed following the same protocol. Since a specific protocol for feather processing was not attached, the gDNA protocol for mammal tissue and rodent tail was applied.

Amplification of the 749 bp fragment of the mitochondrial DNA COI gene was performed with PCR (Polymerase Chain Reaction) by using the following primer pairs (Awans et al., 2013) forward: 5'-TTCTCCAACCACAAAGACATTGGCAC-3'; reverse: 5'-ACGTGGGAGATAATTCCAAATCCTG-3'. The 10 µl reaction volume contained 1 µl dNTP (2mM), (Thermo Scientific, USA), 2 µl buffer (5u/µl) (Promega, USA), 2 µl $MgCl_2$ (2mM) (Promega, USA), 0.4 µl primer (10 pmol/µl) (Sigma, USA), 0.2 µl GoTaq polymerase (1.25 U) (Promega, USA), 2.4 µl dH_2O-t and 2 µl DNS template.

PCR reaction conditions were the following: at 94 °C for 5 minutes, then for 35 cycles: at 94 °C for 1 minute, at 60 °C for 1 minute, at 72 °C for 1 minute then at 72 °C for 5 minutes. 3 µl PCR product was amplified on 2 % agrose gel (1 X TAE buffer (Thermo Scientific, USA), 0.5 mg/ml GelRed (Biotium, USA), 2% SeaKem agrose (Lonza, USA), then the result was checked under UV ray. The PCR product – after considered suitable based on the results- was prepared for sequencing. Until posting it was stored at –20 °C. Sequencing was performed by Macrogen Europe Laboratory in the Netherlands. The resulting sequences was checked by MEGA6 (TAMURA et al., 2013) and the possible occurring problems were manually corrected. The fitting of sequences was done by CLUSTALW (LARKIN et al., 2007).

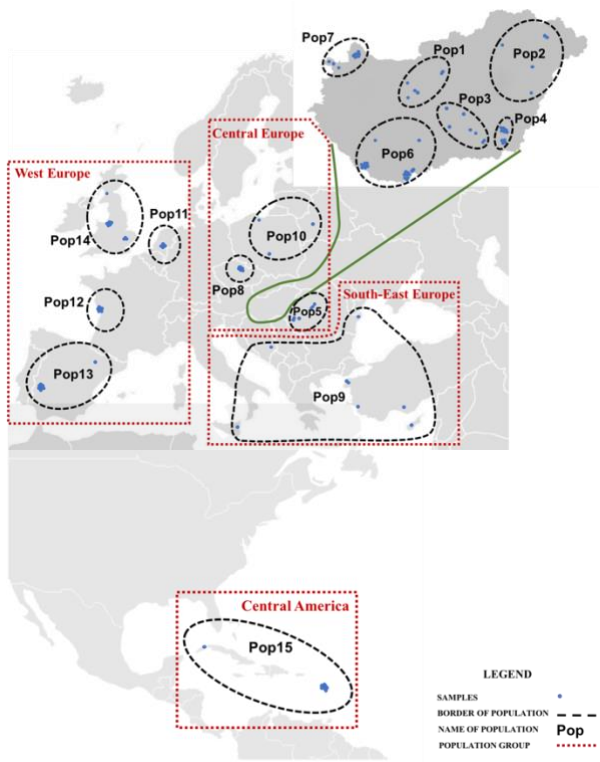

Figure 1: Assigned populations for examination of divergence between populations

MEGA6 software was used for dividing the sequences into equal fragments (658 bp). It was presumed that there are genetic differences between the examined individuals based on geographical location and groups were assigned (n=15) containing approximately equal number of individuals each (Figue 1). For each group and subsequently for 4 larger geographical areas, diversity indexes (total number of haplotypes(Ht), haplotype diversity (H_d), nucleotide diversity (π), and In/Del positions) were determined with ARLEQUIN 3.11. software (EXCOFFIER et al., 2005). During the determination of variable positions the whole mitochondrial *Streptopelia decaocto* genome downloaded from NCBI gene bank was used (KX372273). All the available Eurasian Collared Dove sequences downloaded from NCBI gene bank were used in further analysis of the identified haplotypes in order to detect the relation between halpotypes with the inclusion of Asian territories. The figure was made with Median-Joining Network Analysis, Hasegawa-Kishino-Yano (HKY) Model using Network 4.6 (BANDELT et al., 1999) software.

The analysis of the spatial arrangement of molecular variance between the assumed populations was performed by AMOVA (Analysis of Molecular Variance) (WEIR and COCKERHAM, 1984; EXCOFFIER et al., 1992) with the software Arlequin 3.11 (EXCOFFIER et al., 2005). The method examines mutational differences during the examination of stocks in addition to gene frequency comparisons. When assigning populations to be used in the study we took into consideration the presence of geographical distance and the possible geographical barriers (higher mountain chains and water surfaces). The bootstrap consensus tree describing the genetic distance of COI haplotypes was constructed by MEGA6 (TAMURA et al., 2013) software with HKY-model-based Maximum Likelihood method (HASEGAWA et al., 1985), implementing more than 1000 bootstrap repetitions (FELSENSTEIN, 1985).

Population structure and the most likely genetic classification within it was determined with the admixture model of STRUCTURE 2.3.4 software (FALUSH et al., 2003) which compares the allele patterns of the individuals in pairs and assigns genotypes to groups without pre-hypothesis. In the present study the 15 previously selected populations were applied. Markov Chain Monte Carlo (MCMC) algorithm was used which generates a Markov chain sequences of probability variables that converge to the aimed classification. The convergence is facilitated if the probability of the initial state is high in the aimed classification. For this reason samples are taken after the so-called burn-in phase (BODZSÁR, 2012). In the present study MCMC algorithm was used in 100 000

repetitions in addition to 10 000 burn-in steps and 10 iterations were set up for each different K value (K= number of groups). The results of STRUCTURE analysis were processed by Harvester (EARL and von HOLDT, 2012) applying the method by Evanno (EVANNO et al., 2005) to determine the most probable classification. This process equals the measurement of Delta K figures based on the probability figures generated by STRUCTURE. Result presentation was done by DISTRUCT software (ROSENBERG, 2004) with default settings. Principal Coordinates Analysis (PCoA) and Spatial Autocorrelation Analysis were performed using GenAlEx 6.501 software (PEAKALL and SMOUSE, 2006; 2012).

Due to the haploid feature of the data it was not possible to assign the populations with high certainity, therefore the process by WILLIAMS et al. (2007) was applied during spatial autocorrelation analysis, making haploid data applicable in the examination. The point of the process is that all samples were treated as a single population during spatial autocorrelation analysis because isolating populations cannot be implemented with high certainty. This enable the program to process each individual as a single unit and thus the examination of the genetic and geographical relations between data could be done.

Genetic discontinuity examination was performed using BARRIER software (MANNI et al., 2004). Sequences attained from NCBI green bank were also involved in the study. The geographical coordinates of the samples and the genetic distance matrix applied in PCoA analysis were used here. A bootstrap phase is needed to find the adequate number of barriers – but the process was not possible due to the lack of diploid data. Since no previous information was available to us about the exact number of geographical obstacles that possibly hinder the movement of doves, the number of set barriers was the equivalent of number of previously determined populations, that is 14 (number of barriers= number of populations-1).

Four indicators were applied in the examination of demographical changes. The null hypothesis of Tajima-*D* (Tajima's test of selective neutrality) (TAJIMA, 1989) is that polymorphism is the result of neutral mutations. The model assigns different sample units to different confidence intervals. Provided that „*D*" falls into the given confidence interval ($P<0.05$) and significantly differs from 0, null hypothesis is dismissed, which means that polymorphism is not the result of neutral mutation. As long as the population is not neutral we can come to various conclusions depending on the pre-indicator. If „*D*" takes negative value the population is expanding e.g. after a bottleneck- or founder effect, because more polymorphism sites will be present with low frequency than the expected

level. If „*D*" takes positive value it point to natural selection (or possibly a decreasing population). In this case the rate of polymorphisms with high frequency is low (TAJIMA, 1989). The statistical sensitivity of this indicator is the highest when the number of sample units is low. Fu's *Fs* examines the dispersal of haplotypes making it one of the most relevant tests to detect population growth but an extensive number of samples are needed to apply it reliably. When there are a low number of samples Tajima-*D* value is more suitable to be used. When high number of variable is available Fu's *Fs* is more suitable (LARSSON et al., 2013; TÓTH, 2014). Mismatch distribution (differential distribution curve) (ROGERS and HARPENDING, 1992) measures distribution value based on the differences of haplotype per pair found in samples in addition to using the method of least square (SCHNEIDER and EXCOFFIER, 1999) to measure demographical or spatial expansion. In case of continuous demographic expansion (even after founder effect) the curve peaks once indicating Poisson distribution, while a curve that peaks twice or more indicates a differentiated population (SLATKIN and HUDSON, 1991; ROGERS and HARPENDING, 1992). The null hypothesis of the test is that genetic samples come from a population with permanent numbers and random pairings. The probability of the model is given by „p" (SSD) value. Raggedness value indicates the point where the mismatch curve peaks (HARPENDING et al., 1993). During the examination of Tajima-*D*, Fu's *Fs*, Raggedness and mismatch distribution 100.000 repetitions were used. Analysis was run by Arlequin 3.11 software (EXCOFFIER et al., 2005).

2.2. Morphological examination

The Eurasian Collared Dove (*Steptopelia decaocto*) individuals (n= 25) used in the morphometrical examination were collected from the towns Előszállás and Hajdúnánás between August and October 2014. Birds were stored at -20 °C until preapartion. After defrosting, primary and secondary feathers were removed from the bodies. Before storing, feathers were individually signed and separately packed. Feral Pigeon (*Columba livia domestica*) individuals (n=11) were also collected from the agglomeration of the towns

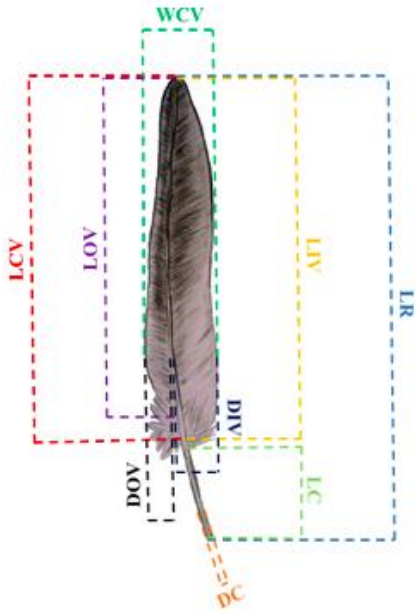

Figure 2: Variables on feather

Előszállás and Hajdúnánás and handled according to the process described above. The specific identification codes of the feathers and the explanations of abbreviations related to the examination are featured in Figure 1 and 2. In the examination primary feathers of the birds were used because DNA isolation in smaller feathers is much less effective in our experience, therefore larger feathers have more significance during sample taking. Rectrices are also suitable for this purpose due to their size and this feather of the two studied species are more distinguishable based on their color than primary feathers.

Table 1: Abbreviations used during morphometrical examination

ABBREVIATION	MEANING
P	primary
PL1-PL10	primary,left
PR1-PR10	primary, right
LR	length of rachis
LCV	length of complete vane
WCV	width of complete vane
LIV	length of inner vane
DIV	depth of inner vane
LOV	length of outer vane
DOV	depth of outer vane
LC	length of calamus
DC	diameter of calamus

The morphometrical data of the feathers were taken with caliper (Digital Meßschieber 150 mm) and graph paper. Measurement points were determined for each feather (Figures 1-2) and the resulting values characterize the given feather. Since two feathers of the same position (right and left) were taken from each individual it was reasonable to assess these data series by variables in later studies. By doing this we managed to reduce the number of variables and increase the number of elements.

Paired t-test was done for assessing examination by which the variance data series of feathers from the same position but opposite sides were compared by variables. In order to do the statistical separation analysis of the values of the two species within

variables, first Levene's test was used to check variance homogenity. In case of identical variances 2 sample t-test was used while in case of different variances Welch's test was applied. These tests show if the means of the two groups significantly differ from one another. The values of the varaibles that are characteristic of the species were gained by descriptive statistical analysis. In our case confidence interval is highly applicable. During interval estimation an interval was deterimend based on the sample that contains the trait to be estimated with the probability given in advance. The process intervals which charcterize the given species at the given siginificance level were provided. In terms of applicability is was important to reduce the number of variables used for species separation. It was done by highlighting the variables having the highest predictive impact, which was achieved by using 2 statistical tests. As the first step the predictive impact of varaibale was compared to species with discriminant analysis. Discriminant analysis is a method suitable for separating observed groups by considering more quantitaive variables simultaniously (FIDY and MAKARA, 2005). Chosing the variable combination that ensures the greatest explanatory impact was carried out with optimal Reression model. In the present study the optimal model was Binomial Logistics Regression. In this model qualitative variables are expalined by quantitative varaibles. Logistic Regression is a model where the dependent variable is binary categorical (dichotome) and the independent variable can be of any type: interval, ordinal or nominal (LÁZÁR, 2011). The two values of the dependent variable were the two species in this study while independent variables were the measure data of the feathers, of the type interval. The model enables us to select the combination of variables measured on ratio scale, providing us the combination that has the greatest explanatory impact in case of quantitive variables.

Binomial Logistic Regression applies Maximum Likelihood Tree estimation after transforming the dependent variable into logit variable. In this respect Logical regression estimates the possibility of a certain event to happen. Analysis was performed by Forward Stepwise method. The procedure keeps involving a new variable from the given ones (and may omit one that is already involved) with F test. If the value of F is higher then the set value the involvement of the variable takes place and the process starts again (FIDY and MAKARA, 2005). SPSS 21.0 softwre was used in every statistical analysis (IBM, 2012).

3. Results

3.1. mtDNA

During the examination of all the 134 samples 171 polymorphisms and 52 haplotypes were found. In case of all samples haplotype diversity was 0.843 (±0.037), and nucleotide diversity was 0.026 (±0.013). The number of In/Del positions was 2. In order to perform genetic diversity and structure studies 15 populations were assigned based on the guidelines detailed in the material and methods chapter. The highest haplotype diversity (1.000) was measured in the Western Hungarian population (Pop7) but figures were high in the other populations too. The lowest haplotype diversity was measured in the Dutch population (Pop11) with only haplotype Ht1 appearing. According to the reference data Ht1 frequency was high (70%) in the Caribbean population originated in the Netherlands. Nucleotide diversity exhibited low values in all the 15 populations. Subsequent results made it necessary to assign the populations to regions. The sequences of the regions related to diversity indicators were also measured. These are the number of polymorphism, total number of halpotypes (Ht), diversity value of haplotypes (Hd), nucleotide diversity value (π), and the number of In/Del positions. Larger geographical regions were also defined and 7 haplotypes and 117 polymorphisms appeared in South-Eastern Europe. Haplotype diversity was 0.064 (±0.036). In Central Europe the presence of 33 haplotypes, 118 polymorphisms and a value of 0.871 (±0.035) haplotype diversity and 0.023-os (±0.012) nucleotide diversity were detected. In Western European populations 20 haplotypes and 111 polymorphisms were found. Haplotype diversity was 0.836± (0.061), and nucleotide diversity was 0.023 (±0.012). In case of Central American population 82 polymorphisms in addition to 4 haplotypes, 0.491 (±0.175) haplotype diversity and 0.024-os (±0.013) nucleotide diversity could be determined. It can be determined in conclusion that the number of polymorphisms and haplotypes is high in relation to the number of samples in the joint examination of populations, geographical regions and all the sequences. Even thought haplotype diversity in the Central American region is significantly lower compared to other geographical regions it can still be considered a high value.

The difference can probably be explained by the fact that the Central American population is younger as it is present in the region only since 1970s. The high number of haplotypes is not an uncommon phenomenon within the Columbidae populations. Previously CALDERÓN et al. (2016) reported similar rates as he found 40 halpotypes

when examining the cytochrome-b sequences of 95 European Turtle Doves. Besides high haplotype diversity low nucleotide diversity value is also characteristic of each group which is one of the common features of rapid demographic expansion starting from a small, effective population (after bottleneck- or founder effect). Signs of the bottleneck effect were discovered by CALDERÓN et al. (2016) when examining the demographic history of the European Turtle Dove. He reported a significant and radical fluctuation in population size (Ne) but the molecular genetic signs of the fluctuation are less peceivable.

Figure 3 performed with Network Median-Joining analysis shows the relations of the halplotypes from individuals involved in the study.

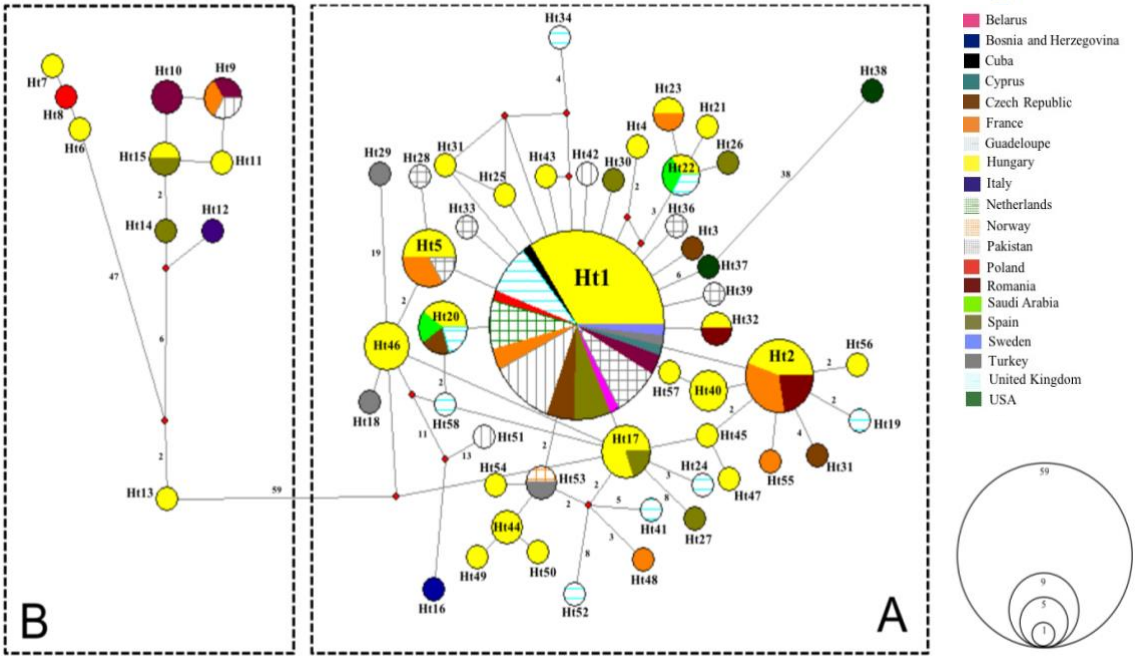

Figure 3: Median-Joining Network based on the joint (original and published sequences) data set from mtDNA COI region of *Streptopelia decaocto.* Each circle represents a haplotype with the size proportional to the frequency of collapsed sequences. Solid branches connecting circles represent nucleotide changes among haplotypes. Numbers represents the numbers of mutations. The branch length is not proportional to the number of mutations. Colours and patterns within circles illustrate the relative frequency of sequences from different geographic areas.

The high number of individuals of haplotype 1 (Ht1) is pervalent in Figure 3 (44.03%). BAJC et al. (2011) mentions in his study of wood grouse (*Tetrao urogallus*) that the stellar topography of the Network Tree, in which other haplotypes connect radially to a central haplotype (signed Ht1 in the present study), is characteristic of demographic expansion. Area "A" in Figure 3 also shows this stellar arrangement. In the present case haplotype Ht1 is the most likely common ancestor. However in the smaller figure more

distant groups begin to form especially in area “B” which can be interpreted as developing genetic isolation (JOSHI et al. 2013; TÓTH, 2014).

Haplotype Ht1 was present in 75% of the origins of the used sequences. Due to its central position and geographical distribution range it represents the most ancient haplotype, which is also indicated by similar traits in case of other species as well (POSADA and CRANDALL, 2001; NI et al., 2015). The limited geographical distribution of other haplotypes may point to a genetic differentiation process between populations (SUN et al., 2015). No obvious correlation could be demonstrated between the network of COI haplotypes and geographical distribution. The genetic structure analysis of populations was performed with AMOVA test. Geographically-based classification of the populations revealed the majority of variance. While looking for the source of genetic variance between groups ("A" and "B") supported by Network Median-Joining Figure and Maximum Likelihood Tree made by Mega6 showing phylogenic relations between haplotypes (Figure 4), it was found significant between groups (91.25%). The joint examination of the total number of samples variance within population was significant too (98.7%). These results underline the assumption that genetic variance in the species is primarily present within populations at individual level. Geographically-based isolation cannot be demonstrated between populations.

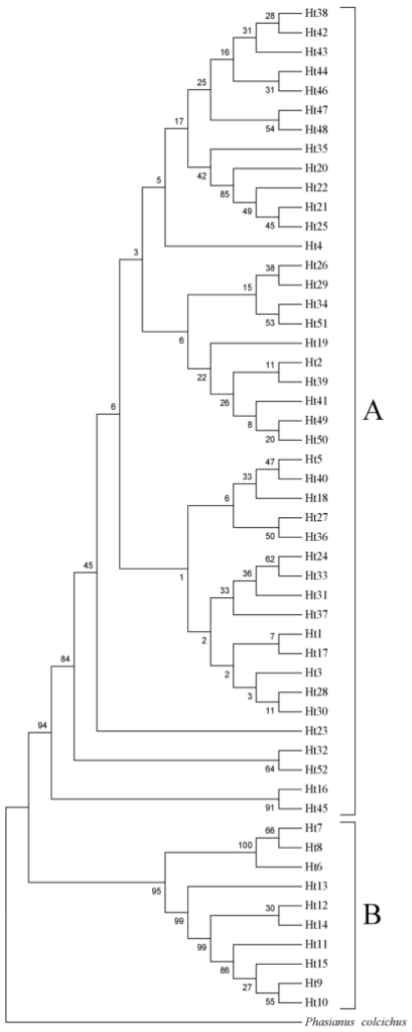

Figure 4: Maximum Likelihood bootstrap tree phylogeny based on haplotypes. Numbers above the branches refer to NJ bootstrap values. Brackets highlight the two genetic groups.

The number of genetic clusters was examined with STRUCTURE software package (FALUSH et al., 2003). Comparing all populations (K: 1-15) in relation to Delta K, we found that K value reached its first peak at K=2 and the second at K=3 (Figure 5). Based on the figure K=2 classification is the most likely as it is suggested by the highest peak in the figure. No correlation between the samples of the same genetic cluster and their geographical origin could be observed. There was no correlation between genetic and geographic data either. K=2 classification reinforces the conclusion that there are no relevant genetic differences between the populations of the species.

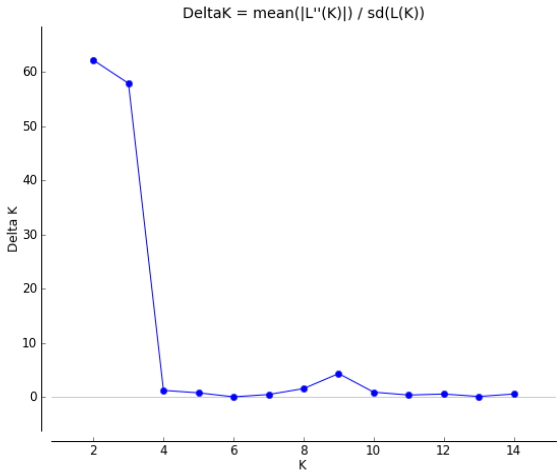

Figure 5: Plot of delta K values from the structure analyses of assigned populations

For detecting the possible interrelation between genetic and geographical distances aerial autocorrelation analysis and PCoA were used. In Figure 6 describing spatial autocorrelation analysis lines "U" and "L" represent the 95% confidence values of the null hypothesis (there is no special structure) with "r" representing correlation coefficient. As demonstrated by Figure 6 a positive correlation could be demonstrated between genetic variance and geographical areas within a 2000 km (r=0,124; P=0,001) distance. The find indicates that genetic structuring can be detected up to this distance. Over this distance gene flow stops in case of negative correlation (ÁLVARES-CARVALHO et al., 2016). The correlation value is considerably higher in the 1000 km class that is r=0.781; P=0.001 then declines steeply. For such a dispersive species, whose individuals have no difficulties covering great distances populations of large distribution range can be anticipated. Based on the steepness of the correlation

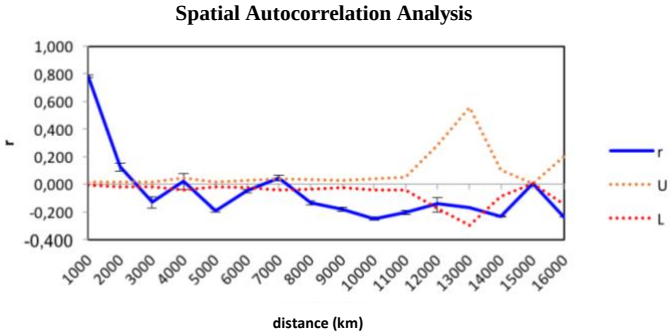

Figure 6: Spatial autocorrelation correlogram plots. The plot depicts results obtained from all geographic regions. The analysis considered geographic distances with even distance classes of 1000 km. Dashed lines encompass the 95% confidence interval of the null hypothesis, and each point represents the autocorrelation coefficient (r).

coefficient population barriers are expected to be found within a distance of 1000 km. The related data could be more specified by marking smaller sample taking sites and selecting a higher number of items in them. As the result of Principal Coordinate Analysis samples, which were taken from large geographical areas distant from one another, also appear. Consequently, it can be inferred that genetic structures that characterize specific geographical regions have not developed yet in case of the Eurasian Collared Dove. No expansion pattern could be identified based on our results. It can be partly explained by the very short time the species spread in addition it remains uncertain if Columbiane can exhibit such genetic features at all. CALDERÓN et al. (2016) examined 3 different migration routes of the Eurasian Collared Dove populations and did not find specific genetic structures related to them. BARRIER software (MANNI et al., 2004) was applied for the study of genetic discontinuity. In this examination the geographical coordinates of the samples and the genetic distance matrix used in PCoA were applied. Figure 7 represents the assumed expansion routes, population barriers and hidden genetic barriers in Europe. In Asia and the Americas the traces of genetic isolation could not be demonstrated because of the low number of items. It can also be explained by their short presence as the few decades since the colonization from Europe did not provide enough time for major genetic variations to evolve. Genetic barriers were identified only in the Hungarian territory. This population was isolated on the South-Eastern part of the Great Plain and another isolated one was found in the South, in South-Western Hungary. Both are highly developed agricultural areas where the members of the species find all the necessary resources to thrive on a relatively small area not having to migrate or wander over large territories. Identifing further population barriers will be possible if the number of samples is increased. It would enable a better understanding of the species' land use, which is needed because of the discrepancy in the trend data of nesting and wintering stocks. While the size of nesting stocks has been declining for years, wintering stocks have been increasing. Under these circumstances it is useful to know population barriers

Figure 7: The genetic and geographical isolation context on the study area (blue: Hypothetical geographic border of population, green: Hypothetical expansion path, red: Genetic barrier

and migration routes in terms of planning wildlife management and disease spreading (e.g.: bird flu).

Examining all the sequences together Tajima-*D* and Fu's *Fs* values were negative but they were not siginifcant values in either case. However, for Tajima-*D* it can be considered borderline significant (P=0.03) (Table 2). These values do not indicate expansion but is has to be noted that the study was performed with a low number of items and in such cases Raggedness value needs to be weighted more in examinations. In case of all samples neither mismatch distribution nor Raggedness value showed siginificant results (Table 2) which suggests a past expansion here (JOSHI, et al. 2013). The distribution curve has more peaks which indicates that isolated populations may have developed on the distribution range (ROQUES és NEGRO, 2005; TÓTH, 2014). Therefore, when the two genetically isolated gropus were examined separately for group "A" Tajima-*D* and Fu' F_S were negative and siginificant, and Raggedness was not significant (Table 2). The one-peak curve of mismatch distribution evidently supports demographic expansion that has taken place lately. In case of group "B" Tajima-*D* and Fu's F_S were positive and not significant and the mulit-peak curve of mismatch distribution point to a stagnating population. At the same time SSD and Raggeddness values suggest expansion in group "B" too. It is noticeable that neutral tests by the joint application of SSD and Raggedness values – with the excpetion of group "A" – failed to detect the evident genetic traces of a demographic expansion, which indicates that since the expansion in the last century demographic equilibrium has developed in cerain populations and isolation to a certain degree has began. If the short generation interval (1 year) is considered, our previous conclusion is affirmed.

Table 2: Results of neutrality tests and mismatch analysis

	Neutrality test				**Mismatch**			
Group	**Tajima-*D***	**P**	**Fu-*Fs***	**P**	**SSD**	**P**	**Raggedness**	**P**
A	-2.606	**0.000**	-25.914	**0.000**	0.414	0.000	0.010	**1.000**
B	0.674	0.779	1.811	0.787	0.050	**0.590**	0.043	**0.800**
All	-1.566	**0.030**	-6.399	0.121	0.010	**0.980**	0.007	**0.990**

4.2. Morphometrical examination

Selecting the variables that have the highest predictive impact was necessary to improve the method developed by us. During the analysis the impact of size variables was first examined with Discriminant aAnalysis (Table 3).

Table 3: Predictive Impact of variables based on Discriminate Analysis

Variable	Wilks' Lambda	Predictive Power (%)	Predicted Group Membership (%)	
			Dove	Pigeon
DC	0.144***	85.600	100	100
DIV	0.167***	83.300	98	95.500
DOV	0.296***	70.400	96	90.900
LC	0.263***	73.700	100	95.500
LCV	0.214***	78.600	100	90.900
LIV	0.224***	77.600	100	90.900
LOV	0.211***	78.900	100	90.900
LR	0.114***	88.600	100	95.500
WCV	0.161***	83.900	100	100

***P<0,001

Wilk's Lambda distribution is an indicator measuring predictive impact. 1 is subtracted from this value, and then it is multiplied by 100. As the result, the predictive impact can be gained in percentage. Classification Results (correct and incorrect) are presented in Table 4. showing in what percent the model is able to determine if a variable belongs to a category. These results are featured in Table 4 in the column „Predicted Group Membership" (%).

Table 4: The selection of variables to ensure the greatest explanatory impact combination by logistic regression. Numbers indicate in which step of the model the variables were used. "a" Nagelkerke R Square was 1 and Classification Results were 100% in case of both species

	DC	DIV	DOV	LC	LCV	LIV	LOV	LR	WCV
P10							1; 2; 3[a]	1	1; 2[a]
P9		1						1; 2[a]	
P8	1; 2[a]	1							
P7									1[a]
P6					1; 2; 3[a]			1; 2[a]	1
P5								1[a]	
P4	1		1; 2; 3[a]						1; 2[a]
P3			1; 2; 3[a]; 4[a]; 5[a]			4[a]; 5[a]	1; 2; 3[a]; 4[a]		3[a]; 4[a]; 5[a]
P2	1			1; 2; 3[a]		1; 2			
P1	1; 3; 4; 5; 6[a]; 7[a]; 8[a]	2; 3; 4		6[a]; 7[a]; 8[a]	7[a]; 8[a]			3; 4; 5; 6[a]; 7[a]	4; 5; 6[a]; 7[a]; 8[a]

Binomial Logistic Regression Model was used to determine the combination of variables that has the biggest predictive impact (Table 4). The fitting of the model was checked based on two methodologically different indicators. One of them is Nagelkerke R-squared, an indicator used to measure predictive impact. It shows in what percent result variables are explained by predictive variables. The other used indicator was the so-called Accuracy Table which shows in what percent of the cases the model found the species that the variable values characterize. Based on the above results, the consideration of the three variables with the highest predictive impact is suggested in isolating the primary feathers of the Feral Pigeon and Eurasian Collared Dove with an objective method. In application it is recommended to take the measurements of the diameter of the calamus (DC), length of rachis (LR) and the width of complete vane (WCV) of the collected

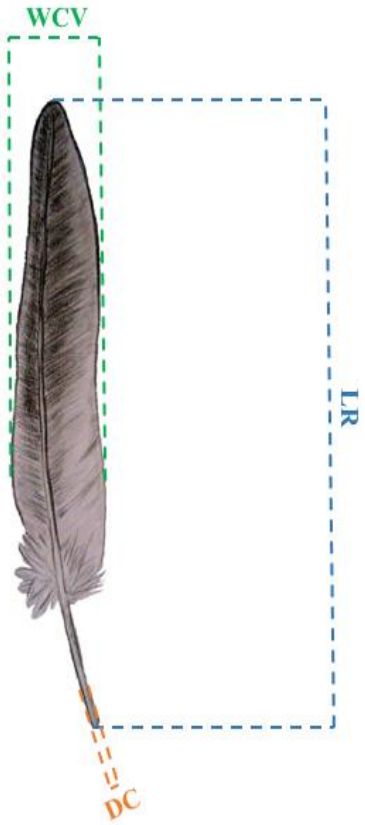

Figure 8: The applicable variables for separating both species on feather

feathers (Figure 8) then assess the data with confidence intervals determined at 95% significance level. In case of a found feather identifying the exact position of the feather and therefore the selection of the correct confidence interval is more difficult during identification. In terms of this problem, examining the shapes of feather tips is of help because in the majority of bird species the tip of the first outer 5-6 primary feathers are sharper than those that are located in inner regions. The angles of the feather tips are gardually increasing towards the inner region of the body. This visible difference helps us approximately locate the found feather on the wing. In case of uncertainity the number of variables involved into the identification can be increased.

4. New scientific results of the thesis

1/a. Based on our knowledge such large-scale research on the genetic diversity and structure of the Eurasian Collared Dove (*Streptopelia decaocto*) was firstly performed by us. Haplotypes in the 658 bp fragment of the citochrome-oxydaze (COI) domain I was first describe in this thesis. 58 haplotypes were detected based on 152 individuals with 52 out of them having been identified based on own sequences. The dominance of haplotype Ht1 is independent of geographical regions (44.03%) and genetic variance within a species is not associated with geographical distribution.

1/b. 2 genetically well separated groups were described within the species and designated „A" (n=120) and „B" (n=14). The presence of a demographic expansion following a bottleneck effect was proved with genetic methods which supports and reinforces the observations and hypotheses about the Eurasian Collared Dove. Genetic distances between Eurasian Collared Dove populations are characterized by low values. Gene flow within populations is also of importance which is supported by the low nucleotide diversity (π=0.026±0.013) and the fact that gene flow is detectable up to distance of 2000 km (r=0.124; P=0.001).

2. By examining the primary feathers of the Eurasian Collared Dove and the Feral Pigeon the possibility of isolating the shed and collected primary feathers of the two species in an exact way was proved. The descriptive statistical results in the database we developed enable species-level identifications of feathers. In case of the examined species the diameter of the calamus, length of rachis, and the width of complete vane are the most suitable indicators for isolating and identifying species and it has the biggest predictive impact.

5. Applicability of the results

1. The genetic diversity and structure of the Eurasian Collared Dove was firstly examined in the world with such a comprehensive sample taking. The results can serve as a factual and comparative basis for similarly researches in the future.
2. The sequences of the collected samples uploaded into the data bank can be used in taxonomical, philogenetic and population genetic researches in addition to diversity examinations.
3. The result regarding the gene flow and the genetic barriers of populations can be applied in addressing the issue of presence and numbers of the species, such as in terms of wildlife management, agricultural damage management and epidemiology.
4. Species identification based on the morphometrical parameters of feathers could play a relevant role primarily in genetic studies since the elimination of feathers of uncertain origin from the examination can save time and money.
5. Further utilizations fields of the morphometrical feather identification method may include differentiating Collared Doves from subspecies that are difficult to distinguish and protected or huntable species that are similar in appearance. In addition to this species identification is important in forensic investigating cases when planes collide with birds. In general DNA-based species identification was used for this purpose but if the remains of birds are available morphometrical examination of feathers can be a less expensive alternative.

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7. Publications

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Subject: PhD Publikációs Lista

Candidate: Zoltán Bagi
Neptun ID: U3K65G
Doctoral School: Doctoral School of Animal Husbandry
MTMT ID: 10038226

List of publications related to the dissertation

Hungarian scientific articles in Hungarian journals (2)

1. **Bagi, Z.**, Kusza, S.: A balkáni gerle (Streptopelia decaocto) genetikai diszkontiunitás vizsgálata. *Agrártud. Közl. 73*, 5-11, 2017. ISSN: 1587-1282.
2. **Bagi, Z.**, Kusza, S.: Molekuláris genetikai módszerek alkalmazása madárfajok esetében (irodalmi áttekintés). *Agrártud. Közl. 69*, 37-41, 2016. ISSN: 1587-1282.

Foreign language scientific articles in Hungarian journals (2)

3. **Bagi, Z.**, Posta, J., Kusza, S.: Morphometric characterization and exact separation of Eurasian Collared Dove (Streptopelia decaocto) and Common Pigeon (Columba livia forma domestica) moulted feathers. *Acta Agron. Óvár. 58* (1), 21-32, 2017. ISSN: 1416-647X.
4. **Bagi, Z.**, Posta, J., Kusza, S.: Chromatometric comparison of Eurasian Collared Dove (Streptopelia decaocto) and Feral Pigeon (Columba livia domestica) feathers. *Agrártud. Közl. 70*, 19-22, 2016. ISSN: 1587-1282.

Foreign language scientific articles in international journals (2)

5. **Bagi, Z.**, Dimopoulos, E. A., Loukovitis, D., Eraud, C., Kusza, S.: MtDNA genetic diversity and structure of Eurasian Collared Dove (Streptopelia decaocto). *PLoS One. 13* (3), e0193935, 2018. EISSN: 1932-6203. DOI: http://dx.doi.org/10.1371/journal.pone.0193935 IF: 2.806 (2016)
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Hungarian conference proceedings (2)

7. **Bagi, Z.**, Kusza, S.: Tollból történő DNS Izolálás a Debreceni Egyetem Állatgenetikai Laboratóriumában.
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Total IF of journals (all publications): 2,806
Total IF of journals (publications related to the dissertation): 2,806

The Candidate's publication data submitted to the iDEa Tudóstér have been validated by DEENK on the basis of Web of Science, Scopus and Journal Citation Report (Impact Factor) databases.

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12 March, 2018