

Theses of Doctoral (PhD) Dissertation

**GENETIC RESOURCES OF HUNGARIAN PIGEON BREEDING:
A GENETIC INVESTIGATION**

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1. INTRODUCTION AND AIM OF THE THESIS

The relationship between humans and the domestic pigeon (*Columba livia domestica*) dates back several millennia; the species was likely domesticated 3,000–10,000 years ago, although the exact timing remains debated (LEVI, 1996; HERNÁNDEZ-ALONSO et al., 2023). Throughout history, domestic pigeons have played important roles in multiple contexts: as symbolic and cult animals, as messengers, in sport and recreation, and as a source of food. Among these, meat production remains a key utilization pathway today, as pigeon meat can be produced with relatively low input while providing a high-quality protein source (MACKROTT, 1998; ASADUZZAMAN et al., 2012). The formerly significant Hungarian meat pigeon sector has declined in recent decades: breeding populations have decreased, and the competitiveness of local genotypes has weakened. Currently, domestic breeding systems rely largely on imported breeding stock, which poses both economic and genetic risks. At the same time, the widespread use of high-performance hybrids has narrowed the global genetic base (VEKIĆ et al., 2023), further increasing the importance of conserving and utilizing local genetic resources. Due to the limited availability of comprehensive genetic data on Hungarian pigeon populations, the application of molecular genetic approaches is essential to establish sustainable and cost-effective breeding strategies. Based on these considerations, the aim of this dissertation was to investigate the genetic diversity, population structure, and phylogenetic relationships of large-bodied domestic pigeon populations in Hungary, with particular emphasis on indigenous Hungarian breeds. In addition, the study aimed to identify single nucleotide polymorphisms (SNPs) associated with economically important traits in squab pigeon production, which may be utilized in selection programs. The results are expected to contribute to the conservation of domestic genetic resources and to meeting the increasing demand for high-quality animal protein.

Research objectives:

mtDNA-based diversity and origin analysis – Study I

1. Assessment of the genetic diversity of Hungarian and international-origin domestic pigeon populations relevant for meat production.
2. Investigation of genetic relationships among breeds and the domestication process using reference populations.

Multimarker-based population genetic analysis – Study II

3. Comprehensive analysis of the genetic diversity, population structure, and phylogenetic relationships of large-bodied domestic pigeon breeds using mtDNA (COI region) and 13 microsatellite (SSR) markers.
4. Comparison of the information content and applicability of different marker systems (mtDNA vs. SSR).

SNP (single nucleotide polymorphism)-based applied genetic analysis – Study III

5. Evaluation of the applicability of SNP chip technology developed for domestic chicken (*Gallus gallus domesticus*) in domestic pigeons.
6. Identification of potential SNPs associated with production traits and analysis of differences among utilization types.

2. MATERIAL AND METHODS

The study consisted of three methodologically distinct parts. In all cases, samples were collected from pigeons selected on the basis of the available pedigree information (ring numbers, as well as breeders' own records and knowledge of their breeding stocks) to ensure that no close kinship existed among the sampled individuals. During sample collection, breeders were specifically asked to identify unrelated birds for inclusion in the study, and additional individuals were sampled from a given loft only as long as this criterion could be met.

As part of the sampling strategy, efforts were made to recruit nationally recognized and well-established breeders who were active members of pigeon breeding organizations and had achieved long-term success in breeding the respective breeds. These breeders possess extensive knowledge of the domestic populations of the breeds they maintain and are widely respected within the breeding community. Consequently, the sampled individuals originated from multiple breeding lofts and different geographical regions. However, it should be noted that no unified pedigree registry exists for Hungarian pigeon breeds, and up-to-date information on population size and structure is not consistently available. Therefore, it is difficult to obtain an accurate estimate of the size of the studied populations. Nevertheless, all available information was utilized during sampling to assemble a dataset that was as representative as possible.

For all investigations, blood samples were collected from the brachial (wing) vein of unrelated pigeons. While the same sampling procedure was applied throughout the study, the subsequent sample preparation protocols differed according to the specific requirements of each type of analysis.

2.1. Sample Collection and Preparation

2.1.1. *Sampling and DNA Isolation*

Blood samples required for the analyses were collected from Hungarian breeds and internationally distributed foreign pigeon breeds between 2018 and 2023 from breeding lofts located in Hungary and Romania. Approximately 2 mL of blood was collected into tubes containing EDTA (ethylenediaminetetraacetic acid) as an anticoagulant. In contrast, samples from the Iraqi pigeon breeds were collected in Iraq between 2022 and 2023 by applying blood directly onto FTA (Flinders Technology Associates) cards.

In all cases, sampling was performed from the brachial vein (*vena brachialis*). Prior to blood collection, the puncture site was disinfected using a colorless alcohol-based antiseptic solution (Softasept, B. Braun, Germany). Each sample was assigned a unique identifier and stored at -20°C until laboratory processing. In the case of Iraqi samples, blood was immediately applied to FTA cards on-site, followed by a drying period of at least 6 hours prior to transport. Sampling did not result in mortality; all individuals remained in the breeding populations after sampling. The sampling procedure was approved by the local ethics committee of the University of Debrecen (approval number: 20/2023/DEMÁB). DNA isolation was performed at the Agricultural Genomics and Biotechnology Center of the University of Debrecen. Genomic DNA was extracted from a total of 395 blood samples using the protocol of ZSOLNAI and ORBÁN (1999), while 97 FTA card samples were processed using the MagCore® 401 protocol (RBC Bioscience Corp., Belgium) with a MagCore® Automated Nucleic Acid Extractor at the Department of Genetics and Genomics, Hungarian University of Agriculture and Life Sciences (Gödöllő). DNA concentration was measured using a NanoDrop1000 spectrophotometer (Thermo Fisher Scientific, USA).

2.1.2. Logical framework of the applied analyses

The analyses presented in this dissertation were structured in a stepwise, progressively narrowing framework (Figure 1). The study began with a broad-scale phylogenetic and phylogeographic analysis aimed at characterizing the genetic diversity, relationships, and origins of the investigated domestic pigeon breeds. Subsequently, the focus shifted to large-bodied breeds of particular relevance at the national level, allowing for a more targeted, multi-marker-based comparison. This phase enabled detailed analyses of population structure, inbreeding, and demographic patterns. In the third phase, the scope of the study was further refined to compare two distinct utilization types, with particular emphasis on identifying polymorphisms associated with production-related traits. Thus, the applied classification framework reflects both the gradual narrowing of the study scope and the increasing specificity and application-oriented nature of the research objectives.

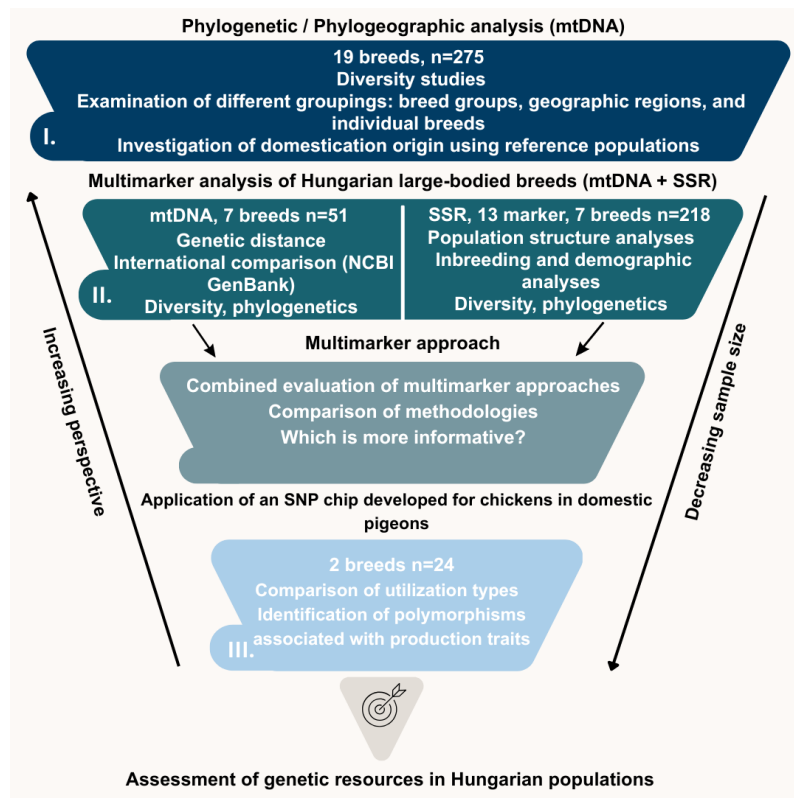


Figure 1: Logical structure of the applied analyses

2.2. Experimental protocols

During the mitochondrial analyses, specific but distinct fragments of the cytochrome oxidase I (COI) region of the mitochondrial genome were targeted.

2.2.1. Study I

Primer design and polymerase chain reaction (PCR) amplification

To optimize the analyses, a custom primer pair was designed to amplify a 664 bp fragment. Primer design was based on the complete mitochondrial genome of the domestic pigeon available in the NCBI GenBank database (GenBank ID: NC_013978.1). Among the tested primer sets, the G_728 primer pair proved to be the most efficient and stable, and was therefore used for PCR amplification.

PCR reactions were performed in a total volume of 50 μ L, containing 18 μ L distilled water (dH₂O), 5 μ L dNTP mix (2 mM), 10 μ L 5 $\times$ GoTaq Flexi buffer, 8 μ L MgCl₂ solution (25 mM), 1 μ L each of forward and reverse primers, 1 μ L DreamTaq Flexi DNA polymerase (Thermo Fisher Scientific, USA), and 6 μ L genomic DNA. Amplifications were carried out in a Biometra Tone thermal cycler. The cycling conditions included an initial denaturation (94 $^{\circ}$ C, 4 min),

followed by 35 cycles of denaturation (94 °C, 1 min), annealing (64 °C, 1 min), and extension (72 °C, 1 min), with a final extension step at 72 °C for 10 min. PCR products were held at 10 °C until further processing. Amplification success was verified by 2% agarose gel electrophoresis using a 100 bp DNA ladder. Sequencing was performed by MacroGen Europe B.V. (Amsterdam, Netherlands).

Data processing and statistical analyses

Raw sequence data and electropherograms were checked using Chromas 2.6.6 and manually validated. Sequence alignment was performed using the ClustalW algorithm, followed by editing and trimming in MEGA11. Haplotype number, distribution, and polymorphism and nucleotide frequency parameters were calculated using DnaSP 6. Genetic differentiation among populations was assessed using FST, genetic distances, and AMOVA in Arlequin 3.5.2.2, while pairwise distances were visualized in R (version 2.11.1). Evolutionary relationships among haplotypes were analyzed using Tamura–Nei-based dendrograms (MEGA11) and Neighbor-Joining phylogenetic trees (Network 5.0.1.1). The Eurasian collared dove (*Streptopelia decaocto*; MF381976.1) was used as an outgroup. Population structure was inferred using STRUCTURE 2.3.4 (MCMC: 100,000 iterations, 10,000 burn-in, 10 runs per K), and the optimal number of clusters was determined using STRUCTURE Harvester with the Evanno method. Genetic relationships among individuals were further explored using principal coordinate analysis (PCoA). Identified haplotypes were deposited in GenBank (PP952127–PP952153).

2.2.2. Study II

PCR amplification and fragment analysis

For the analysis of the mtDNA COI region, the widely used BirdF1 and BirdR1 primer pair was applied (AWAN et al., 2013), amplifying a 611 bp fragment. PCR reactions were performed in a total volume of 30 µL, containing 7.2 µL dH₂O, 6 µL DreamTaq Flexi buffer, 6 µL MgCl₂ solution (25 mM), 3 µL dNTP mix, 0.6 µL of each primer (1 pmol/µL), 0.6 µL DreamTaq DNA polymerase, and ~6 µL genomic DNA. The cycling protocol consisted of initial denaturation (94 °C, 5 min), followed by 35 cycles (94 °C, 1 min; 56 °C, 1 min; 72 °C, 1 min), and a final extension at 72 °C for 10 min. PCR products were verified on 2% agarose gels and sequenced by MacroGen Europe. For microsatellite analysis, 13 SSR markers were selected based on literature sources (TRAXLER et al., 2000; LEE et al., 2007). PCR reactions (10 µL) were

optimized into two protocols (“A” and “B”) with different annealing temperatures (60 °C and 55 °C). Reaction compositions and cycling conditions were adjusted accordingly to primer characteristics.

Capillary electrophoresis

Fragment analysis was performed using a QIAxcel Advanced capillary electrophoresis system (Qiagen, Germany). Multiplex sets were constructed based on fragment size to optimize efficiency. Each plate included a QX DNA Size Marker (25–500 bp), and results were evaluated using QIAxcel ScreenGel software.

Data and statistical analyses

Data processing followed the same workflow as in Study I (Chromas, ClustalW, MEGA11, DnaSP). Genetic differentiation was assessed using Arlequin, complemented by mismatch distribution analysis in R. Phylogenetic relationships were analyzed using Neighbor-Joining trees (MEGA11) and Median-Joining networks (PopART). To improve phylogenetic resolution, 50 additional COI sequences were retrieved from GenBank. The common wood pigeon (*Columba palumbus*; MF381976.1) was used as an outgroup. Newly identified haplotypes were deposited in the European Nucleotide Archive (ENA; accession numbers: GCA_965637565–GCA_965637685).

Microsatellite data analysis

Genetic diversity parameters (allele frequencies, N_a , private alleles, H_o , H_e , F_{IS}) were calculated using GenAlEx v6.5. F-statistics (F_{ST} , F_{IT} , F_{IS}), gene flow (N_m), and polymorphic information content (PIC) were estimated in R (version 4.4.3) using the ape, poppr, adegenet, and hierfstat packages. AMOVA was conducted in Arlequin and visualized in R. Bruvo distance matrices were calculated at the population level and visualized using dendrograms and heatmaps. Population structure was analyzed using STRUCTURE 2.3.4 (MCMC: 500,000 iterations, 100,000 burn-in, 10 runs per K; $K=2-15$), and the optimal clustering was determined using STRUCTURE Harvester with the Evanno method.

2.2.3. Study III

SNP-chip cross-application

The Illumina Chicken_50K_CobbCons SNP array (57,636 SNPs) was applied to pigeon samples. Genotyping was performed by Neogen Corporation (Lansing, MI, USA). Quality control of raw data was carried out using SNPviewer 4.1.2 (GenCall and GenTrain scores), followed by filtering and data processing in PLINK v1.9 and the argyle R package. Due to karyotypic differences between chicken and pigeon, PLINK parameters were adjusted (--chr-set 40; --allow-extra-chr). SNPs with high missingness (--geno 0.05) and low minor allele frequency (MAF<0.01) were removed. Linkage disequilibrium (LD)-based pruning was performed (--indep-pairwise 50 5 0.5 and 0.9). Principal component analysis (PCA) was conducted on the filtered dataset to compare genetic patterns between production types. Subsequently, literature-based filtering was applied to identify SNPs associated with meat quality traits and relevant QTL regions.

3. RESULTS AND DISCUSSION

3.1. Results of Genetic Diversity Analyses (Studies I and II)

3.1.1. Genetic diversity indexes

Genetic diversity and relationships among populations were investigated using both mitochondrial and nuclear markers. In Study I, genetic diversity indices based on the traditional breed classification are summarized in Table 1.

Table 1: Genetic diversity indices by traditional breed groups

Indexes Groupings	Number of elements (n)	Number of polymorphisms	Number of haplotypes	Haplotype diversity (Hd) $\pm$ SD	Nucleotide diversity (p) $\pm$ SD
Utility pigeons	159	111	17	0.396 $\pm$ 0.049	0.0150 $\pm$ 0.0087
Cropper pigeons	14	2	3	0.275 $\pm$ 0.148	0.0014 $\pm$ 0.0017
Trumpeter pigeons	7	1	2	0.286 $\pm$ 0.196	0.0014 $\pm$ 0.0019
Tumbler pigeons	47	4	4	0.125 $\pm$ 0.065	0.0010 $\pm$ 0.0014
Squab pigeons	20	35	4	0.363 $\pm$ 0.131	0.0173 $\pm$ 0.0103
Structure pigeons	10	120	6	0.778 $\pm$ 0.137	0.1894 $\pm$ 0.1019
Poule Type pigeons	19	1	2	0.105 $\pm$ 0.092	0.0005 $\pm$ 0.0010

The number of polymorphisms was highest in the Structure pigeon group (120), and was also notably high in the Utility (111) and Squab (35) pigeon groups compared to the other groups. The lowest number of polymorphisms was observed in the Poule Type (1) and Trumpeter (1) pigeons. Due to differences in sample size, these absolute values are only partially comparable; however, it is noteworthy that the Structure pigeons exhibited remarkably high polymorphism

despite its small sample size ($n = 10$) and the inclusion of only a single breed. This suggests that the genetic variability of this group may indeed be higher, which is further supported by the high haplotype diversity ($H_d = 0.778 \pm 0.137$) and nucleotide diversity ($\pi = 0.1894 \pm 0.1019$). In line with the number of polymorphisms, relatively high haplotype diversity was also detected in the Utility pigeons ($H_d = 0.396 \pm 0.049$) and Squab ($H_d = 0.363 \pm 0.131$) pigeon groups, whereas the lowest values were observed in the Poule Type and Trumpeter pigeon groupings. Nucleotide diversity values were generally low across most breed groups; however, in addition to the Structure pigeons, higher-than-average values were also observed in the Utility ($\pi = 0.0150 \pm 0.0087$) and Squab ($\pi = 0.0173 \pm 0.0103$) pigeons. The similar haplotype and nucleotide diversity values observed in Utility pigeons and Squab pigeons may be consistent with the contribution of Utility pigeon breeds to the development of Squab varieties.

The data were also evaluated based on the geographical regions of the breeds, the genetic diversity indexes of the resulting regional groups are summarized in Table 2.

Based on Table 2, the number of polymorphisms was high in both the Asian (129) and the Great Plain (91) groups, which is consistent with the number of haplotypes observed. The highest number of haplotypes was detected in the Asian (15) and Great Plain (13) groups, while lower values were found in the other geographical groups.

Table 2: Genetic diversity indexes by geographic region

Indexes Groupings	Number of elements (n)	Number of polymorphisms	Number of haplotypes	Haplotype diversity (H_d) $\pm$ SD	Nucleotide diversity (π) $\pm$ SD
Breeds from the Hungarian Great Plain	73	91	13	0.486 $\pm$ 0.071	0.0245 $\pm$ 0.0133
American pigeons	30	2	3	0.191 $\pm$ 0.093	0.0009 $\pm$ 0.0014
Asian pigeons	114	129	15	0.305 $\pm$ 0.057	0.0313 $\pm$ 0.0165
Hungarian squab pigeons	19	18	2	0.105 $\pm$ 0.092	0.0092 $\pm$ 0.0061
Mediterranean pigeons	40	65	6	0.576 $\pm$ 0.078	0.0181 $\pm$ 0.0104

The high haplotype diversity observed in the Mediterranean group ($H_d = 0.576 \pm 0.078$) is likely related to the more complex origin and breeding history of these breeds. According to the literature, the genetic patterns of domestic pigeon breeds have been shaped by long-term artificial selection, repeated crossbreeding and introgression, as well as geographical and breeding history differences (STRINGHAM et al., 2013). Accordingly, the higher diversity of the Mediterranean group may reflect their longer and more complex breeding history. This is particularly evident when compared to the American ($H_d = 0.191 \pm 0.093$) and Hungarian squab

pigeons ($H_d = 0.105 \pm 0.092$), which also included smaller sample sizes. The results of the geographical analysis suggest the antiquity of the Carpathian Basin (Great Plain) group, however, a historical-genetic connection between Mediterranean and Carpathian Basin breeds cannot be excluded. While pigeon breeding is well documented in the American, Asian, and Mediterranean regions, direct evidence from the Carpathian Basin is limited. Nevertheless, the relatively high haplotype diversity of the Great Plain group ($H_d = 0.486 \pm 0.071$), comparable to that of the Mediterranean ($H_d = 0.576 \pm 0.078$) and Asian ($H_d = 0.305 \pm 0.057$) groups, suggests that large-bodied domestic pigeons may have been present in the region for a long time. This is supported by historical records, such as references to the Hungarian Giant pigeon dating back to the 17th century (SZÜCS, 1990). A similar pattern was observed for nucleotide diversity (π). The highest value was found in the Asian group ($\pi = 0.0313 \pm 0.0165$), followed by the Great Plain ($\pi = 0.0245 \pm 0.0133$) and Mediterranean groups ($\pi = 0.0181 \pm 0.0104$). In contrast, Hungarian squab pigeons ($\pi = 0.0092 \pm 0.0061$) and especially American breeds ($\pi = 0.0009 \pm 0.0014$) exhibited low nucleotide diversity, indicating a more homogeneous maternal gene pool. Overall, nucleotide diversity was relatively high in the Asian and Great Plain pigeons, moderate in the Mediterranean group, and low in Hungarian squab pigeons and American breeds. Despite differences in sample size, relatively balanced nucleotide diversity values were observed among the groups, even though the Mediterranean and Asian regions have a longer evolutionary history. As Asia represents the center of domestication, it is expected to exhibit the highest genetic variability. The Carpathian Basin contains numerous contact zones characterized by high species and population diversity, and is therefore often considered a biodiversity hotspot (KAJTOCH et al., 2016).

3.1.2. Genetic distance values based on Fixation index

Genetic distance analysis using a multi-marker approach

Pairwise F_{ST} values calculated from mtDNA and microsatellite data in Study II generally indicated low levels of genetic differentiation among the seven large-bodied breeds included in the analysis; however, marker-specific patterns were observed. The complete distance matrices are presented as heatmaps in Figures 2A–B.

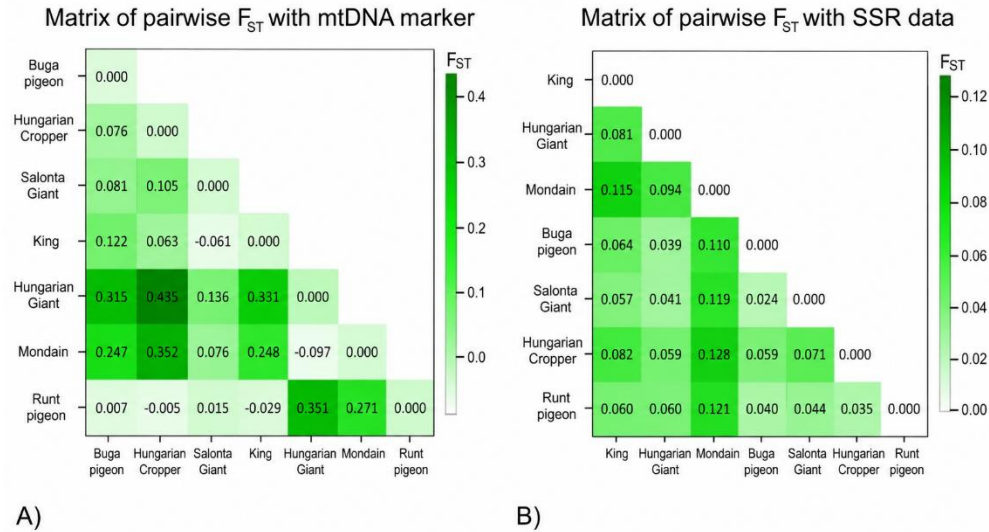


Figure 2: Genetic distance values visualized as a heatmap for both markers

Based on the mitochondrial marker, no consistent clustering pattern was observed (Figure 2A), and genetic distances were generally low. The smallest distance was detected between the Mondain and the Hungarian Giant pigeon, while the largest was found between the Hungarian Giant pigeon and the Hungarian Cropper pigeon. This differs from the microsatellite-based results, where these two Hungarian breeds showed a closer relationship; therefore, the greater mtDNA-based distance likely reflects differences in maternal lineages rather than overall genetic differentiation. In contrast, the heatmap based on microsatellite markers (Figure 2B) revealed a more structured pattern, the Mondain was clearly separated, while the Hungarian Giant pigeon and the Hungarian Cropper pigeon appeared more closely related. This suggests that biparentally inherited microsatellite markers provide a more comprehensive representation of overall genetic relationships than mtDNA-based analyses. Among the international breeds, the Runt pigeon and the King were genetically closer to the Hungarian breeds, whereas the Mondain appeared more isolated according to both marker types, which was also confirmed by the microsatellite heatmap (Figure 2B). The Hungarian Giant pigeon showed the greatest distance from the Mondain, in general agreement with the mtDNA results, although with moderate consistency. The differing variability of the two marker types resulted in differences in F_{ST} values and genetic distance estimates. The F_{ST} values obtained were higher than those reported in some studies on other pigeon species and feral populations (MONCEAU et al., 2013; GIUNCHI et al., 2020), but were comparable to those described for European–Mediterranean domestic pigeon breeds (BIGI et al., 2016). Compared to Polish populations

(PODBIELSKA and RADKO, 2022), stronger differentiation and reduced gene flow were observed, which can be attributed more to targeted selection and local breeding preferences than to geographic isolation. As none of the F_{ST} values exceeded 0.430, the limited gene flow is more likely the result of breeding decisions rather than physical barriers (HALL et al., 2022).

3.1.3. Analysis of Molecular Variance (AMOVA)

To assess the genetic structure of the studied samples, analysis of molecular variance (AMOVA) was performed in both Study I and Study II. In Study I, the results obtained from the traditional breed group classification (IA) were compared with those based on breed-level classification (IB). In Study II, genetic differentiation among breeds was evaluated using COI-based mtDNA data (IIA) and microsatellite markers (IIB) on the same set of individuals (Table 3).

Table 3: AMOVA results for all grouping types

	Source of variation	df	Sum of squares	Variance components	Variance (%)
IA. Based on traditional breed groups	Among populations	6	191.143	0.92804	35.07
	Within populations	269	462.231	1.71833	64.93
IB. By breeds	Among populations	18	217.926	0.74415	30.52
	Within populations	257	435.447	1.69435	69.48
IIA. COI mtDNA marker analysis	Among populations	6	34.401	0.51290	20.34
	Within populations	44	88.403	2.00915	79.66
IIB. microsatellite marker analysis	Among populations	6	178.439	0.39413	6.84
	Within populations	429	2301.123	5.36392	93.16

In Study I (IA), 35.07% of the total genetic variance was attributed to differences among groups, while 64.93% occurred within groups. The breed-based classification (IB) also revealed differentiation; however, the among-group component was lower (30.52%). This indicates that traditional breed groupings represent genetically meaningful units. In Study II, the two marker types revealed different patterns. The COI-based mtDNA analysis (IIA) showed a higher proportion of variance among populations (20.34%) than the microsatellite markers (6.84%) (IIB), despite being based on the same individuals. This is consistent with previous findings, where the majority of genetic variance is typically found within populations (GIUNCHI et al., 2020). Although microsatellite-based AMOVA analyses are less frequently reported in pigeons, the combined results of the two marker types clearly indicate that most genetic variation resides within populations. These differences can be explained by the distinct inheritance patterns of the markers. Maternally inherited, non-recombining mtDNA reflects deeper historical

relationships, whereas microsatellite markers provide a genome-wide perspective. Accordingly, mtDNA markers are particularly suitable for phylogenetic analyses. Although the compared studies are not fully identical in methodology, the overall results still indicate a relatively strong genetic structure.

3.1.4. Analysis of haplotype relationships

The relationships among haplotypes of the breeds analyzed in Study I and II are illustrated by dendrograms in Figure 3. Figure 3A presents the haplotypes identified in Study I grouped by traditional breed categories, while Figure 3B shows the same haplotypes organized by geographical regions. Figure 3C illustrates the haplotype distribution of the breeds analyzed in Study II.

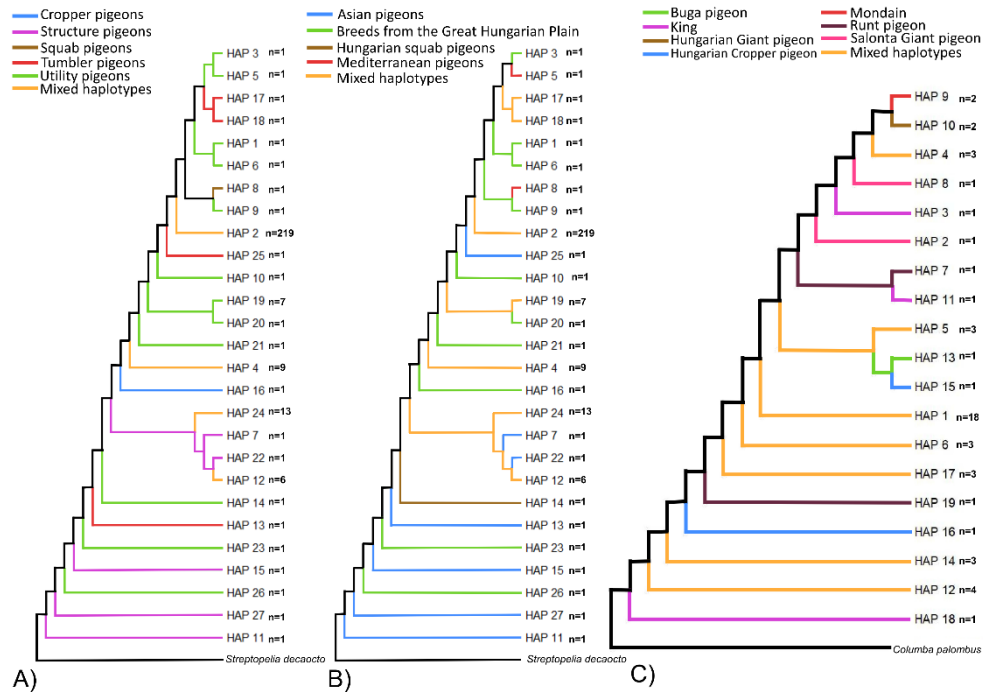


Figure 3: The relationships between the haplotypes of the studied pigeon breeds are shown on dendrograms. (Note: The n values indicated next to the haplotypes indicate the number of individuals belonging to the given haplotype.)

Based on Figures 3A and 3B, four out of the 27 identified haplotypes (HAP_2, HAP_4, HAP_12, HAP_24) were shared across multiple groups, indicating that not all haplotypes can be assigned to a single breed group or geographical region. Notably, HAP_2 was highly dominant (n = 219), widely distributed, and likely of ancestral origin. The remaining haplotypes occurred at low frequencies, often associated with a single individual, indicating high mitochondrial diversity. In the dendrogram based on breed groups (Figure 3A), haplotypes did not form clearly separated clusters but frequently appeared on shared or closely related

branches. Several haplotypes of the Structure pigeon group were located in more basal positions, suggesting the persistence of older maternal lineages. The proximity of haplotypes between Squab and Utility pigeons also suggests a shared origin or closer genetic relationship, consistent with previous SNP-based findings (STRINGHAM et al., 2012). In the geographical grouping (Figure 3B), partial clustering was observed, but no clear separation among regions. The breeds from the Hungarian Great Plain exhibited several unique haplotypes, however, the presence of shared haplotypes indicates that geographical origin alone does not fully explain the observed patterns. The widespread occurrence of shared haplotypes suggests a common origin combined with subsequent breeding interactions, in agreement with previous studies (BIRAY, 2019). In the dendrogram of Study II (Figure 3C), basal branches were primarily characterized by shared haplotypes, including the most frequent HAP_1 ($n = 18$). In contrast, terminal branches showed a higher proportion of breed-specific haplotypes, including several associated with Hungarian breeds (e.g., HAP_13, HAP_15, HAP_2, HAP_8, HAP_10). This pattern indicates the coexistence of a common origin and partial differentiation. Excluding HAP_1, the lower and upper branches contained similar numbers of individuals (16 vs. 17), but differed in haplotype counts (7 vs. 11), suggesting higher diversity within Hungarian large-bodied breeds. To further investigate relationships among haplotypes, haplotype network analysis was performed. Figure 4 illustrates the grouping of haplotypes based on traditional breed groups and geographical regions in Study I.

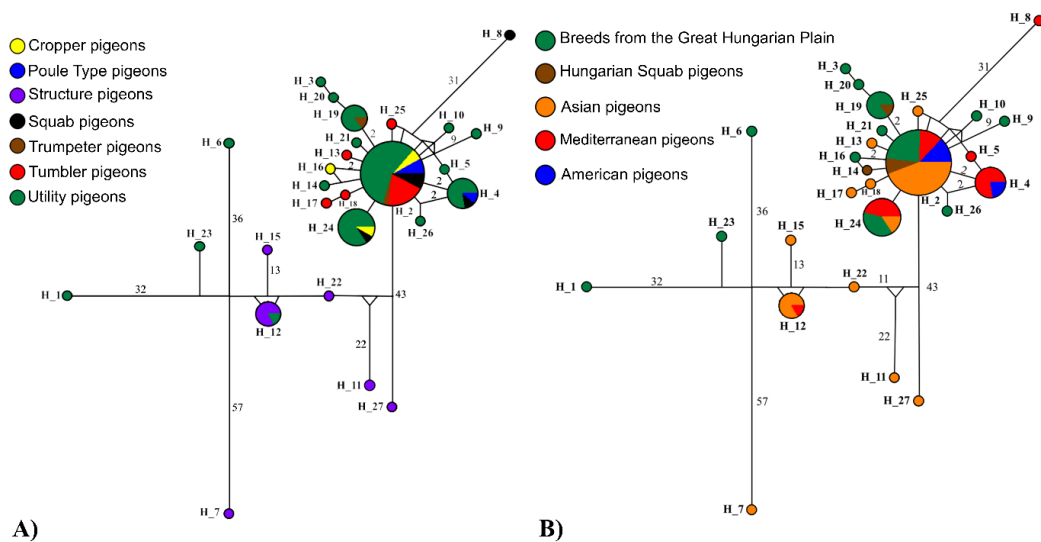


Figure 4: Neighbor-Joining Network diagram A) based on traditional breed groups, B) based on geographical regions. (Note: The size of the circles indicating haplotypes is proportional to the number of individuals. The length of the branches does not always represent evolutionary distance. The numbers on the branches indicate mutation steps (if > 1) between the sequences. The red diamonds/nodes indicate intermediate haplotypes estimated by the network but not identified among the examined samples.)

Figure 4A illustrates the distribution of haplotypes according to traditional breed group classification. Utility pigeons are represented by multiple haplotypes that are widely dispersed across the network, indicating higher internal diversity. Within the Tumbler pigeons group, rare and unique haplotypes were also observed, which in this study were exclusively associated with the Iraqi Red pigeon. The distinct position of the Jacobin pigeon, representing the Structure pigeons, suggests a different maternal background, consistent with its complex breeding history. Overall, breed groups do not form clearly separated maternal units; however, multiple independent haplotype lineages are present within groups, indicating partial discordance between phenotypic classification and genetic structure.

Based on Figure 4B, the geographical distribution of haplotypes also does not show complete separation. A substantial proportion of American samples are associated with Mediterranean haplotypes, suggesting the influence of Mediterranean origin. In contrast, samples from the Carpathian Basin harbor several rare, partly local haplotypes, indicating the presence of distinct evolutionary lineages. Within the network, haplotypes from the Carpathian Basin more frequently show direct connections with Asian samples, while relationships with the Mediterranean group appear mainly as partial overlaps. Although this pattern does not support

a single origin model, it highlights the importance of Asian connections and suggests a potential “genetic bridge” role of the Carpathian Basin between Asia and the Mediterranean region.

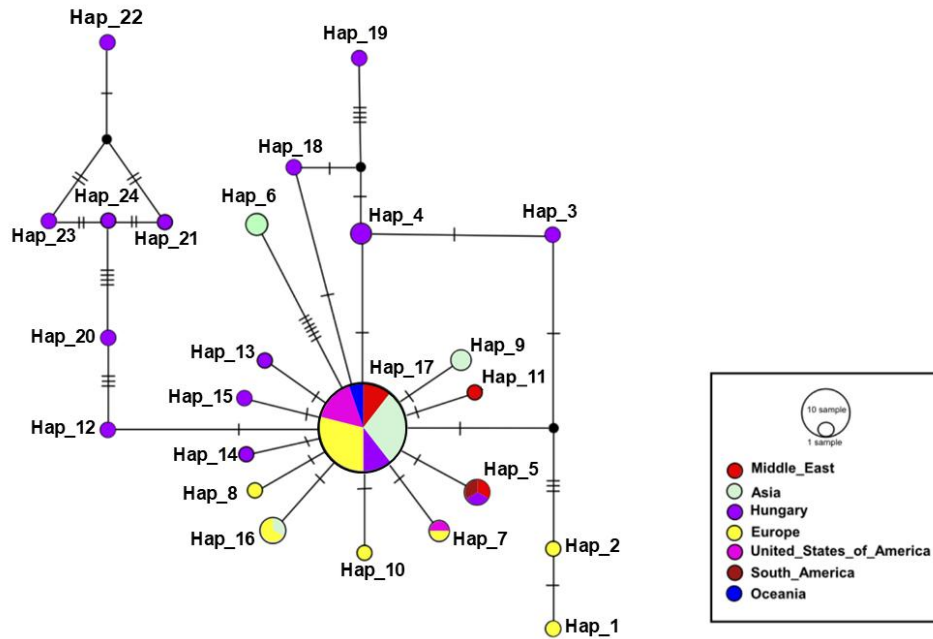


Figure 5: Study II Neighbor-Joining haplotype analysis based on mtDNA sequence data, consisting of our own samples and sequences from the NCBI GenBank database. (Note: The size of the circles indicating haplotypes is proportional to the number of individuals. The lengths of the branches do not always represent evolutionary distances.)

The results of Study II (Figure 5) confirm this pattern. A total of 24 haplotypes were identified, of which 13 were found exclusively in Hungarian samples and had no corresponding sequences in public databases, thus representing novel haplotypes. This indicates substantial internal genetic diversity. In addition, several shared haplotypes were observed, suggesting broader geographical connections of the Hungarian populations; for example, HAP_5 was present in Argentine, Saudi Arabian, and Hungarian samples. Importantly, despite differences in the datasets of Study I and II, the network structures revealed a similar overall pattern. This pattern is consistent with a common origin followed by subsequent regional diversification and possible introgression. Accordingly, our results support a model of diversification from a shared maternal background rather than multiple independent domestication events. This interpretation is in agreement with recent studies identifying the Levant region as the primary center of domestication (HERNANDEZ-ALONSO et al., 2023).

3.1.5. Analysis of population structure using Bayesian clustering (Study I and II)

Population structure was inferred using the STRUCTURE program under an admixture model without *a priori* population assignment, based on two datasets: recoded mtDNA data from

Study I and microsatellite markers from Study II. The optimal number of clusters (K) was determined using the ΔK criterion. In Study I (19 breeds), ΔK peaks were observed at K = 3 and K = 11. At K = 3, most breeds exhibited highly admixed cluster membership, with only the Jacobin, Mondain, and Salonta Giant showing more homogeneous profiles. At K = 11, a finer substructure emerged; however, admixture remained dominant, and cluster membership varied at the individual level (Figure 6).

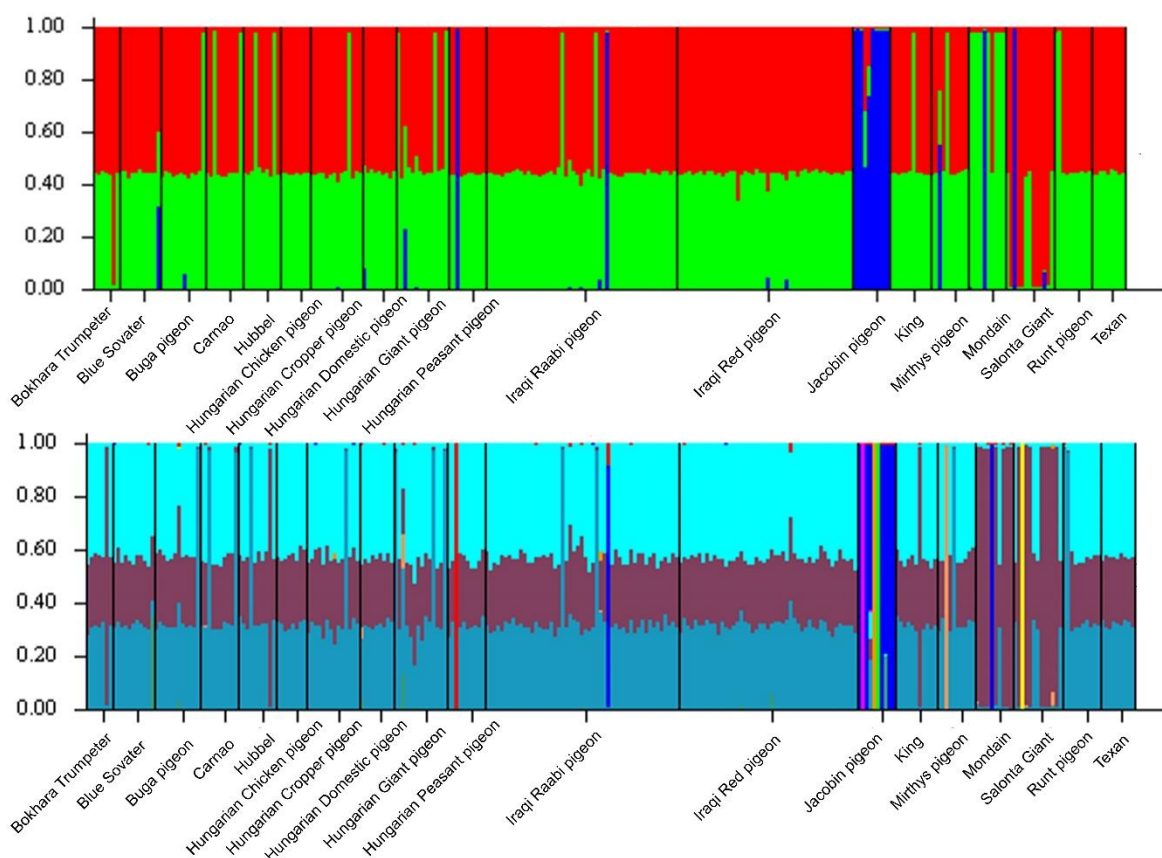


Figure 6: Results of Structure analysis for K=3 and K=11 based on data from study I. (Note: Each column represents an individual, and the colors within the columns indicate the proportion of genetic components belonging to different genetic clusters.)

In Study II, the ΔK analysis showed the strongest support at K = 4, with a secondary peak at K = 5 (Figure 7). At K = 4, the main differences among breeds became apparent; however, the breeds still exhibited highly admixed genetic composition. For example, the Mondain and Szalontai Giant showed higher assignment proportions to certain components, whereas the Hungarian Giant, Hungarian Giant Pouter, and Roman pigeon displayed more pronounced admixture. At K = 5, the resolution increased and an additional component emerged, resulting

in greater variability in individual assignment proportions. However, this did not alter the main clustering pattern observed at $K = 4$, but rather refined its finer structural details.

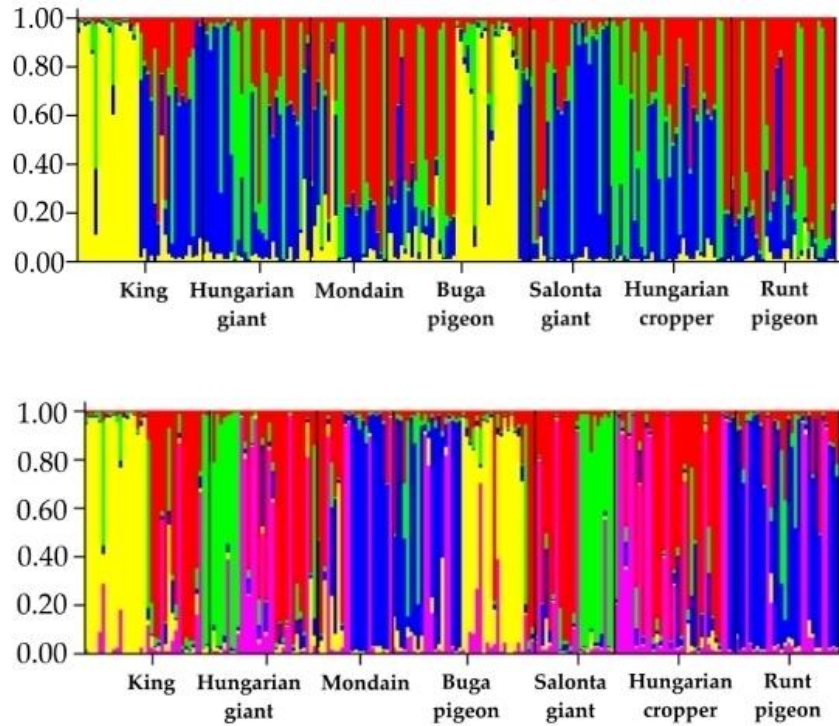


Figure 7: Results of the Structure analysis in $K=4$ and $K=5$ breakdown for the 7 large breeds based on data from study II. (Note: Each column represents one individual and the colors within the columns indicate the proportion of breeds belonging to different genetic clusters.)

The extensive admixture observed can be explained by frequent crossbreeding practices in pigeon breeding, which reduce genetic differentiation among groups. Accordingly, STRUCTURE clusters cannot be directly equated with traditional breed group classifications, but rather reflect shared breeding history and the extent of admixture (STRINGHAM et al., 2012; SHAPIRO et al., 2013; BIRAY et al., 2019). Therefore, the interpretation of these results should be carried out in conjunction with other analytical approaches, such as dendrograms, haplotype networks, and distance-based heatmaps.

3.2. SNP-chip analysis in domestic pigeon (Study III)

The aim of this analysis was to investigate genetic differences between meat-type (Mirthys hybrid) and racing-type (homing pigeon) populations through the cross-application of a chicken-derived SNP chip in domestic pigeons. The Illumina Chicken_50K_CobbCons SNP array was applied to 24 samples ($n = 12-12$), of which 53,313 SNPs were successfully detected

out of the total 57,636 markers. The average sample-level call rate was 0.474 (meat-type: 0.501; racing-type: 0.447), while the allele-level call rate was approximately 49%. This relatively low rate can be attributed both to the small sample size and to the considerable evolutionary distance between pigeon and chicken (~85 million years; CLARAMUNT and CRACRAFT, 2015). Similar observations have been reported in SNP-chip studies involving phylogenetically distant species (HOFFMAN et al., 2013; FOUNTAIN et al., 2021). Linkage disequilibrium (LD) was characterized using the R^2 metric, with approximately 27% of pairwise comparisons showing complete linkage ($R^2 = 1$). Following quality control, 356 SNPs remained for further analysis. Subsequent LD-based pruning resulted in the removal of 179 SNPs at a threshold of 0.5 and 38 SNPs at a threshold of 0.9. Principal component analysis (PCA) based on the 356 SNPs revealed substantial genetic overlap between the two utilization types, with only one meat-type and two racing-type individuals appearing as outliers (Figure 8).

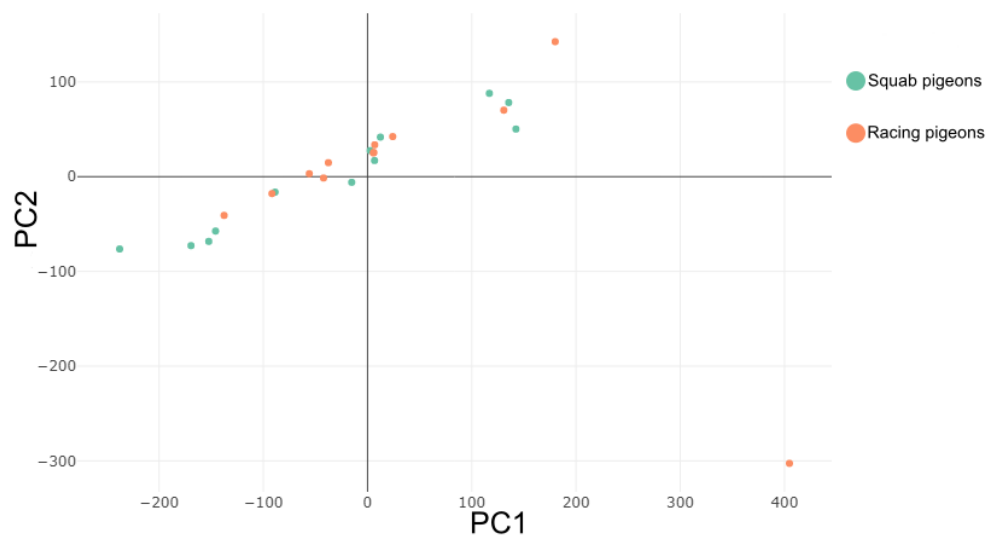


Figure 8: Principal component analysis with 356 SNPs for the two utilization types

4. NEW SCIENTIFIC RESULTS

1. During the analysis of the mitochondrial DNA (mtDNA) COI region in Hungarian and international domestic pigeon breeds, 19 breeds (Buga pigeon, Hungarian Peasant pigeon, Bokhara Trumpeter, Hubbel, Iraqi Raabi pigeon, Iraqi Red pigeon, Carnao, King, Hungarian Chicken pigeon, Hungarian Domestic pigeon, Hungarian Giant pigeon, Hungarian Cropper, Mirthys, Mondain, Jacobin pigeon, Runt pigeon, Salonta Giant, Blue Sovater, and Texan) comprising 275 individuals were examined. The investigated populations exhibited high genetic diversity. A total of 27 novel haplotypes were identified in Study I and 13 novel haplotypes in Study II within the same gene, all of which are uniquely associated with the geographical region of the Carpathian Basin.
2. Based on genetic relationship and domestication analyses, we demonstrated that the genetic structure of domestic pigeon breeds reflects a partially differentiated evolutionary pattern originating from a common ancestral population. AMOVA analyses revealed that, across the different grouping levels evaluated in Study I, 35.07% of the total genetic variance was attributable to differences among breed groups, while 30.52% was explained by variation among breeds. These findings confirm the genetic relevance of the traditional breed-group classification.
3. A multilocus genetic analysis of large-bodied domestic pigeon breeds was conducted using one mtDNA marker and 13 microsatellite loci in seven breeds (Buga pigeon, King, Hungarian Cropper, Hungarian Giant pigeon, Mondain, Runt pigeon, and Salonta Giant). The results demonstrated considerable differences among populations in both genetic diversity and inbreeding levels. The Runt pigeon exhibited the highest mtDNA haplotype diversity ($H_d = 0.964 \pm 0.077$), whereas the Hungarian Cropper pigeon showed the lowest ($H_d = 0.583 \pm 0.183$). Microsatellite analyses revealed the highest inbreeding coefficients in the Buga pigeon ($F_{IS} = 0.502$) and the Salonta Giant ($F_{IS} = 0.499$).
4. Genetic and phylogenetic analyses demonstrated that the investigated domestic pigeon breeds originated from a common ancestral population, however, their evolutionary history has not been linear but has followed a partially divergent and admixed pattern. Hungarian breeds, particularly the large-bodied indigenous breeds, are genetically more closely related to one another than to the foreign populations and possess a substantial proportion of unique haplotypes, indicating a relatively isolated and regionally distinct evolutionary history.

5. We demonstrated that the Illumina Chicken_50K_CobbCons SNP array, originally developed for the domestic chicken, has limited applicability for genetic studies in the domestic pigeon. Despite a relatively low genotype call rate (0.474), 356 reliably detectable SNPs were identified, of which eight markers have been associated with production-related traits in other species according to the literature. These findings indicate that the chicken-derived SNP array may serve as an useful preliminary tool for identifying potentially informative genetic markers in domestic pigeons. However, accurate genetic evaluation and marker validation will require the development of a pigeon-specific SNP array and analyses involving larger sample sizes.

5.PRACTICAL RESULTS

1. The results obtained from the phylogenetic, genetic diversity, and population structure analyses have practical relevance, as they provide breeders with an objective assessment of the genetic status of the populations, the level of inbreeding, and the impact of previous breeding practices. These findings can be directly applied to breed management, particularly for optimizing mating strategies, maintaining genetic diversity, reducing inbreeding, and supporting the monitoring and documentation of breeding lines.
2. In this study, we were the first to successfully evaluate the applicability of the Illumina Chicken_50K_CobbCons SNP array, originally developed for the domestic chicken, in the domestic pigeon. Although the platform exhibited limited efficiency, it enabled the reliable identification of informative SNP markers, providing a valuable foundation for subsequent validation studies and the development of pigeon-specific genomic approaches.

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7.PUBLICATION LIST



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Doctoral School: Doctoral School of Animal Husbandry
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List of publications related to the dissertation

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1. **Balog, K.**, Al-Sallami, A. S. W., Lakhmi, C. M., Kusza, S., Bagi, Z.: Initial steps in the study of genetic diversity of pigeon breeds in the Middle East and Hungary.
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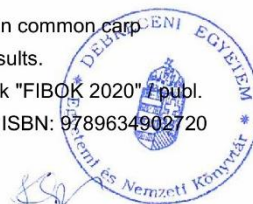




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