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Article

Population structure analysis of the Border Collie dog breed in Hungary

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Simple Summary: The appearance of dog breeds is constantly changing according to many reasons. The Border Collie breed has several lines, depending on the sport, show or work performance of the past decades, assuming closed breeding practices within these lines. The aim of the study was to map the current population in Hungary and determine the possible inbreeding levels in and between the different subpopulations. Regarding the outcome of the research, it was outlined, that the size of the active breeding population decreased dramatically in the past years, however, there are many dogs in the country without pedigree. The calculated results pointed out the genetic divergence of the show and working line is appreciable, in addition, there are several favourised sires in each line, decreasing genetic variability. As a consequence, it can be seen, that despite the proportion of registered breeders, dog owners are still not preferring to buy purebred dogs, so most of the pups born in Hungary are exported to other countries.

Abstract: Pedigree data of the Border Collie dog breed was constructed in Hungary, to examine genetic diversity within the breed and between its different lines. The database based on available herd books from the development of the breed (the late 1800s) until now. The constructed pedigree file consisted of 13 339 individuals from which 1567 dogs (born between 2010 and 2016) composed the reference population that are still alive and active from breeding aspect. Since the breed is subdivided by phenotype, the reference population was dissected according to the existing lines. The number of founders was 894 but only 8 individuals were responsible for contributing 50% of the genetic variability. The reference population had a pedigree completeness 99.6% until 15 generations and inbreeding coefficient of 9.86%, respectively. Due to the changing breed standards and the requirements of the potential buyers the effective population size substantially decreased between 2010 and 2016. Generation intervals varied between 4.09 and 4.71 years where the sire paths were longer due to the later ages when males begin their breeding carrier compared to females. Genetic differences among the existing lines calculated by fixation indices are not significant, nonetheless ancestral inbreeding coefficients are able to show the contrasts.

Keywords: Border Collie, inbreeding**,** pedigree analysis, population size, subpopulations

1. Introduction

The Border Collie dog nowadays is considered as one of the most intelligent dog breeds originating England Northumbria region. The breed's name is related to the words „border" (between England and Scotland), „Coal" (basic colour) and „Koolie" (useful) [11, 12]. Breeding of the collie-type dogs began at the British Islands at the 19th century in order to help the shepherds performing gathering, driving, singling, penning, loading in a trailer and shedding race. Thus the main objectives in the breed's selection were herding instinct, acceptance of human guiding and speed, respectively. The name „Border Collie" was first used by the International Sheep Dog Society (ISDS) in 1915 in order to distinguish this breed and the smooth and Bearded Collies which at the beginning had similar breeding aspects. From the 1860s the exhibitions became more and more popular and their appearance was more consistent the breed was registered by the British Kennel Club. The first public sheep herding event

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took place at Wales in 1873, where Old Hemp, one of the founders of the breed appeared. Contrary to his conspecifics his herding work was performed without barking, carefully approaching the sheep and controlled the flock with an intensive stare, or "eye". These characteristics were defining the basics of today's collecting style herding.

The Border Collie breed was officially recognized by the FCI (Féderation Cynologique Internationale) in 1977, and the valid official breed standard was published in 1987 when also the selection for appearance has been started. Obtaining the status „show champion" was however only possible after passing the so-called working exam in several countries.

Regarding the Hungarian Border Collie population, the first two females were imported in the country in 1995. The present population is not consistent; the number of registered breeders is 154. The Border Collie dogs are bred based on a closed herd book which predisposes the inbreeding level of the population to be increased. It is also a common practice for dog breeders, to choose sires and dams with a common ancestor, to fix some specific traits in the appearance or working ability. This so-called line breeding tries to avoid the closely related matings, however, the breeding association sometimes permits it. Using specific lines within one breed was previously reported in France [18], where more than 49% of the breeders claimed to use line breeding in practice. There are three specific lines within the breed worldwide, which are also represented in Hungary, such as show line, working line and the so-called "mixed" line, originating from Australia and New-Zealand. This "mixed" line combines the appearance of show dogs (heavier bones, elegant head, more and thicker coat) with the energy and stamina of the working-lined dogs, creating suitable SAR (Search and Rescue), therapy or other specific dogs for sport.

In case of working and show dogs, there are slight differences among breed standards between countries, thus import of breeding animals is not always appropriate for the breeder's point of view. Hence the objective of this study was to analyze the effects of closed breeding on the population structure of the Hungarian Border Collie dog population and examine the genetic diversity in-and between the subpopulations.

2. Materials and Methods

The pedigree dataset of the Hungarian Border Collie population was constructed using available electronic herd books and pedigrees from Hungarian breeders. These websites could be searched but their content could not be downloaded therefore all genealogy data had to be retyped manually. First, the reference population was defined as the living and active animals (from the aspect of breeding) born between 2010 and 2016. The reference population was composed of 1567 dogs (703 males and 863 females). Then the available genealogy information of these dogs was traced back and was recorded creating the pedigree of the whole population from the late 1800s until now. The created Hungarian Border Collie pedigree dataset contained 13 339 individuals (5649 males and 7750 females).

The genealogy records used in this study were created using the software „Equihun Pedigree Builder" (Bokor, 2004). The following information was entered:

- individual identity number
- male parent
- female parent
- date of birth
- country code (i.e. county of origin)
- colour (not used in this study)
- sex

After exporting the pedigree records their correctness was checked, then pedigree analysis was performed applying ENDOG software [13]. The structure Hungarian Border Collie population was characterized by the following parameters:

- number of founders (f: Ancestors with two unknown parents)
- effective number of founders (fe: the number of equally contributing founders that would be expected to produce the same genetic diversity as in the population under study)

- effective number of ancestors (fa: similar to fe but replacing the contributions of founders by marginal contributions of ancestors)
- fa50 (Number of ancestors responsible for the 50% of the genetic variability)
- generation interval (average age of parents at the birth of their progeny kept for reproduction)
- pedigree completeness (proportion of its known ancestors per generation)
- inbreeding coefficient (the probability that the two alleles at any locus in an individual are identical by descent)
- average relatedness (the probability that an allele randomly was chosen from the whole population belongs to a given animal)
- effective populations size (realized effective population size) from individual increase of inbreeding (Gutiérrez et al. 2008)

All these parameters were explained in detail by [14] therefore equations related to the listed parameters will not be repeated here.

Then, the database was dissected into three groups, the inbreeding coefficients were also adjusted in the three lines, in addition fixation indices (F_{IS}, $F_{ST)}$ was calculated to detect the reduction of heterozygosity among subpopulations and individuals for measuring the total population differentiation [29].

For the calculation of the fixation indices, coancestry and kinship distance was used [6, 7], using the following equations:

$$F_{IS} = \frac{\bar{F} - \bar{f}}{1 - \bar{f}}$$

$$F_{ST} = \frac{\bar{f} - \bar{f}}{1 - \bar{f}} = \frac{\bar{D}}{1 - \bar{f}}$$

Where: $\bar{f}$ is the mean coancestry for the metapopulation; $\bar{F}$ is the mean inbreeding coefficient for the metapopulation; $\bar{D}$ is the average genetic distance between the subpopulations

Moreover, ancestral inbreeding coefficients proposed by [1, 16, 17] and determined with GRain 2.0 software [2] to obtain, weather these distinct measurements for inbreeding are able to describe the differences between the lines. For the determination of the cumulative proportion of the genome that was exposed to inbreeding effects, ancestral inbreeding (F_BAL) was calculated in the subpopulations. In addition, inbreeding coefficient was also calculated by the method of [16] by dividing inbreeding into two parts, based on weather one part of the identical alleles were inbred in the past (F_KAL) or it became inbred in the recent generations (F_KAL_NEW).

3. Results

3.1 The probability of gene origin

Trends in the probability of gene origin fe, fa50 and their ratios are presented in Table 1.

Table 1. Demographic parameters of the border collie breed in Hungary

f	894
fg	806
fe	117
fa	20
fa50	8
fe/fa ratio	0,13

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f: number of founders; fg: equivalent number of founders; fe: Effective number of founders; fa: Effective number of ancestors; fa50: Number of ancestors responsible for the 50% of the genetic variability;

Nevertheless, compared to a great number of founders, large part of the genetic variability is maintained based on only 8 ancestors (Table 1). Looking at the observed ratio of *fa* and *fe* it can be concluded that the Hungarian Border Collie population has suffered a very strong gene loss.

3.2 Effective population size

Trends in the realized effective population size are presented in Figure 1.

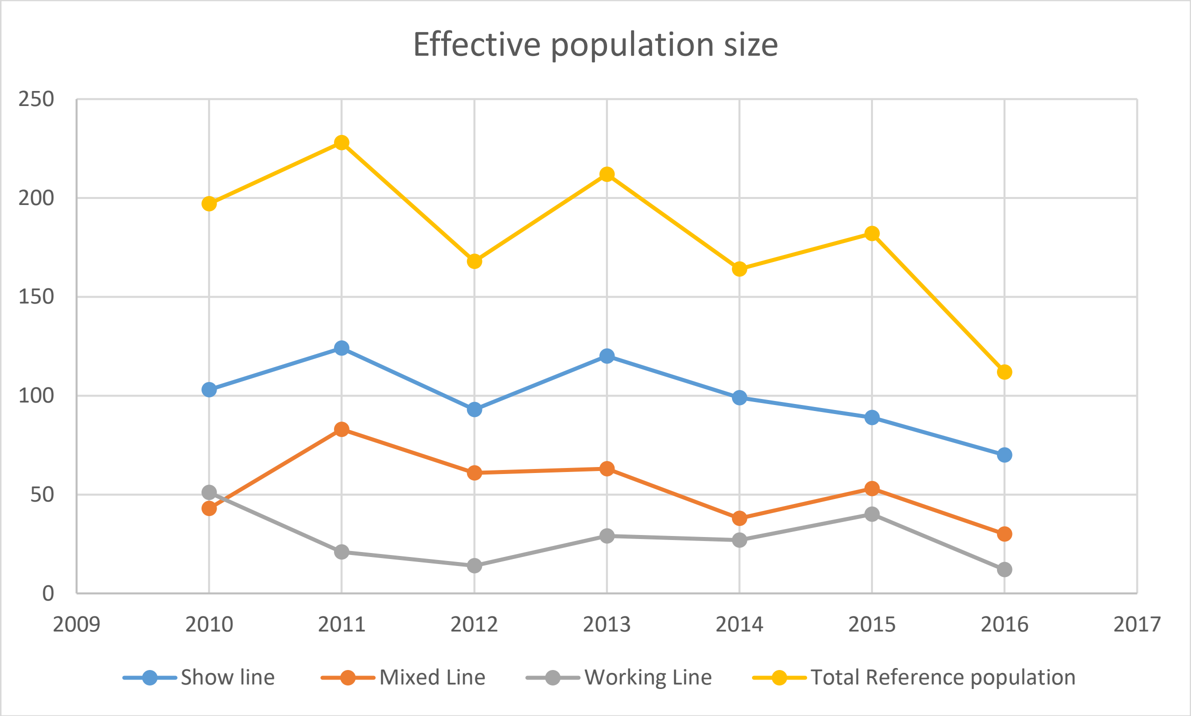

Figure 1. Effective population size (Ne) of the reference population

3.3 Generation interval

The generation interval was calculated as the average age of parents at the birth of their progeny kept for the reproduction, and it was computed for all four parent-progeny pathways (Table 2) represented in the total reference population and per line.

Table 2. Descriptive statistics of the generation interval (T) for the reference population (2010-2016)

	N	T	SD	SE
Father-Son	67	4.43	2.63	±0.341
Father-Daughter	107	4.71	2.64	±0.335
Mother-Son	67	4.17	1.65	±0.220
Mother-Daughter	106	4.09	1.63	±0.217
		Show line		
Father-Son	13	4.84	2.93	±0.813
Father-Daughter	25	5.01	3.12	±0.865
Mother-Son	13	4.41	1.81	±0.504

Mother-Daughter	25	4.22	2.10	±.584
	Mixed line			
Father-Son	7	2.71	0.92	±0.348
Father-Daughter	15	4.33	1.95	±0.738
Mother-Son	7	3.29	1.60	±0.607
Mother-Daughter	15	3.44	1.25	±0.472
	Working line			
Father-Son	14	3.42	1.24	±0.717
Father-Daughter	26	4.22	1.87	±1.08
Mother-Son	14	4.34	1.38	±0.80
Mother-Daughter	26	4.48	2.07	±0.158

N: number of individuals in the reference population; T: generation interval; SD: standard deviations; SE: standard errors of means

The length of the generation interval (T) can be substantially divergent across the different species. In the present study, the sire paths were longer as the males kept in breeding for longer ages than females and the requirements for breeding for males are also stricter for the females. Intervals within the show and working lines were similar, however, the mean age of the father when the offspring was born was somewhat lower in the mixed line (Sire-Son path: 2.71 years, Sire-daughter path: 4.33 years).

3.4 Inbreeding and average relatedness

Evolution of the inbreeding coefficient and the average relatedness of the reference population is provided in Table 3.

Table 3. Inbreeding (F) and average relatedness (AR) of the reference population

Birth Year	N	F	F_BAL	F_KAL	F_KAL_NEW	AR
2010	269	8,71	61,1	7,97	1,98	7,38
2011	245	9,32	61,4	7,39	1,92	7,39
2012	199	10,6	61,9	8,83	2,33	7,32
2013	233	10,5	61,9	8,69	2,14	7,11
2014	188	9,3	62,3	7,98	1,75	7,23
2015	214	10,1	59,9	8,26	1,92	7,06
2016	219	10,5	50,3	4,56	1,59	7,42

N: Number of individuals; F: inbreeding coefficient; F_BAL: Ballou's formula to ancestral inbreeding; F_KAL: Kalinowski's formula to ancestral inbreeding; F_KAL_NEW: Kalinowski's new formula to ancestral inbreeding; AR: Average relatedness

Ancestral inbreeding coeffiticients were added to determine if inbred alleles in the past may influenced the characterisations of these different phenotypes (Table 4).

Table 4. Ancestral inbreeding coefficients in subpopulations (%)

Birth Year	N	F	F_BAL	F_KAL	F_KAL_NEW	AR
Show line						
2010	104	9.67	63.7	7.93	1.73	7.3
2011	119	9.5	6.,4	7.61	1.94	7.7
2012	93	11.9	62.3	9.38	2.58	7.17
2013	120	12.4	63.5	10	2.35	7.06
2014	99	10,8	65.3	9.05	1.77	7.23
2015	101	11.3	64.6	9.75	2.45	7
2016	100	11.7	63.9	9.6	2.1	7.2
Mixed line						
2010	43	11.5	62.6	8.94	2.63	7.37
2011	70	10.2	61.7	7.82	2.18	7.55
2012	52	12.1	63.2	8.91	2.4	7.39
2013	63	10.5	62.8	7.64	2.85	7.31
2014	38	8.79	63.1	7.26	1.53	7.27
2015	61	10	64.5	9.77	1.73	7.31
2016	-	-	-	-	-	-
Working line						
2010	51	5.69	54.2	4.35	1.43	7.5
2011	12	4.62	53.6	3.82	0.63	7.63
2012	14	5.18	53.7	4.8	0.3	7.67
2013	29	4.6	52.4	5.14	0	7.14
2014	27	6	51.5	4.33	0.17	7.22
2015	40	4.68	45.3	3.66	0.1	6.45
2016	12	3.53	43.9	2.57	0.09	6.46

N: Number of individuals; F: inbreeding coefficient; F_BAL: Ballou's formula to ancestral inbreeding; F_KAL: Kalinowski's formula to ancestral inbreeding; F_KAL_NEW: Kalinowski's new formula to ancestral inbreeding; AR: Average relatedness

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The differences between the show and working lines regarding Ballou's formula are 20.4%, in addition the working line also differs from the mixed line by 20%. Furthermore, Both Kalinowski's formulas point out, that working line suffered the less inbreeding in the past few generations.

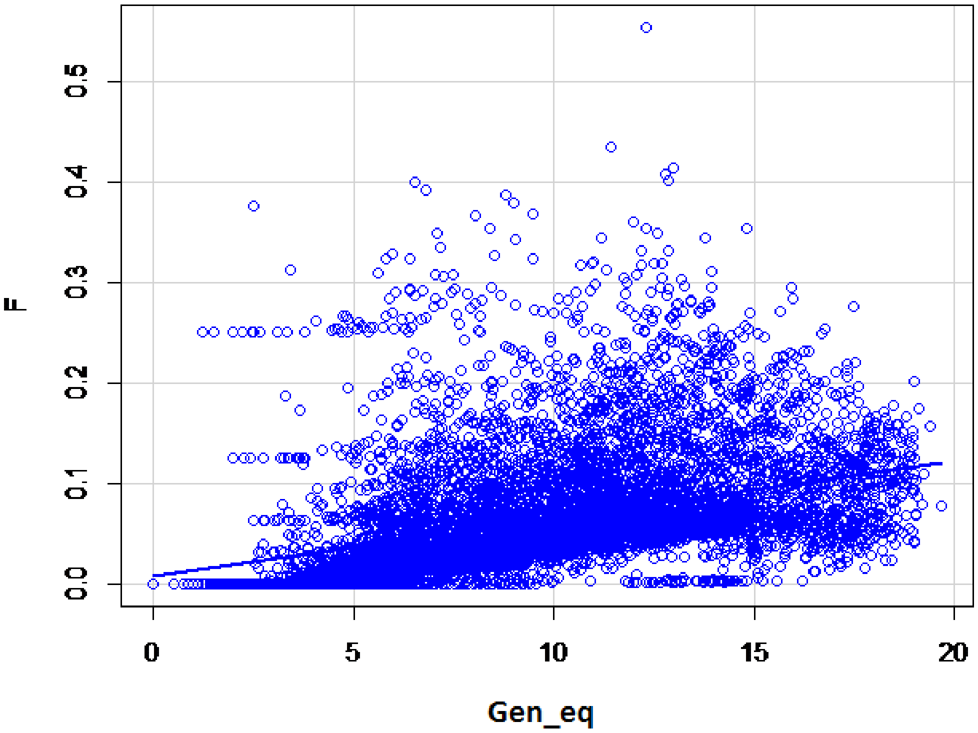

Figure 2. Association between inbreeding coefficient and complete generation equivalents in the total population

F: Inbreeding coefficient; Gen_eq: Number of complete generation equivalents

In the total population, only 2.77% of the matings were highly inbred (0.16% between full sibs, 1.74% between half-sibs and 0.87% between parent-offspring). Inbreeding coefficients differed among the studied lines, average inbreeding coefficient was 4.9% in the reference population of the working line, while it reached 10.51% and 11.03% between 2010 and 2016 in the mixed and show line.

The maximum and average number of complete generation equivalents were 25.04 and 4.47 respectively. The slow but continuous increase of the inbreeding coefficient based on the increasing complete generation equivalent is obvious (Figure 2). For the first 15 generation, the pedigree completeness was 99.6% which decreased to 87.6%/ by the 40th generation.

3.5 *Fixation indices in subpopulations*

Table 5. Genetic similarities within the population

Mean coancestry within Subpopulations F_{ij}	0.079
Mean self-coancestry (s_i)	0.541
Dij	0.024
F_{ST}	0.026

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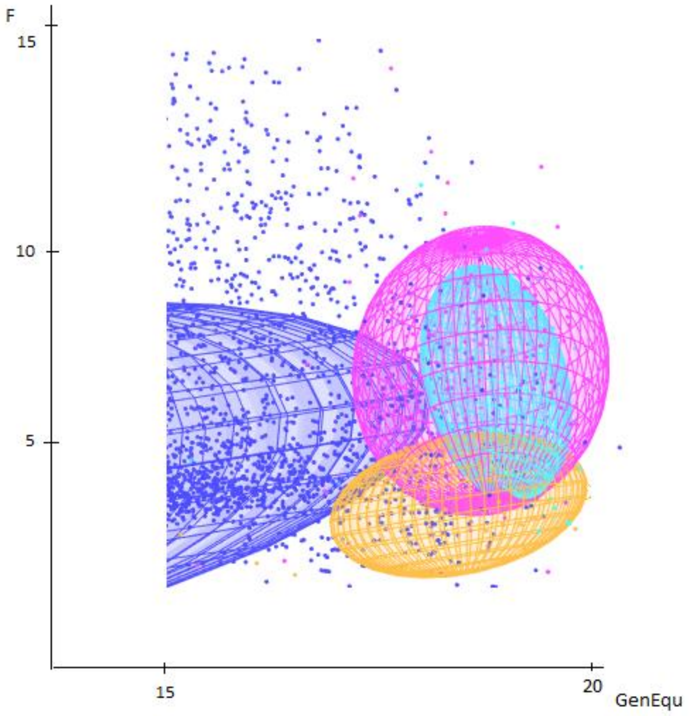
FIS	0.0036

Fij: Mean coancestry within subpopulations; si: self-coancestry; Dij: Nei's minimum distance; FST: Inbreeding caused by the differentiation of the subpopulation; FIS: Inbreeding coefficients within the subpopulations

Figure 3. represents the effects to the subdivision on the reference population, highlighting that the studied lines started to separate, nonetheless this is not statistically proven.



● Show line, ⬭ Mixed line, ● Working line

Figure 3. The inbreeding coefficients of the different lines depending on the total generation equivalent

Where: F is the inbreeding coefficient of an individual; and GenEqu is the number of complete generation equivalents.

4. Discussion

In many populations, all estimates related to the probability of gene origin decrease most during the first years. Unfortunately, in this study, the analyzed period covered more than a century, therefore, giving annual numbers was not possible. Similar findings were also reported in the French Beauceron and Braque Francais dog populations [10, 19]. The presence of preferential breeding can be shown by calculating the ratio of fe and fa. Small values signal the so-called bottleneck effect [3]. If *fe* is larger compared to *fa,* the population suffer from gene loss and consequently decrease of genetic variation [23]. Comparing this result to other populations the medium value (0.75) of fa/fe ratio of the Braque Francais dog population shows a more balanced use of animals for breeding and an absence of a bottleneck in that population [10]. The observed small ratio of *fa* and *fe* of the Hungarian Border Collie population can be explained by its closed herd book, intense selection for appearance and by the favoritism of some relevant individuals

Due to the unequal contribution of the breeding animals to the next generation, the effective population size was always smaller compared to exact population size. One of the reasons for decreasing the effective population size is that most of the puppies born in Hungary are sold abroad due to the lack of suitable owners for the breed. However, the dog-keeping culture improves, there are still many backyard breeders, who are selling puppies often half of the cost of the breeder’s price, making a huge border collie mix population. Besides, accommodating to the breed standards also decreases the effective population size. Unfortunately, this decreasing trend may coincide with the loss of genetic variability and with the appearance of genetic diseases [20]. Similar tendencies were reported in several dog breeds [8].

For the generation intervals, the result is not surprising as the reproductive life of sires is usually longer compared to dams. Similar results were found in the Nova Scotia Duck Tolling Retriever and the Lancashire Heeler dog breeds [22] and for several French dog breeds [10, 19]. The lower length of the mixed line generation interval can be attributed to the fact, that these dogs are bred with fewer show and working performance.

In dog breeding, matings of close relatives is a common practice where the objectives to create an outstanding individual [27], however, after few generations, the increased inbreeding level escalates juvenile mortality [28]. As the population size of the Border Collie breed in Hungary is relatively large the increase of the inbreeding level was relatively small (10% per 23 years). The decrease of the average inbreeding coefficients between 2011 and 2014 can be explained by the intense import of breeding animals. Because inbreeding coefficients are always dependent on the length and on the completeness of the pedigree the inbreeding coefficients were plotted on the complete generation equivalents [23].

Adding ancestral inbreeding coefficients, Ballou’s formula showed that individuals in the working line had less probability inheriting an allele which has undergone inbreeding in the past at least once, than individuals in the show and the mixed lines. Estimating the proportion of each dog’s genome that was identical by descent in an ancestor, to alleles identical by descent for the first time in that dog’s linage by gene dropping method, F_{KAL} and F_{KAL_NEW} pointed out similar results. Calculations for ancestral inbreeding were previously used by [1, 16, 17].

For the pedigree completeness, the obtained values show that the available electronic herd books register all ancestors and the Hungarian border collie population has an exceptionally long and complete pedigree. This pedigree quality is only comparable to that of Thoroughbred horse and Pannon White rabbit populations [5, 24].

As calculating the subdivision of the lines, within variety fixation index (F_{IS}) was 0.36%, showing that matings within lines were not random, in contrast with sheep and horse breeds, where this value is negative [21] representing that individuals in farm animal species are less related. In the reference population, the overall F_{ST} was 2.6% resulting decreasing heterozygosity on the subpopulation level, however the genetic differences are still not significant, despite of the diversity of the pheotype of the lines in the past 20 years. Analogous fixation indices were measured studying native Italian hunting dog breeds with microsatellite markers [18].

Conclusions

Based on the obtained results the genetic contribution of the different males could be limited and consequently by planning the mating scheme could be possible in order to maintain genetic variability. The decreasing tendency of the effective population size points out a trend, that dog owners do not prefer to buy from registered breeders. Since the definite purposes such as show and sport require different anatomical structures, the importance of these lines are outstanding, however the contrasts of the selection of these dogs may increase the genetic distance. In Hungary, the working line is at the greatest risk, regarding the number of breeding animals and the number of litters. Import cannot be the only solution to this problem, due to the slightly different breeding standards between the countries.

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