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Genetic Analysis of the Hungarian Population of Endangered Hucul Horses

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ABSTRACT

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The population genetic evaluation of the Hungarian Hucul horse population was performed based on pedigree records. Herd book data of registered Hucul horses available up to 2016 were analysed using ENDOG (Gutierrez and Goyache 2005) and POPREP (Groeneveld et al. 2009) on the whole population (WP) as well as on the reference stock (RS) (breeding stock registered in 2016). Inbreeding coefficients were 5.57% (WP) and 7.18% (RS). Average relatedness was 10.39% in WP and higher in RS (12.67%). Effective population size was 52.32. Generation interval was 13.01 years for WP and 10.99 years for RS. The values for equivalent complete generations were 6.07 and 8.75, for the maximum number of generations 14.11 and 19.16, and for the number of full generations traced 3.77 and 5.50 for WP and RS, respectively. The effective number of founders (f_e) was 23 both for WP and RS. The effective number of ancestors (f_a) was 20 in WP and lower in RS (16). The f_a/f_e ratio was 0.869 in WP and 0.696 in RS. Founder genome equivalent (f_g) was 9.618 in WP and 5.790 in RS. The f_g/f_e ratio was 0.481 in WP and 0.361 in RS. The study revealed that both the inbreeding coefficient and the average relatedness were high. The above mentioned ratios indicated loss of genetic diversity in the Hungarian Hucul population.

Keywords: genetic diversity; pedigree analysis; genetic protection; endangered breed

Before World War I, Huculland was located at the borders of Bucovina, Galicia, and Hungary, in the forested Carpathian region. Thus, Hungary has been linked to the Hucul horse since its existence. Hucul horses occurred in large estates within the Hungarian countryside as well.

After World War I, Hungary bought 4 Hucul stallions and 13 mares from the original breeding stock. Some Hucul horses came from Poland and in 1939 the Hucul stock of Turjaremete (Ukraine) was moved to Hungary. This stock became the victim of World War II, only several horses survived, mainly in clerical estates. The rescue of the breed started with these few animals. Some stallions were imported from Czechoslovakia. Only two of the rescued mares (Aspiráns and Árvácska) established mare families and there was not enough diversity

on the paternal side as well. After the reorganization of civil breeding organizations, from 1992, the Association of Pony and Small Horse Breeders received the right to organize the breeding of Hucul horses in Hungary. Firstly, 5 mares and 2 stallions (from Ousor and Goral stallion lines) were imported from Lucina (National Stud in Romania), and later on a stallion from the Polan stallion line (Poland) was imported in the middle of the 1990s. These three stallion lines and two mare families dominated the breed for a long time, the growth of mare families was slow. When the number of breeding animals exceeded 200, the huge willingness of the breeders resulted in the appearance of all seven stallion lines (Hroby, Goral, Prislop, Pietrosu, Ousor, Polan, Gurgul) in the Hungarian breeding. Nowadays, there are more

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than 300 broodmares and more than 30 breeding stallions in the active population representing the seven mentioned stallion lines.

In the case of endangered breeds due to the bottleneck effect during the population history, population genetic calculations have become essential as a tool that may help maintain a breed genetic variance. By slowing down inbreeding progress and avoiding the mating of related individuals, genetic diversity can be maintained or at least its decreasing can be slowed down whereby the preservation of the breed may be attained during a longer period. In the case of breeds under gene conservation and especially in the case of the Hucul, the import of foreign breeds is not allowed. Because of the closed stud book and small population size, carefully planned mating is especially important and may be facilitated by pedigree analyses. The theoretical basis of pedigree analysis was first described by Wright (1931), later on by James (1962, 1971, 1972), MacCluer et al. (1986), and Lacy (1989). Since the method of Boichard et al. (1997), pedigree analyses for various horse breeds (e.g. Dunner et al. 1998; Curik et al. 2003; Royo et al. 2007; Vostry et al. 2011; Pjontek et al. 2012; Mackowski et al. 2015) as well as other animal species (e.g. Martin de la Rosa et al. 2016) have been published. The ENDOG program created and further developed by Gutierrez and Goyache (2005) revealed further opportunities.

The aim of the current study was to analyse pedigree information of the registered Hungarian Hucul population. Our research focused on the Hungarian population of the protected and endangered Hucul breed. The results might be used for long-term preservation of the breed.

MATERIAL AND METHODS

The herd book data of registered Hungarian Hucul population up to 2016 were analysed. The dataset covered birth years between 1895 and 2016. The breeding stock registered in 2016 was chosen as the reference to evaluate the genetic structure. The indicators analysed in the study are described below.

Pedigree completeness. It can be characterized by the values of the number of full generations traced, the maximum number of generations, and the equivalent complete generations. The equivalent

complete generations can be computed as the sum over all known ancestors of the terms computed as the sum of $(1/2)^n$, where n is the number of generations separating the individual from each known ancestor (Maignel et al. 1996). The first is defined as the farthest generation in which all the ancestors are known. Ancestors with unknown parents were considered as founders (generation 0). The second is the number of generations separating the individual from its farthest ancestor.

ENDOG calculates using Wright's (1922) formula where the inbreeding coefficient (F) of a given individual (X) is:

$$F_X = \Sigma(1/2)^{n+n'+1} \times (1 + F_A)$$

where:

- A = common ancestor in the chains of origin of the father and mother of the individual X
- n, n' = number of generations between the individual X and the ancestor A on father's and mother's side, respectively
- F_A = inbreeding coefficient of the common ancestor
- Σ = sum of all common ancestors and ancestry roads in the chains of origin of the individual X 's father and mother. Its precision depends on the length and completeness of the pedigree (Boichard et al. 1997).

The coefficient of inbreeding (F) of an individual is equal to the additive genetic relationship between its parents or the coefficient of co-ancestry, i.e.

$$F_i = f_{sd}$$

where:

- i = the individual i
- s, d = sire and dam of the individual i , respectively (Falconer and Mackay, 1996).

Under random mating, the rate of inbreeding (ΔF) is equal to the rate of additive genetic relationships (Δf). Thus, the effective population size (N_e) can be obtained from either $1/2\Delta F$ or $1/2\Delta f$. Therefore, the discrepancy between the two effective sizes indicates a deviation from a random mating system. The rate of additive genetic relationship equals to:

$$\Delta f = f_t - f_{t-1}/1 - f_{t-1}$$

where:

- f_t = average additive genetic relationship of the cohort born in generation t (or the current year)
- f_{t-1} = the cohort born a generation earlier

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The rate of inbreeding per generation (ΔF) was calculated as:

$$\Delta F = F_t - F_{t-1}/1 - F_{t-1}$$

where:

F_t, F_{t-1} = average inbreeding of offspring and their parents, respectively (Falconer and Mackay 1996)

The rate of additive genetic relationships and the rate of inbreeding were computed using the POPREP program (Groeneveld et al. 2009).

Average relatedness coefficient. The average relatedness coefficient (Colleau 2002) shows the likelihood of an allele randomly chosen from the pedigree covering the whole population belonging to an individual. It was calculated according to the equation:

$$c' = (1/n) l'A$$

where:

c' = row vector where c_i is the average of the coefficients in the row of the individual i in the numerator relationship matrix A , of the dimension n

A = relationship matrix of the size $n \times n$.

Effective population size. The estimation based on individual increase in inbreeding (ΔF_i) was calculated following the approach proposed by Gutierrez et al. (2009). The ΔF_i coefficients are computed simply as

$$\Delta F_i = 1 - \sqrt[t-1]{1 - F_i}$$

where:

F_i = individual coefficient of inbreeding

t = equivalent complete generations (Maignel et al. 1996).

This estimate of effective population size (\bar{N}_e), called realized effective size by Cervantes et al. (2008), can be computed from ΔF as $\bar{N}_e = 1/(2\Delta F)$.

Effective number of founders. All individuals of the population can be traced back to the founders, which, however, contribute to the formation of the population's genetic stock to various extents. This latter is what is adjusted by the effective number of founders (f_e) in a way as if the founders had contributed to genetic diversity to the same extent. This can be computed as:

$$f_e = 1/\sum_{k=1}^f q_k^2$$

where:

q_k = probability of gene origin of the k ancestor

Therefore the effective number of founders (f_e) is always lower than the number of founders (Vigh et al. 2008).

The **effective number of ancestors** (f_a) is lower than (or the same as) the f_e . This can be computed as:

$$f_a = 1/\sum_{k=1}^f q_k^2$$

where:

q_j = marginal contribution of an ancestor j , which is the genetic contribution made by an ancestor that is not explained by other ancestors chosen before

Ancestors are selected on the basis of their genetic contribution to the population, since certain individuals are not necessarily founders, so in view of relatedness genetic contributions may be overlapping (and their totality may be more than 100%). In the case of ancestors we consider their marginal contribution (using the non-overlapping part of genetic contributions).

The **f_a/f_e ratio** implies a bottleneck effect suffered. If f_e is higher than f_a , the population suffered from a bottleneck effect. The bottleneck effect means that the number of individuals in a population falls due to the impact of some outside factor, and this shrunk population starts reproducing. While their population size can grow, their genetic variance cannot, since it cannot be higher than the genetic variance of the lowest population size before reproduction. This means nothing else but that the genetic variability of the survived population is significantly lower than in the original population (with a high number of individuals). At later stages the population is only able to draw from the retained genetic diversity and practically never attains the genetic diversity of the original population.

The **founder genome equivalent** (f_g) (Ballou and Lacy 1995) can be defined as the number of founders that would be expected to produce the same genetic diversity as in the population under study if the founders were equally represented and no loss of alleles occurred. Following Caballero and Toro (2000), parameter f_g was obtained by the inverse of twice the average coancestry of the individuals included in a pre-defined reference population. This indicator considers each effect that played a role in the reduction of the genetic stock and therefore f_g is usually lower than f_e and f_a (Solkner et al. 1998).

The f_g/f_e *ratio* indicates whether the analysed population was affected by a genetic drift (Boichard et al. 1997).

The *generation interval* shows the average age of parents at the time of their offspring's birth (James 1977). The value was calculated along four different pathways (sire-to-daughter, sire-to-son, dam-to-daughter, and dam-to-son) on the basis of the recorded individuals' and their parents' birth dates.

The above described parameters were estimated using the ENDOG program (Gutierrez and Goyache 2005). The appropriate formulas and methods are more detailedly explained in the instructions to the software.

RESULTS

Quality of the pedigree. The three different pedigree completeness values of the whole population (WP) and the reference stock (RS) are summarised in Table 1. The equivalent complete generations calculated for WP was, on the average, 6.07 generations (with values ranging between 0 (founders) and 10.48); in RS the average was 8.75 generations (with the extreme values of 4.39 and 10.48).

Both in WP and RS we were able to trace back the origin up to maximally 23 generations. In the case of 38% of RS we are familiar with ancestors up to 20–23 generations, in the case of 35% up to 19 generations, and in the case of 26% up to 16–18 generations. The mean value of the maximum number of generations was 14.11 in WP (values ranging

Table 1. Description of the quality of the pedigree

Pedigree completeness		Whole population	Reference stock
Equivalent complete generations	minimum	0	4.39
	maximum	10.48	10.48
	average	6.07	8.75
Maximum number of generations	minimum	0	16
	maximum	23	23
	average	14.11	19.16
Number of full generations traced	minimum	0	2
	maximum	7	7
	average	3.77	5.50
Known ancestor at generation (%)	1	95.21	100
	2	90.34	100
	3	83.37	99.85
	4	76.07	99.63
	5	67.75	98.72
	6	57.98	95.91
	7	46.77	86.62
	8	34.88	70.54
	9	23.47	50.30
	10	14.43	31.93

between 0 (founder) and 23), while a significantly higher value was obtained in RS (19.16 generations; values varying between 16 and 23).

We are familiar with the full ancestry of 88% of RS up to 5–7 generations; of 12% up to 2–4 generations. Considering the WP, only 41% can be traced back to 5–7 generations and 46% to 2–4 generations. The mean value of the number of full generations traced is 3.77 generations in WP, in RS it grew to 5.5.

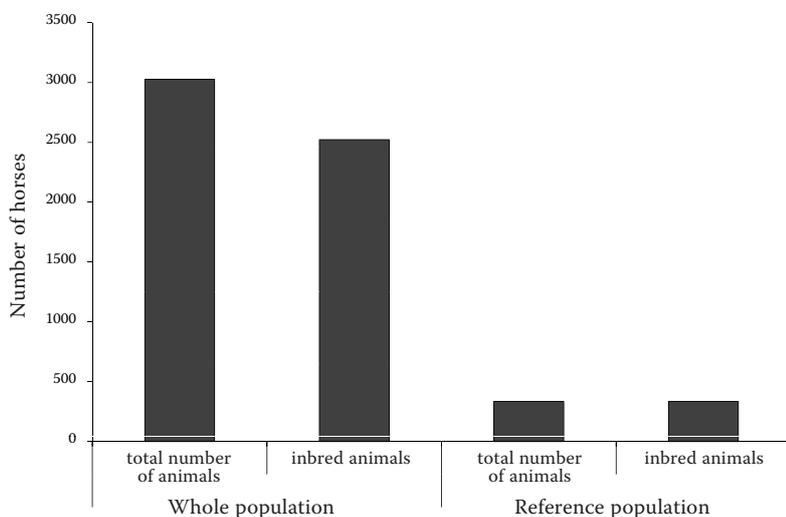


Figure 1. Description of inbred animals

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Table 2. Inbreeding and inbreeding-related variables in the whole population and in the reference stock

	Whole population	Reference stock
Average inbreeding (%)	5.57	7.18
Average inbreeding of inbred animals (%)	6.68	7.18
Rate of inbreeding	0.007	
Expected inbreeding (%)	2.02	
Average relatedness (%)	10.39	12.67
Rate of co-ancestry (relatedness)	0.006	
Effective population size	52.32	

Known ancestors were above 90% up to the 6th generation for RS, and only up to the 2nd generation for WP.

Inbreeding coefficient, average relatedness, and effective population size. The average inbreeding coefficient of WP (3026 individuals) was 5.57%, that of RS (336 individuals) was significantly higher – 7.18%. There were 2523 inbred animals within WP and 335 within RS, so the proportion of inbreeding was 83.38% and 99.7% in WP and RS, respectively (Figure 1). The rate of inbreeding was 0.007 and average relatedness was 0.006, the computed effective population sizes based on these parameters were 73 and 85.67. Due to the differences between the two numbers, there is non-random mating within the population. The expected inbreeding was 2.02% (Table 2).

Average relatedness in WP was 10.39%, which is lower than the 12.67% of RS. This implies that the mating of related individuals could not be avoided. Effective population size was 52.32.

Probability of gene origin. The number of founders in WP is 152; the effective number of founders (f_e) is 23. In RS the number of founders is lower than 110, while f_e is the same (23). The number of ancestors in WP is 144; the effective number of ancestors (f_a) is 20. In RS, both the number of ancestors (75) and f_a (16) are lower. The f_a/f_e ratio is 0.869 in WP and 0.696 in RS. The f_e is higher than f_a , which confirms that there is a bottleneck effect in the population. The founder genome equivalent (f_g) in WP and RS is 9.618 and 5.790, respectively. The f_g reflects all the effects that may have resulted in the shrinkage of the genetic stock. The f_g is lower than f_e and f_a , which indicates further genetic loss, i.e. diversity in the population has shrunk. The f_g/f_e ratio is 0.481 in WP and 0.361 in RS. The obtained value supports the occurrence of the population genetic drift.

Generation interval. Surprisingly, the longest generation interval was obtained in WP for the sire-to-daughter pathway. This was followed by the sire-to-son and the mare-to-daughter pathways whereas the shortest value was calculated for the mare-to-son pathways. In RS, it is the sire-to-daughter pathway that has the longest generation interval, followed by the dam-to-son and sire-to-son pathways with approximately the same values. The shortest generation interval was calculated for the dam-to-daughter pathway. The average generation interval in WP and in RS is 10.99.

Ancestors with the greatest genetic impact. The individuals of RS included in Table 4 (11 stallions and 2 mares) are responsible for 70.65% of the genetic variability. 100% of the RS genetic composition comes from 75 ancestors (Table 3).

Table 3. Parameters of gene origin

	Whole population	Reference stock
Number of founders	152	110
Effective number of founders (f_e)	23	23
Number of ancestors	144	75
Effective number of ancestors (f_a)	20	16
Effective number of ancestors/effective number of founders ratio (f_a/f_e)	0.869	0.696
Founder genome equivalent (f_g)	9.618	5.790
Founder genome equivalents/effective number of founders ratio (f_g/f_e)	0.481	0.361
Number of ancestors contributing		
50% of the gene pool	7	6
80% of the gene pool	21	15
100% of the gene pool	144	75

The individuals collected in Table 4 (9 stallions, 3 mares) make up 63.01% of WP. There are 144 ancestors (Table 3) responsible for 100% of the WP genetic diversity. The ancestor with the greatest impact in RS is Goral III from Lucina. His impact on the increase has not been apparent in WP yet but has been continuously raising in recent years. The second place is held, through his numberless offspring and grandchildren, by 3139 Polan (Pol) which, in comparison with the other stallions, has a shorter breeding history but still a great impact on the current stock. His involvement in the breeding changed the genetic variability in RS (10.36%), while it influenced WP only to the extent of 1.96%. The impact of the stallions Hroby VIII (Lu), Ousor (Lu), 162 Ousor 02-7 Turek (Murány), Pietrosu II (Lu), and Pietrosu VIII (Lu) on the genetic structure in RS continued to grow. Owing to the effect of the two Pietrosu individuals and their offspring the distribution among the studs changed. The impact of certain individuals in RS (e.g. stallions Goral I (Lu), Hroby (Bukovina), 21 Gurgul (Top), Goral (Halicsi), and of 76 Taras mares) decreased.

DISCUSSION

Quality of the pedigree. Royo et al. (2007) reported 2.97 generations (equivalent complete generations) for Asturcon ponies and Pinheiro

et al. (2013) 6.14 for Sorraia horses; these values are lower than the ones (Table 1) we attained. Mackowski et al. (2015) and Pjontek et al. (2012) reported somewhat higher equivalent complete generations for the Polish (3.8–7) and Slovak Hucul populations (7.1) as well as Druml et al. (2009) for the Austrian Noriker draught horses (12.28) compared to our study. As it was expected, Bokor et al. (2013) obtained almost twice as high indicator (15.64 generations) for the Hungarian population of English Thoroughbred horses. A lower number of generations than their maximum number (Table 1) – only 5.76 – was obtained with reference to Slovak Sport Pony (Pjontek et al. 2012); 13 generations were recorded for Sorraia horses (Pinheiro et al. 2013), and 14.59 generations for Andalusian horses (Valera et al. 2005). The value of 17.54 generations for the Slovak Hucul horses reported by Pjontek et al. (2012) is close to the value recorded in the case of the Hungarian population. Bokor et al. (2013) recorded 28.96 generations for the Hungarian Thoroughbred; Druml et al. (2009) 31 generations for Austrian Noriker draught horses. The value 34.82 published by Pjontek et al. (2012) for Shagya Arabian horses indicates a significantly longer period, which can be explained by the fact that the ancestors can be traced back as far as before the 1800's. Pjontek et al. (2012) published 4.29 generations (number of full generations traced) for the Slovak Hucul population, which is somewhat

Table 4. Description of the most important ancestors

Animal	Gender	Year of birth	Coverage rate in the variability (%)	
			whole population	reference stock
Proportion of genes contributed by:				
Goral I (Lu)	stallion	1907	13.64	3.11
3 Tatarca (Lu)	mare	1913	8.67	–
Hroby (Bukovina)	stallion	1895	8.14	3.93
Ousor (Lu)	stallion	1929	6.88	7.14
Hroby VIII (Lu)	stallion	1933	4.48	8.53
21 Gurgul (Top)	stallion	1927	3.69	2.76
Pietrosu II (Lu)	stallion	1937	3.58	6.45
85 Manaila (Lu)	mare	1924	3.56	3.56
Goral (Halicsi)	stallion	1898	3.50	1.03
76 Taras	mare	–	2.86	1.96
162 Ousor 02-7 Turek (Murány)	stallion	1969	2.05	4.95
3139 Polan (Pol)	stallion	1984	1.96	10.36
Goral III (Lu)	stallion	1926	–	15.18
Pietrosu VIII (Lu)	stallion	1967	–	4.80

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lower in our study (Table 1). Bokor et al. (2013) calculated 6.69 generations for the Hungarian Thoroughbred. Naturally and characteristically, the values of all the three pedigree indicators are higher in RS. Lines of descendants have become longer and more complete. Considering that the history of the Hucul goes back to the 1870's and that ancestry data were lost at the times of war, the pedigree completeness values obtained may be regarded as favourable.

Inbreeding coefficient, average relatedness, and effective population size. The inbreeding coefficient has been increased in the Hungarian population. The inbreeding coefficient (Table 2) values obtained were significantly higher than those reported by Vostry et al. (2011) for Noriker horses (1.51%) and Silesian Noriker horses (3.23%), or those in the study of Alvarez et al. (2010) for Mallorqui horses (4.7%). Lower values (2.7% and 4.7%) were published by Dunner et al. (1998) and Royo et al. (2007) for Asturcon ponies compared to our results. The values for the Polish Hucul (6.26%; Mackowski et al. 2015) and for the Slovak Hucul (7.7%; Pjontek et al. 2012) populations were quite similar to those for the Hungarian ones, which might be the result of the common origin as well as the limited population size in the individual countries. We obtained higher values (5.57% and 7.18%) than those reported by Valera et al. (2005) for Andalusian horses (8.48%), Curik et al. (2003) and Zechner et al. (2002) for Lipizzan horses (10.3% and 10.81%, respectively), Avdi and Banos (2008) for Greek Skyros horses (11%), and Sevinga et al. (2004) for Friesian horses (15.7%). Most of the animals in the reference population were inbred (Figure 1), so it seems to be difficult to keep the average inbreeding low in the future.

Significantly lower average relatedness (Table 2) values were reported by Pjontek et al. (2012) for Shagya Arabian horses (3.08%) and Lipizzan horses (3.73%), by Dunner et al. (1998) and Royo et al. (2007) with reference to Asturcon ponies (6.8% and 9.2%). Pjontek et al. (2012) obtained a somewhat lower value (9.34%) for the Slovak Hucul population. Although these authors estimated higher inbreeding value compared to our results, average relatedness was nevertheless by more than 3% lower, which indicates a lower level of close breeding in the Slovak Hucul population. Alvarez et al. (2010) recorded values similar to ours (11.2%) with reference to Mallorqui horses

whereas Valera et al. (2005) reported quite similar results for Andalusian horses (12.25%) than our values calculated for RS.

The level of inbreeding and average relatedness in RS exhibited a growing trend (inbreeding coefficient rose from 5.57 to 7.18%; average relatedness from 10.39 to 12.67%), which is unfavourable from the viewpoint of genetic diversity and the long-term sustainability of the breed. Unfortunately, the average inbreeding of both WP and RS exceeds the expected inbreeding (2.02%). In order to reduce inbreeding, the import of individuals having ancestors not appearing among the ancestors of the current Hungarian population is recommended. An example of this method was the import of 3139 Polan (Pol), which was unrelated to the Hungarian breeding stock and nowadays has the second highest genetic impact in RS. The impact of this stallion might be higher than desirable for maintaining the long term genetic diversity. The deviation from non-random mating could be a sign of selection within a population posing a risk to maintaining genetic diversity in an endangered population.

The effective population size was 52.3. This value is slightly higher than 50 what is considered as the limit of sustainability reported by Frankham et al. (2002) and predicts the possibility of maintaining the breed in the following generations. This effective population size is quite close to those reported in previous studies – Pjontek et al. (2012) reported 47.67 for the Slovak Hucul horse population and Vostry et al. (2011) computed 43.14 for Silesian Noriker horses. Our finding is more favourable compared to the effective population size of the Friesian Horse (27) reported by Sevinga et al. (2004). The genetic variability of Austrian Noriker horses (79.11) (Vostry et al. 2011) and Lipizzan horses (102) (Zechner et al. 2002) seems to be more favourable based on the effective population sizes compared to our results.

Probability of gene origin. In comparison with the values published by other authors, an indicator similar to ours (26; Table 3) was obtained for the effective number of founders in the Slovak Hucul population by Pjontek et al. (2012). The indicator of 7.46 published by Pinheiro et al. (2013) for Sorraian horses and the value of 11 recorded by Alvarez et al. (2010) for Mallorqui horses are lower than those we obtained. Significantly higher is, on the other hand, the value of 40 recorded by Mackowski et al. (2015) for the Polish Hucul

Table 5. Generation intervals (years) of the whole population and of the reference stock for different pathways

Parent–offspring lineages	Generation interval (years)	
	whole population	reference stock
Sire-to-son	11.40	10.50
Sire-to-daughter	12.15	13.21
Dam-to-son	9.92	10.52
Dam-to-daughter	9.93	8.90
Average	10.99	10.99

population. Druml et al. (2009) obtained a value of 117.2 for Austrian Noriker draught horses, which is five times higher than our findings. The effective number of ancestors for RS (Table 3) is in agreement with Mackowski et al. (2015) and Pjontek et al. (2012) for the Polish and Slovak Hucul population. Pinheiro et al. (2013) for Sorraia horses and Alvarez et al. (2010) for Mallorqui horses (4 and 11, respectively) published lower values for the effective number of ancestors compared to our study, whereas Druml et al. (2009) obtained higher value (29.3) for Austrian Noriker draught horses. The values for the effective number of ancestors/effective number of founders ratio obtained by Mackowski et al. 2015 (0.4) and by Druml et al. 2009 (0.25) are lower than our values (Table 3). Values similar to ours were obtained for the founder genome equivalent by Mackowski et al. (2015) (6 and 10) for the Polish Hucul population, Alvarez et al. (2010) for Mallorqui horses (7), and Druml et al. (2009) for Austrian Noriker draught horses (10.63). The founder genome equivalent and the effective number of founders are in agreement with values reported by Vostra-Vydrova et al. (2016) in Old Kladruber horses.

Generation interval. The average generation interval in WP and RS is 10.99 (Table 5). This cannot be considered ideal from the viewpoint of breeding, since it may reduce genetic diversity per time unit. The longer the generation interval, the longer the genealogical lineage; a mare family, an individual with a rare pedigree is able to survive from the viewpoint of gene preservation, whereby genetic diversity can be sustained. This fact or requirement is also favourable with a view to reducing inbreeding. There were significant differences ($P < 0.05$) between sire-to-son and dam-to-son, sire-to-son and dam-to-daughter as well as sire-to-daughter and dam-to-son, sire-to-

daughter and dam-to-daughter pathways for WP based on independent samples t -test. For RS, the pathways were significantly ($P < 0.05$) different only between sire-to-daughter and dam-to-son as well as sire-to-daughter and dam-to-daughter. Lower values for the generation interval were recorded by Druml et al. (2009) for Austrian Noriker draught horses (7.9 years), Vostry et al. (2011) for Czech Silesian Noriker horses (8.53 years) and Noriker horses (8.88 years), as well as by Pinheiro et al. (2013) for Sorraia horses (7.94 years). The value of 10.99 years recorded for RS and WP was close to that reported by Alvarez et al. (2010) for Mallorqui horses (11.1 years) and Pjontek et al. (2012) for the Slovak Hucul population (11.4 years). Higher values (mares 10.24–12.6, stallions 8.64–13.94) were calculated by Glazewska and Jezierski (2004) for Polish Arabian horses.

CONCLUSION

The pedigree completeness values were higher and more complete in RS, which enabled us to obtain more precise and reliable data for the inbreeding coefficient calculation. The multiple decreasing/increasing of the Hungarian Hucul breeding stock, genetic diversity decreasing, the genetic drift and the bottleneck effect were supported by the f_g , f_a/f_e , and f_g/f_e values calculated in our study. In order to facilitate the long-term sustainability of the Hucul breed under genetic conservation, the exchange or purchase of breeding animals among breeding countries is inevitable. The import of breeding animals with the genotype not appearing in the Hungarian population from Hucul breeder countries is reasonable. Because of the genetic relationships among the breeding stock of the breeder countries, the task is difficult, however not impracticable. Genetic diversity may be increased by importing animals with alleles not or just rarely appearing in the Hungarian population.

REFERENCES

- Alvarez J., Royo L.J., Perrez-Pardal L., Fernandez L., Payeras L., Goyache F. (2010): Assessing losses of genetic variability in the endangered Mallorqui horse. *Czech Journal of Animal Science*, 55, 456–462.

<https://doi.org/10.17221/54/2017-CJAS>

- Aydi M., Banos G. (2008): Genetic diversity and inbreeding in the Greek Skyros horse. *Livestock Science*, 114, 362–365.
- Ballou J.D., Lacy R.C. (1995): Identifying genetically important individuals for management of genetic variation in pedigreed populations. In: Ballou J.D., Gilpin M., Foose T.J. (eds): *Population Management for Survival and Recovery: Analytical Methods and Strategies in Small Population Management*. Columbia University Press, New York, 76–111.
- Boichard D., Maignel L., Verrier E. (1997): The value of using probabilities of gene origin to measure genetic variability in a population. *Genetics Selection Evolution*, 29, 5–23.
- Bokor A., Jonas D., Nagy I., Bokor J., Szabari M. (2013): Pedigree analysis of Hungarian Thoroughbred population. *Livestock Science*, 151, 1–10.
- Caballero A., Toro M.A. (2000): Interrelations between effective population size and other pedigree tools for the management of conserved populations. *Genetics Research*, 75, 331–343.
- Cervantes I., Goyache F., Molina A., Valera M., Gutierrez J.P. (2008): Application of individual increase in inbreeding to estimate effective sizes from real pedigrees. *Journal of Animal Breeding and Genetics*, 125, 301–310.
- Colleau J.J. (2002): An indirect approach to the extensive calculation of relationship coefficients. *Genetics Selection Evolution*, 34, 409–421.
- Curik I., Zechner P., Solkner J., Achmann R., Bodo I., Dovc P., Kavari T., Marti E., Brem G. (2003): Inbreeding, microsatellite, heterozygosity, and morphological traits in Lipizzan horses. *Journal of Heredity*, 94, 125–132.
- Druml T., Baumun R., Solkner J. (2009): Pedigree analysis in the Austrian Noriker draught horse: genetic diversity and the impact of breeding for coat colour on population structure. *Journal of Animal Breeding and Genetics*, 126, 348–356.
- Dunner S., Checa M.L., Gutierrez J.P., Martin J.P., Canon J. (1998): Genetic analysis and management in small populations: the Asturcon pony as an example. *Genetics Selection Evolution*, 30, 397–405.
- Falconer D.S., Mackay T.F. (1996): *Introduction to Quantitative Genetics*. Longman Green, Harlow, UK.
- Frankham R., Ballou J.D., Briscoe D.A. (2002): *Introduction to Conservation Genetics*. Cambridge University Press, Cambridge, UK.
- Glazewska I., Jezierski T. (2004): Pedigree analysis of Polish Arabian horses based on founder contributions. *Livestock Production Science*, 90, 293–298.
- Groeneveld E., Westhuizen B.V.D., Maiwashe A., Voorde-wind F., Ferraz J.B.S. (2009): POPREP: a generic report for population management. *Genetics and Molecular Research*, 8, 3, 1158–1178.
- Gutierrez J.P., Goyache F. (2005): A note on ENDOG: a computer program for analysing pedigree information. *Journal of Animal Breeding and Genetics*, 122, 172–176.
- Gutierrez J.P., Cervantes I., Goyache F. (2009): Improving the estimation of realized effective population sizes in farm animals. *Journal of Animal Breeding and Genetics*, 126, 327–332.
- James J.W. (1962): The spread of genes in random mating control population. *Genetics Research*, 3, 1–10.
- James J.W. (1971): The founder effect and response to artificial selection. *Genetics Research*, 16, 241–250.
- James J.W. (1972): Computation of genetic contributions from pedigrees. *Theoretical and Applied Genetics*, 42, 272–273.
- James J.W. (1977): A note on selection differentials and generation length when generations overlap. *Animal Production*, 24, 109–112.
- Lacy R.C. (1989): Analysis of founder representation in pedigrees: founder equivalents and founder genome equivalents. *Zoo Biology*, 8, 111–123.
- MacCluer J.W., Van de Berg J.L., Read B., Ryder O.A. (1986): Pedigree analysis by computer simulation. *Zoo Biology*, 5, 147–160.
- Mackowski M., Mucha S., Cholewinski G., Cieslak J. (2015): Genetic diversity in Hucul and Polish primitive horse breeds. *Archives Animal Breeding*, 58, 23–31.
- Maignel L., Boichard D., Verrier E. (1996): Genetic variability of French dairy breeds estimated from pedigree information. *Interbull Bulletin*, 14, 49–54.
- Martin de la Rosa A.J., Cervantes I., Gutierrez J.P. (2016): Equivalent effective population size mating as a useful tool in the genetic management of the Ibicenco rabbit breed (Conill Pages d'Eivissa). *Czech Journal of Animal Science*, 61, 108–116.
- Pinheiro M., Kjollerstrom H.J., Oom M.M. (2013): Genetic diversity and demographic structure of the endangered Sorraia horse breed assessed through pedigree analysis. *Livestock Science*, 152, 1–10.
- Pjontek J., Kadlecik O., Kasarda R., Horny M. (2012): Pedigree analysis in four Slovak endangered horse breeds. *Czech Journal of Animal Science*, 57, 54–64.
- Royo L.J., Alvarez I., Gutierrez J.P., Fernandez I., Goyache F. (2007): Genetic variability in the endangered Asturcón pony assessed using genealogical and molecular information. *Livestock Science*, 107, 162–169.
- Sevinga M., Vrijenhoek T., Hesselink J.W., Barkema H.W., Groen A.F. (2004): Effect of inbreeding on the incidence of retained placenta in Friesian horses. *Journal of Animal Science*, 82, 982–986.

<https://doi.org/10.17221/54/2017-CJAS>

- Solkner J., Filipcic L., Hampshire N. (1998): Genetic variability of populations and similarity of subpopulations in Austrian cattle breeds determined by analysis of pedigrees. *Animal Science*, 67, 249–256.
- Valera M., Molina A., Gutierrez J.P., Gomez J., Goyache F. (2005): Pedigree analysis in the Andalusian horse: population structure, genetic variability and influence of the Carthusian strain. *Livestock Production Science*, 95, 57–66.
- Vigh Zs., Csato L., Nagy I. (2008): Application of pedigree analysis in the animal breeding programs. (*Hungarian Journal of Animal Production*, 57, 549–564. (in Hungarian))
- Vostra-Vydrova H., Vostry L., Hofmanova B., Krupa E., Zavadilova L. (2016): Pedigree analysis of the endangered Old Kladruber horse population. *Livestock Science*, 185, 17–23.
- Vostry L., Capkova Z., Pribyl J., Hofmanova B., Vydrova H.V., Mach K. (2011): Population structure of Czech cold-blooded breeds of horses. *Archives Animal Breeding*, 54, 1–9.
- Wright S. (1922): Coefficients of inbreeding and relationship. *American Neptune*, 56, 330–333.
- Wright S. (1931): Evolution in Mendelian populations. *Genetics*, 16, 97–159.
- Zechner P., Solkner J., Bodo I., Drum T., Baumung R., Achmann R., Marti E., Habe F., Brem G. (2002): Analysis of diversity and population structure in the Lipizzan horse breed based on pedigree information. *Livestock Production Science*, 77, 137–146.

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