GENETIC VARIABILITY OF HOLSTEIN CATTLE ASSESSED BY PEDIGREE ANALYSIS

Ivan PAVLÍK[1]*, Ondrej KADLEČÍK[2], Ján HUBA[1], Dana PEŠKOVIČOVÁ[1], Martina GONDEKOVÁ[1]

[1]NPPC – Research Institute for Animal Production Nitra, Lužianky, Slovak Republic
[2]Slovak University of Agriculture in Nitra, Department of Animal Genetics and Breeding Biology, Nitra, Slovak Republic

ABSTRACT

The aim of this paper was to evaluate the genetic variability within Holstein cattle population in Slovakia using the methods of pedigree analysis. Totally, 76,176 animals were included into the reference population. Pedigree completeness assessed by index of pedigree completeness was satisfying; the proportion of known ancestors in the first three generations was over 95 %. The value of average inbreeding coefficient was not alarming (0.95 %), but regular increase of average inbreeding was observed in recent years (R^2 = 0.963). The difference between the effective number of founders and the effective number of ancestors showed unequal contributions of individuals into reference population caused by the bottleneck effect. Very low effective numbers of founder genomes reflected the loss of founder gene pool within the population. Regular monitoring of genetic diversity is an essential part of breeding work within the population. Farmers should focus on appropriate mating strategies, e.g. individual mating programs limiting inbreeding.

Key words: founder; gene origin; inbreeding; relatedness

INTRODUCTION

Holstein is considered to be the most common dairy cattle breed world-wide as well as in the Slovak Republic. Nowadays, Holstein represents more than 60 % of dairy cattle population in Slovakia. Slovak Holstein population is open and intensively interacted with the other important Holstein populations (USA, Canada, Germany, France and Netherlands). Genetic variation or diversity could be described and observed as a spectrum of alleles and genotypes (Toro *et al.*, 2011). For the Holstein breed, results obtained in different countries, with various indicators, showed that managing the genetic variability of this world-wide breed deserves much attention (Danchin-Burge *et al.*, 2012). Genetic variation and its maintenance are of the utmost relevance to selection and conservation; therefore, one of the first steps is to estimate the current state and predicted changes in variation. Genealogical information would yield comprehensive parameters to assess the actual levels of diversity, and, therefore should be preferred to assessing the state of variation, although molecular markers, and in the future even whole genome sequences of individuals, are also useful in describing variation (Toro *et al.*, 2011). Knowing the level of genetic diversity within local livestock breeds plays important role in preservation, utilization and production quality in these populations (Kasarda *et al.*, 2015). The breeding strategies currently applied in dairy cattle are very effective in generating genetic gain. However, the reproductive technologies have

increased the focus on a small number of superior animals, especially bulls, and the advanced methods of breeding value estimation have increased the accuracy of prediction by using information on all available relatives. Both of these advancements in animal breeding have increased the probability of generating inbred animals (Sørensen *et al.*, 2005). The trend in inbreeding is doubtlessly the tool most frequently used to quantify the rate of genetic drift. Another complementary approach is to analyse the probabilities of gene origin. In this method, the genetic contributions of the founders, i.e. the ancestors with unknown parents, of the current population are measured. This method assesses how an original gene pool has been maintained across generations (Boichard *et al.*, 1997). Pedigree analysis as a tool for diversity evaluation was published by various authors (Baumung and Sölkner, 2002; Bouquet *et al.*, 2011; Danching-Burge *et al.*, 2012; Gutiérrez *et al.*, 2003; Hammami *et al.*, 2007; Maignel *et al.*, 1996). Previously, genealogical analysis in Slovak cattle populations was presented by Kadlečík *et al.* (2013) in three dairy breeds in Slovakia, Kadlečík *et al.* (2011) in Pinzgau population, Kadlečík and Pavlík (2012) in four beef breeds, Hazuchová *et al.* (2012) and Hazuchová *et al.*, (2013) in Simmental cattle; and Pavlík *et al.* (2012) in Holstein cattle and Pavlík *et al.* (2014) in Pinzgau cattle. Intensive selection and using a limited number of superior animals in recent years signify potential risk of genetic diversity loss even within large livestock populations (including Holstein breed). Therefore, the objective of this study was to assess the inbreeding and diversity measures based on the probability of gene origin within the Holstein cattle population in Slovakia by means of pedigree analysis trying to estimate important factors affecting the diversity state.

MATERIAL AND METHODS

Pedigree information was obtained from The Breeding Services of Slovak Republic, s.e. Living cows involved in official animal recording and bulls with reserve of frozen semen doses were taken into account. The reference population was represented by 76,176 animals, of which 75,835 were cows and 341 were bulls. Animals belonging to the reference population with their ancestors represented whole pedigree file (248,474 individuals). Both colour subpopulations of Holstein cattle (Black&White – H and Red&White – R) were considered. The minimal gene proportion of Holstein breed in each individual was 50.0 %. All bulls were considered as purebred (over 93.75 % Holstein gene proportion). In the case of cows, 59.34 % of animals were purebred; the rest of the cow population was represented by various types of crossbred animals (50.0 – 93.74 % Holstein gene proportion). The reference population was divided into groups according to sex and colour subpopulation. The number of animals in the defined subpopulations is presented in Table 1.

Table 1. Number of animals under study

Population	N
Pedigree file	248,474
Reference population	76,176
RP – bulls	341
RP – cows	75,835
RP – H bulls	257
RP – R bulls	84
RP – H cows	52,082
RP – R cows	23,753

The first step of our analysis was to assess the pedigree depth as an important factor affecting reliability of genetic variation evaluation. Pedigree depth was evaluated by an index of pedigree completeness (PEC) according to McCluer *et al.* (1983). PEC was calculated according to the following formula:

$$PEC = \frac{2C_{sire}\ C_{dam}}{C_{sire}\ C_{dam}},$$

where C_{sire} and C_{dam} are contributions from the paternal and maternal lines, respectively.

$$C = \frac{1}{d} \sum_{i=1}^{d} g_i,$$

where g_i is the proportion of known ancestors in generation i; and d is the number of generations that is taken into account.

Inbreeding coefficient (*F*), defined as the probability that an individual has two identical alleles by descent (Malécot, 1948), was computed according to the algorithm of Meuwissen and Luo (1992). Inbreeding trend in the reference population was calculated by means of moving average (two years moving average taken into account).

Genetic variation was evaluated according to measures based on probability of gene origin as well. Following measures based on probability of gene origin were used:

– number of founders (*f*); founder is defined as the animal with unknown genetic connections to other animals in pedigree except its own progeny (Lacy, 1989).

– effective number of founders (*f$_e$*), defined as the number of equally contributing founders that will produce the same genetic diversity as in the assessed population (Boichard *et al.*, 1997), was calculated according to this formula:

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

where q_k represents the probability of gene origin of the *k* ancestor.

– effective number of ancestors (*f$_a$*) defined as the minimal number of ancestors necessary to explain the genetic diversity in the reference population (Boichard *et al.*, 1997) which was computed as:

$$f_a = {}^1\!/\sum_{j=1}^{a} q_k^2,$$

where p_k is the marginal contribution of ancestor *k*.

– effective number of founder genomes (*N$_g$*) defined as the probability that a gene from the founder population has been maintained in the reference population for a given locus if all founders had contributed equally and no alleles had been lost by drift during bottlenecks (Lacy, 1989). Effective number of founder genomes has been computed as:

$$N_g = \frac{1}{2} \sum_{k=1}^{2f} f_k^2,$$

where f_k is the frequency of allele k (Boichard *et al.*, 1997).

The computation of diversity measures, F-statistics and pedigree depth was provided by an ENDOG v. 4.8 software package (Gutiérrez and Goyache, 2005).

RESULTS AND DISCUSSION

Pedigree completeness

Siderits *et al.* (2013) presented that a relatively small improvement of the pedigree information may lead to apparent changes in the measurements of genetic variability. Therefore, deeper pedigrees may offer more reliable information for diversity evaluation. In our case, the pedigree quality was expressed by the index of pedigree completeness (McCluer *et al.*, 1983). As expected, the pedigree completeness was higher in the reference population than in the whole pedigree file. While in the pedigree file, only 69.93 % of animals had both parents known in the first generation, in the reference population, 99.59 % of animals had both parents known. Increasing number of generations taken into account led to decreasing proportion of known ancestors in farther generations. Similar tendency was presented by Sørensen *et al.* (2005) in Danish Holstein population and Hammami *et al.*, (2007) in Holstein populations of Tunisia and Luxembourg. Very similar level of pedigree completeness was observed by Hazuchová *et al.* (2012) and Hazuchová *et al.* (2013) in Slovak Simmental population.

In the case of RP, the ratio of known ancestors in the second generation declined from 95.03 % to 59.24 % in the fifth generation. Significant differences in pedigree completeness were observed between bulls and cows of fifth generation; in farther generations the differences were negligible. The colour variety (H or R) had no impact on the pedigree depth. Pedigree completeness of H and R bulls, as well as cows, was similar with slightly higher tendency in H animals.

Very high pedigree completeness was published by Hagger (2005) in Original Braunvieh cattle in Switzerland, where almost all animals had 100 % completeness of pedigree information in the first five traced generations. Lower level of pedigree depth than in our bulls was presented by Kania-Gierdziewicz (2005) in Polish Holstein sires. Melka *et al.* (2013) found PEC = 97 % in first four traced generations in Canadian Guernsey cattle, while in South African Guernsey cattle it was only 74 %. The quality of pedigrees is different across the countries related to the tradition and history of organized animal breeding. Considerably lower pedigree completeness than in our case
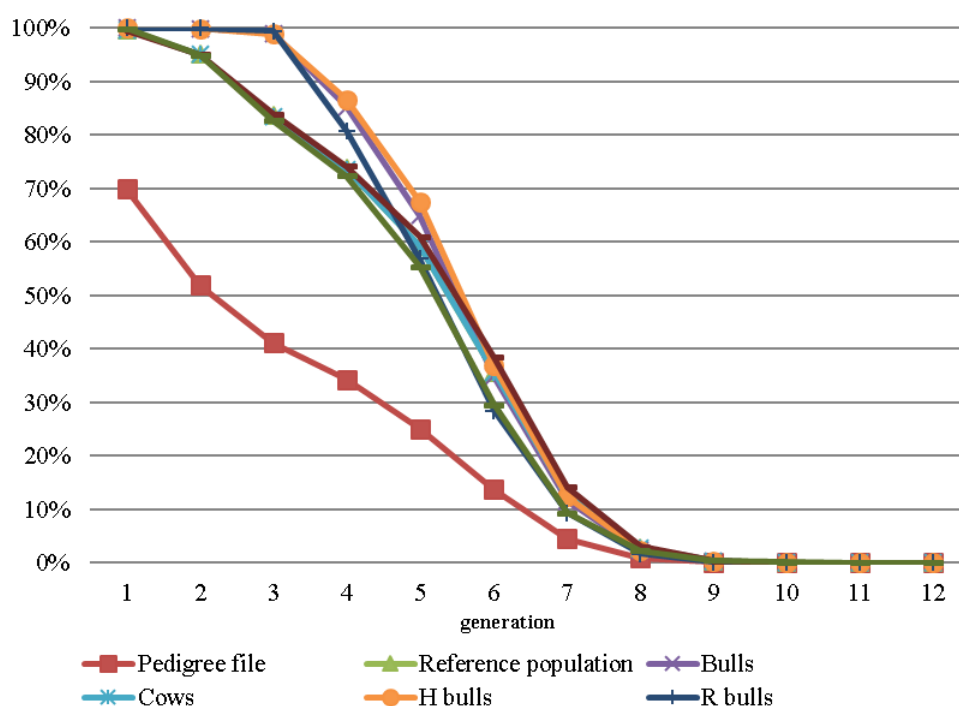
Figure 1. Pedigree completeness in investigated populations

was presented by Malhado *et al.* (2010) in Brazilian Nelore cattle. The overview of pedigree completeness in given populations is presented in Figure 1.

Inbreeding and its evolution

Inbreeding in dairy cattle populations is one of the most important factors affecting the diversity. Many authors confirmed negative effect of inbreeding on different traits (e.g. Maximini *et al.*, 2011; Kasarda and Kadlecik, 2007; Fuerst-Waltl and Fuerst, 2012; Panetto *et al.*, 2010). In addition the average inbreeding value, the trend of inbreeding across the years might be used for managing breeding programs to avoid negative effects of inbreeding depression. In our case, average inbreeding coefficient in the given populations (Table 2) and its evolution across the animals' years of birth (Figure 2) was considered.

The average inbreeding coefficient ranged from 0.34 % in the whole pedigree file to 2.23 % in H bulls. The average inbreeding intensity was 0.95 % in RP. The intensity of inbreeding was more significant in H animals (bulls and cows) than in R

animals. This fact was surprising because the total population size of H animals was almost twice as large as in the Red-Holstein animals. Inbreeding intensity of bulls was more significant than in case of cows in both colour subpopulations. The average values of *F* were not alarming but the proportion of inbred animals was very high. The highest proportion of inbred animals was found in H sires (99.22 %) compared to 94.43 % in all bulls, 80.22 in H cows, 79.76 % in R bulls, 73.59 % in RP, 73.50 % in all cows and finally 58.77 % in R cows. The lower inbreeding intensity and proportion of inbred animals in R cows is related to lowest proportion of purebred animals. The highest proportion of various crossbred animals was in R cows. Although the average inbreeding coefficients were not high, farmers should pay attention on preparation of mating plans. Kadlečík *et al.* (2017) presented lower proportion of inbred animals in reference population of the Slovak Simmental cattle (43 %).

Higher inbreeding coefficient than in our study was published by Danchin-Burge *et al.* (2012) in French Holstein population (*F* = 3.80 %). Higher *F* was presented by Kaerney *et al.* (2004) in British

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Table 2. Average inbreeding coefficient in investigated populations

Population	Inbreeding coefficient (%)	Standard deviation	Minimum (%)	Maximum (%)
Pedigree file	0.34	1.12	0	38.67
Reference population	0.95	1.71	0	36.25
RP – bulls	1.99	1.65	0	11.91
RP – cows	0.95	1.71	0	36.25
RP – H bulls	2.23	1.64	0	11.91
RP – R bulls	1.25	1.49	0	8.08
RP – H cows	1.13	1.80	0	36.25
RP – R cows	0.54	1.40	0	28.32

Holstein (F = 3.06 in bulls, F = 2.64 % in cows) and McParland *et al.* (2007) in Irish Holstein (F = 1.49 %). Maiwashe *et al.* (2006) presented relatively higher inbreeding intensity in Holstein population of South Africa (F = 2.30 %). Very similar inbreeding values as in our study were published by Bouquet *et al.*, (2011) in Charolais populations of Denmark (F = 1.04 %), Ireland (F = 0.99 %) and Sweden (F = 0.92 %). On the other hand, very low inbreeding intensity was found in Brazilian Nelore cattle (F = 0.20 %) presented by Malhado *et al.* (2010), but the authors noted that low inbreeding was a result of lower pedigree completeness in the Nelore population. In Slovakia, lower inbreeding intensity was observed by

Kadlečík *et al.* (2011) in Pinzgau cattle population (F = 0.57 %) and Hazuchová *et al.* (2013) in Simmental cattle (F = 0.36 %).

The evolution of inbreeding coefficient through the years showed that in the recent ten years, there was an increase in the mean F value of 0.5 % during this period in RP. While animals born in 2002 had average F less than 0.6 %, the individuals born ten years later had average F = 1.10 %. The tendency of increase of the inbreeding coefficient was significant (R^2 = 0.963). This fact is related to increasing proportion of inbred animals and global increase of co-ancestry between animals. Stachowicz *et al.* (2011) monitored the evolution

$$y = 0.0473x + 0.338$$
$$R^2 = 0.963$$
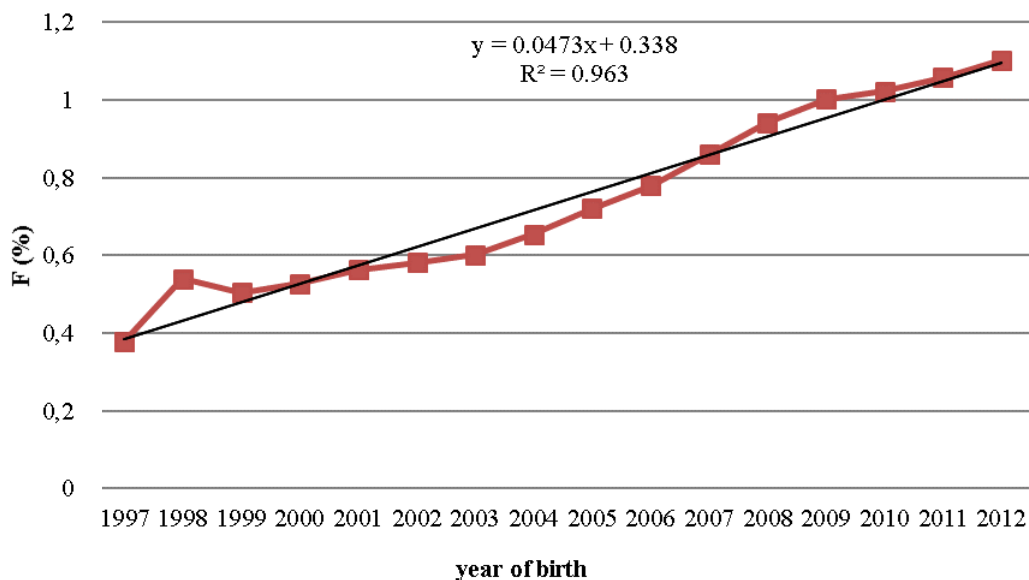
Figure 2. Trend of inbreeding in the reference population

of inbreeding in Holstein population of Canada. They found that animals born in 1968 exceeded the value of 1 % for the very first time. Animals born in 2008 had average *F* over 5 %, which is incomparably higher value than in our population. De Ponte Bouwer *et al*. (2013) observed the highest increase of inbreeding coefficient in the last decade in South African Brown Swiss population. Very similar tendency of *F* increase was presented by Hammami *et al.* (2007) in Holstein populations of Tunisia and Luxembourg. Hazuchová *et al*. (2013) presented significant increase in inbreeding coefficients of Simmental bulls used in the Slovak population born in the recent decade. Similar inbreeding trends were observed by Kadlečík *et al.* (2016) in Slovak populations of beef cattle (Charolais, Blonde d'Aquitaine, Simmental and Limousine).

Probabilities of gene origin

In contrast to the measures based on identity-by-descent (IBD), the characteristics based on gene origin are less susceptible on pedigree quality. Therefore, they represent very useful tool for diversity evaluation. In our case, we focused on number of founders (f), effective number of founders (f_e), effective number of ancestors (f_a) and effective number of founder genomes (N_g). In order to assess the influence of bottleneck effect and genetic drift, the f_e/f_a and f_e/N_g ratios were taken into account. The overview of parameters based on probability of gene origin is presented in Table 3.

In our investigation, there was a significant difference between the total number of founders and their effective number in all analysed populations. Presented difference is caused by unequal use of founder gene pool throughout

the generations. One of the reasons is the using of limited number of superior sires (placed high in rankings) through artificial insemination. The preference of such mating system is responsible for relatively large amount of offspring per sire in comparison with the other sires and dams. The effective number of founders ranged from 47 in H bulls to 182 in the whole pedigree file. The f_e was 132 in RP, 58 in bulls and 132 in cows. The effective number of ancestors was 133 in the pedigree file, 93 in reference population, 38 in bulls and 93 in cows. In case of R animals, there were higher values of such parameters in comparison with H colour variety. The difference between f_e and f_a values is related to unequal contribution of individual animals into reference population caused by bottleneck effect. The effective number of founder genomes points out the maintenance of founder's gene pool in actual population. The highest N_g value was observed in RP and cows (53 in both cases), while the lowest maintenance of founder gene pool was found in H bulls (N_g = 15). For explaining half of diversity, 105 ancestors sufficed in pedigree file, even 52 ancestors in RP. Only 15 ancestors explained half of diversity in bulls, this number was greater in cows (53). Presented results point out that the loss of founders' variability plays an important role in the overall genetic diversity loss. Danchin-Burge *et al*. (2012) found lower f_e and f_a in French Holstein (f_e = 82; f_a = 21). They presented that the comparison between female and male populations strongly suggests that the impact of AI on the breed is so high that in the long run, the genetic variability of the female population is almost a reflection of the genetic variability of a much smaller population, which is

Table 3. Measures based on probability of gene origin

Population	f	f_e	f_a	N_g	f_e/f_a	f_e/N_g	Ancestors explaining 50 % of diversity
Pedigree file	106 953	182	133	-	1.37	-	105
Reference population	106 494	132	93	53	1.42	2.49	52
RP – bulls	664	58	38	19	1.53	3.05	15
RP – cows	106 388	132	93	53	1.42	2.49	53
RP – H bulls	476	47	31	15	1.52	3.13	11
RP – R bulls	304	86	46	21	1.87	4.10	17
RP – H cows	75 932	96	69	37	1.39	2.59	34
RP – R cows	36 490	149	90	49	1.66	3.04	35

considered by the AI bulls. Stachowicz *et al.* (2011) presented higher values of measures based on probability of gene origin in Canadian Holstein females than in males. The same situation was observed in our study. In Canadian Holstein, the effective number of founder genomes was 5.9 in bulls and 7.7 in cows, what indicated massive loss of founders' gene pool in the reference population. The f_e and f_a values of beef cattle breeds were higher than in dairy breeds as presented by Bouquet *et al*. (2011). Similar values of measures based on probability of gene origin were found by Kadlečík *et al*. (2011) in Slovak Pinzgau cattle population (f_e = 141; f_a = 51). Lower values were presented by Hazuchová *et al.* (2013) in the Slovak Simmental cattle.

The ratio of effective number of founders and effective number of ancestors points to the impact of bottleneck effect which reduces the diversity. Greater value of this ratio reflects more significant influence of bottleneck. Presented results showed that the bottleneck reduces the most the diversity in bulls (f_e /f_a = 1.52). Higher impact of bottleneck can be seen in Red-Holsteins (bulls and cows) than in the Black&White variety. The population of bulls was slightly more influenced by the bottleneck than in cows. Differences between the populations were minimal, therefore, it can be concluded that the bottleneck effect has almost the same impact on each population. Bottleneck occurrence in given populations reflects the pedigree construction caused by using small number of superior animals in breeding program. Melka *et al.* (2013) presented that the bottleneck effect reduced the most of the diversity in Canadian Dairy Shorthorn cattle, while the least impact of the bottleneck was observed in Ayrshire cattle. Danchin-Burge *et al.* (2012) found f_e /f_a = 3.90 in French Holstein, what is significantly higher value than in the Slovak Holstein. Moreover, higher impact of the bottleneck effect was found in bulls (f_e /f_a = 4.79). According to the paper of Hazuchová *et al.* (2013), the f_e /N_g ratio in Slovak Simmental cattle was 2.5 times higher than in our study. Therefore, the genetic drift plays more important role in the diversity loss of the Slovak Simmental cattle than in the Slovak Holstein population.

The ratio of effective number of founders and effective number of founder genomes points to the influence of genetic drift on given populations. The highest value was observed in H bulls (f_e /N_g = 3.13),

while the lowest one in RP and cows (f_e /N_g = 2.49). Differences between investigated populations were more significant, therefore the impact of genetic drift, defined as a random change in allelic frequencies throughout the generations, differs within the populations. The results obtained from our analysis showed that the bottleneck effect and genetic drift are important factors reducing genetic variability within Holstein cattle population in Slovakia. Significant decline of Holstein cow's number in Slovakia in recent years has led to a significant bottleneck effect occurrence.

CONCLUSION

Despite the fact that the Holstein represents the largest dairy cattle population in Slovakia, it can be considered as strongly influenced by the diversity loss. The limited number of superior sires used in AI led to increase of co-ancestry and inbreeding level, as well as unequal using of the founder gene pool. The disequilibrium between effective number of founders and ancestors and effective number of founder genomes confirmed important impact of the bottleneck effect and genetic drift. Presented results point out the need to include regular diversity monitoring into the breeding program of Holstein cattle in Slovakia. Genetic diversity within the population is necessary to ensure further production use and fitness of the population. Therefore, optimal mating strategy should be found and used to maintain economical sustainability of the Holstein cattle in Slovakia. Using genomic sires is an option how to reduce inbreeding within the population (knowing "real" genomic inbreeding coefficients and "real" genomic relatedness). Therefore, combination of pedigree data and genomic information (including female population) is the optimal strategy for diversity management in the Holstein population of Slovakia.

REFERENCES

Baumung, R. & Sölkner, J. 2002. Analysis of pedigree of Tux-Zillertal, Carinthian Blond and Original Pinzgau cattle population in Austria. *Journal of Animal Breeding and Genetics*, 119, 175–181.

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(1), 5–23.

Bouquet, A., Venot, E., Laloë, D., Forabosco, F., Fogh, A., Pabiou, T., Morre, K., Eriksson, J. A., Renand, G. & Phocas, F. 2011. Genetic structure of the European Charolais and Limousin cattle metapopulations using pedigree analyses. *Journal of Animal Science*, 89, 1719–1730.

Danchin-Burge, C., Leroy, G., Brochard, M., Moreaux, S. & Verrier, E. 2012. Evolution of the genetic variability of eight French dairy cattle breeds assessed by pedigree analysis. *Journal of Animal Breeding and Genetics*, 129, 206–217.

De Ponte Bouwer, P., Visser, C. & Mostert, B. E. 2013. Analysis of inbreeding of the South African Dairy Swiss Breed. *South African Journal of Animal Science*, 43(1), 1–6.

Fuerst-Waltl, B. & Fuerst, C. 2012. Effect of inbreeding depression on survival of Austrian Brown Swiss calves and heifers. *Journal of Dairy Science*, 95(10), 6086–6092.

Gutiérrez, J. P., Altarriba, J., Díaz, C., Quintanilla, R., Cañon, J. & Piedrafita, J. 2003. Pedigree analysis of eight Spanish beef cattle breeds. *Genetics Selection Evolution*, 35, 43–63.

Gutiérrez, 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.

Hagger, C. 2005. Estimates of genetic diversity in the brown cattle population of Switzerland obtained from pedigree information. *Journal of Animal Breeding and Genetics*, 122, 405–413.

Hammami, H., Croquet, C., Stoll, J., Rekik, B. & Gengler, N. 2007. Genetic diversity and joint-pedigree analysis of two importing Holstein populations. *Journal of Dairy Science*, 90(7), 3530–3541.

Hazuchová, E., Kadlečík, O., Pavlík, I., Kasarda, R. & Žitný, J. 2012. The assessment of genetic diversity and analysis of pedigree completeness in purebred Slovak Spotted cattle. *Acta agriculturae Slovenica*, 97(3), 131–135.

Hazuchová, E., Kadlečík, O., Pavlík, I. & Kasarda, R. 2013. Assessment of genetic diversity using characteristics based on the probability of gene origin in the Slovak Spotted breed. *Acta fytotechnica et zootechnica*, 16(2), 31–37.

Kadlečík, O., Hazuchová, E., Pavlík, I. & Kasarda, R. 2013. Diversity of cattle breeds in Slovakia. *Slovak Journal of Animal Science*, 46(4), 145–150.

Kadlečík, O., Kasarda, R., Pavlík, I. & Hazuchová, E. 2011. Pedigree Analysis of Slovak Pinzgau Breed. *Agriculturae Conspectus Scientificus*, 76(3), 165–168.

Kadlečík, O. & Pavlík, I. 2012. Genealogical analysis in small populations: The case of four Slovak beef cattle breeds. *Slovak Journal of Animal Science*, 45(4), 111–117.

Kadlečík, O., Pavlík, I., Moravčíková, N. & Kasarda, R. 2016. Inbreeding and genetic diversity loss of four cattle beef breeds in Slovakia. *Acta fytotechnica et zootechnica*, 19(2), 59–63.

Kadlečík, O., Hazuchová, E., Moravčíková, N., Kukučková, V. & Kasarda. R. 2017. Genetic diversity in Slovak Spotted breed. *AGROFOR International Journal*, 2(3), 124–130.

Kasarda, R., Trakovická, A., Moravčíková, N., Šidlová, V. & Kadlečík, O. 2015. Research on diversity, utilization and production quality of local breeds in Slovakia. *Poljoprivreda*, 21(1), 11–15.

Kaerney, J. F., Wall, E., Villanueva, B. & Coffey, M. P. 2004. Inbreeding trends and aplication of optimized selection in the UK Holstein population. *Journal of Dairy Science*, 87(10), 3503–3509.

Kania-Gierdziewicz, J. 2005. Inbreeding and relationship in Polish Black-and-White sires. *Journal of Applied Genetics*, 46(2), 187–193.

Kasarda, R. & Kadlečík, O. 2007. An economic impact of inbreeding in the purebred population of Pinzgau cattle in Slovakia on milk production traits. *Czech Journal of Animal Science*, 52(1), 7–11.

Lacy, R. C. 1989. Analysis of founder representation in pedigrees: founder equivalents and founder genome equivalents. *Zoo Biology*, 111–123.

Maignel, L., Boichard, D. & Verrier, E. 1996. Genetic variability of French dairy breeds estimated from pedigree information. *Interbull Bulltein*, 14, 49–54.

Maiwashe, A., Nephawe, K. A., Weisthuizen, R. R., Mostert, B. E. & Theron, H. E. 2006. Rate of inbreeding and effective population size in four major South African dairy cattle breeds. *South African Journal of Animal Science*, 36 (1), 50–57.

Malécot, G. 1948. *Les Mathématiques de l´Hérédite*. Masson et Cie, Paris, France (in French).

Malhado, C. H., Carneiro, P. L., Malhado, A. C., Filho, R., Bozzi, R. & Ladle, R. J. 2010. Genetic improvement and population structure of the Nelore breed in Northern Brazil. *Pesquisa Agropecuária Brasileira*, 45(10), 1109–1116.

Maximini, L., Fuerst-Waltl, B., Gredler, B. & Baumung, R. 2011. Inbreeding depression on semen quality in Austrian dual-purpose simmental bulls. *Reproduction in Domestic Animals*, 46(1), 102–104.

MacCluer, J. W., Boyce, B., Dyke, L., Weitzkamp, D., Pfenning, A. & Parsons, C. 1983. Inbreeding and pedigree structure in Standardbred horses. *Journal of Heredity*, 74, 394–399.

Mc Parland, S., Kaerney, J. F., Rath, M. & Berry, D. P. 2007. Inbreeding trends and pedigree analysis of Irish dairy and beef cattle populations. *Journal of Animal Science*, 85, 322–331.

Melka, M. G., Stachowicz, K., Miglior, F. & Schenkel, F. S. 2013. Analyses of genetic diversity in five Canadian dairy breeds using pedigree data. *Journal of Animal Breeding and Genetics*, 130, 476–486.

Meuwissen, T. H. E. & Luo Z. 1992. Computing inbreeding coefficients in large populations. *Genetics Selection Evolution*, 24, 305–313.

Panetto, J. C. C., Gutiérrez, J. P., Ferraz, J. B. S. , Cunha, D. G. & Golden B. L. 2010. Assessment of inbreeding depression in Guzerat dairy herds: Effects of individual increase in inbreeding coefficients on production and reproduction. *Journal of Dairy Science*, 93(10), 4902–4912.

Pavlík, I., Hazuchová, E., Kadlečík, O. & Kasarda, R. 2012. *Pedigree analysis of Slovak Holstein cattle*. Book of Abstracts of the 63rd Annual Meeting of the European Federation of Animal Science, Bratislava: Slovakia 27 – 31 August 2012, No. 18, p. 246.

Pavlík, I., Sölkner, J., Kadlečík, O., Kasarda, R., Mészáros, G., Fuerst, Ch. & Fuerst-Waltl, B. 2014. Joint genealogical analysis as a tool for diversity evaluation in Pinzgau cattle populations. *Archiv Tierzucht*, 57(14), 1–12.

Siderits, M., Baumung, R. & Fuerst-Waltl, B. 2013. Pedigree analysis in the German Paint Horse: Genetic variability and the influence of pedigree quality. *Livestock Science*, 151, 152-157.

Sørensen, A. C., Sørensen, M. K. & Berg, P. 2005. Inbreeding in Danish dairy cattle breeds. *Journal of Dairy Science*, 88(5), 1865–1872.

Stachowicz, K., Sargolzaei, M., Miglior, F. & Schenkel, F. S. 2011 – Rates of inbreeding and genetic diversity in Canadian Holstein and Jersey cattle. *Journal of Dairy Science*, 94(10), 5160–5175.

Toro, M. A., Meuwissen, T. H. E., Fernández, J., Shaat, I. & Mäki-Tanila A. 2011. Assessing the genetic diversity in small farm animal populations. *Animal*, 5 (11), 1669–1683.