



GENETIC STRUCTURE ANALYSIS OF TATRA SHEPHERD DOG POPULATION FROM TATRA MOUNTAIN REGION*

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Abstract

The aim of the work was to analyze the genetic structure of the population of Tatra Shepherd dogs, registered in branches of Polish Kennel Club from Tatra Mountain Region. Data were pedigrees of 102 Tatra Shepherd dogs (33 males and 69 females) born between 1994 and 2011. Inbreeding and relationship coefficients, as well as effective number of founders and ancestors, were calculated. These statistics give the picture of genetic diversity of the population. Average inbreeding coefficient was 7.17%, whereas average relationship coefficient was 18.20%. The number of inbred animals and the mean F_x values steadily increased over time. Twenty-six of 80 inbred animals had inbreeding coefficients higher than 10%. The effective number of founders was relatively high in relation to the population size (the effective number of ancestors was four times lower) and both were similar to the results of studies of other authors on different dog breeds. The total contribution of only 4 ancestors was enough to explain 50% of the gene pool of the population. Therefore, mating of related animals should be avoided in order to prevent the further increase of inbreeding level, because almost all Polish and foreign Tatra Shepherd dogs living now originate from the population under study.

Key words: founders, ancestors, inbreeding, relationship, Tatra Shepherd dog

The Tatra Shepherd is a Polish native dog breed that has been bred in the mountain region of Zakopane, which is called Podhale in Polish. The Tatra Mountains form a state border and these dogs have lived in isolation from those in Slovakia. The first dog show for Tatra Shepherds was organized in 1937 by the Polish Association of Pedigree Dog Breeders and the Society of Working Dog Breeders. This event became a starting point for breeding the Tatra Shepherd dog in Zakopane. Since many of those dogs were kept in Zakopane during World War II, the breed managed to survive in its native areas. After the war, when the Polish Kennel Club (PKC) was

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reestablished, shows for Tatra Shepherd dogs were organized in Kraków by Prof. T. Marchlewski (Redlicka and Redlicki, 2003; Ściesiński, 2002 a).

In the Zakopane Branch of PKC, Dr H. Dereziński had been searching for typical dogs to be bred in the mountains and, as a result of his efforts, 120 dogs were found for the first post-war show held in 1954. The fact that Tatra Shepherds still appear at dog shows is due to Dereziński's hard work for many years. The breed is now recorded also in other branches of PKC. Since 1967, the Tatra Shepherd dog has been recognized as a breed (FCI Standard No 252a); Prof. M. Trybalski was the first to establish the breed standard. According to the current standard, the Tatra Shepherd is traditionally used as a flock guard dog. It is strong and determined, with good working ability. It is also extremely intelligent and alert, which makes it useful as a guard dog but can also be a companion dog or a therapy dog. It is an excellent partner – friendly towards children and domestic animals. However, the breed representatives are now very limited in number, and breeding problems like hip dysplasia connected with the small size of population arise (Ściesiński, 2002 b). For that reason, the genetic structure of the population requires constant monitoring, especially in the part of the Tatra Shepherd dog population living in Tatra Mountains, where the breed originated.

Recently much more has been published about genetic diversity and its maintenance in farm animals as genetic resources (Kania-Gierdziewicz, 2013) and especially in different dog breeds in the world (Cole et al., 2004; Leroy et al., 2006, 2009; Ólafsdóttir and Kristjánsson, 2008; Coutts and Harley, 2009; Oliehoek et al., 2009; Příbáňová et al., 2009; Voges and Distl, 2009; Mäki, 2010; Martinez et al., 2011). Some papers concerned also Polish dog breeds and their genetic diversity (Drozd and Karpiński, 1997; Głazewska, 2008; Kalinowska et al., 2010; Gierdziewicz et al., 2010, 2011; Kania-Gierdziewicz et al., 2011 a, b; Kania-Gierdziewicz and Gierdziewicz, 2013; Kania-Gierdziewicz et al., 2013; Róžańska-Zawieja et al., 2013). Some authors used molecular or pedigree analysis, or both, to obtain inbreeding and relationship estimates or effective number of founders and ancestors. Some gave advice how to maintain genetic diversity in populations with small number of animals, such as dog populations, and how to minimize the problem of genetic diseases closely related to gradually increasing value of inbreeding.

The aim of this work was to examine the genetic condition of the population of Tatra Shepherd dogs from Tatras, where the breed originated, using estimates of inbreeding and relationship coefficients and also the effective number of founders and ancestors; to find the main founders and ancestors in the active population recorded in the pedigree registry of the Polish Kennel Club branches from Zakopane and Nowy Targ; and to determine the genetic contribution of founders and ancestors to this population.

Material and methods

Pedigrees of 102 Tatra Shepherds: 33 males and 69 females born from 1994 to 2011 were used in this analysis. The pedigrees were obtained from two branches of

Polish Kennel Club in the Tatra Mountains region (Podhale region), namely, from Zakopane (89 pedigrees) and Nowy Targ (13 pedigrees). In total, there were also 250 older animals (98 males and 162 females) in the database. The examined 102 animals were descended from 15 sires and 30 dams. The mean generation interval in this population was 4.94 years (sd=2.15). It was possible to extend the initial four-generation pedigrees of Tatra Shepherd dogs up to 14 generations. The coefficients of inbreeding (F_X) and relationship (R_{XY}) among all animals, for each sex separately, and between males and females were calculated according to the algorithm of Tier (1990). Recursive modification has been applied to this algorithm (Gierdziewicz and Kania-Gierdziewicz, 2007): to save computing time, the values of coefficients F_X and R_{XY} were calculated directly from classic Wright's formulae (Wright 1921, 1922).

The active population of 102 animals was treated as the reference population in founder and ancestor analysis. The total and effective numbers of founders and ancestors were estimated, and the founders and ancestors with the highest gene contribution to the reference population were identified. The effective number of founders (f_e) and the effective number of ancestors (f_a) were calculated according to the method proposed by Lacy (1989, 1995) and modified by Boichard et al. (1996, 1997).

An animal without pedigree is treated as a founder of the reference population. The contribution of a particular founder to the reference population gene pool is defined as the probability that the genes of an animal randomly selected from this population originate from this founder. The contributions of all founders have to sum up to 1. The effective number of founders (f_e) is defined as the number of founders which would equally contribute to the reference population gene pool. The effective number of founders achieves its maximum if the probability of gene origin from each founder is the same, and then f_e is equal to the actual number of founder animals. Otherwise the f_e value is lower. Thus, the effective number of founders defined in such a way estimates the maximum number of founder genotypes, even if some of them have no descendants in the reference population (Lacy, 1989, 1995). The effective number of founders was estimated according to Lacy's formula (Lacy, 1989):

$$f_e = \frac{1}{\sum_{k=1}^f p_k^2}$$

where:

f_e – effective number of founders,

f – number of founders,

k – probability of gene origin from k^{th} founder.

The effective number of ancestors (f_a) takes into account the bottleneck effect, which leads to loss of some part of genes from the population and is the cause of increasing relationship and inbreeding. The effective number of ancestors (f_a) is defined as the number of ancestors with known pedigrees or without them (founders), which would equally contribute genes to the reference population gene pool. Therefore, f_a determines the minimum number of ancestors (founders or not), which is

necessary to explain the whole genetic variability in the reference population. The effective number of ancestors was estimated according to the formula attached below (Boichard et al., 1996, 1997):

$$f_a = \frac{1}{\sum_{k=1}^f p_k^2}$$

where:

- f_a – effective number of ancestors,
- f – number of ancestors,
- p_k – marginal contribution of k^{th} ancestor.

Defined in such a manner, an ancestor would be an animal or, in most cases, one of a few animals responsible for bottleneck effect, for example a famous sire with a lot of progeny. Thus, from the logical and mathematical point of view, the value of the effective number of ancestors will always be lower than the value of f , but if the population gene pool is very limited, even if the number of individuals in a population is large, the effective number of ancestors will decrease significantly faster than the effective number of founders.

Results

Inbreeding and relationship coefficients

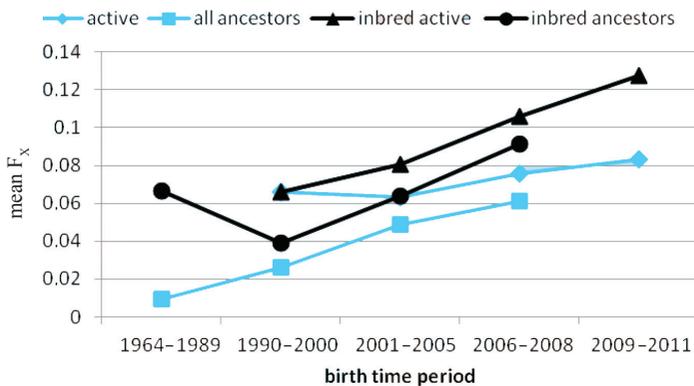
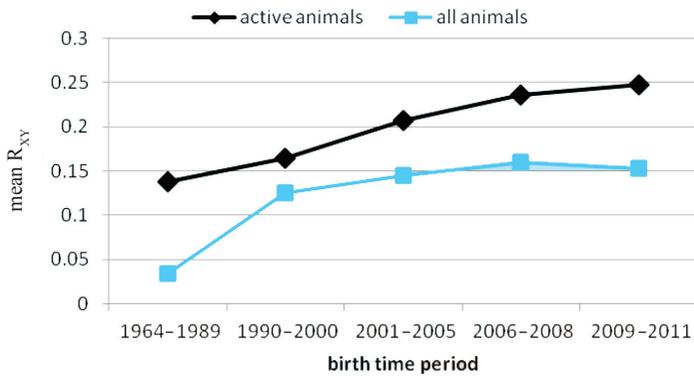
Among the 102 Tatra Shepherds considered in this study, 80 individuals (78.43%) were inbred (i.e. with parents having at least one common ancestor). The group of 33 males comprised 84.85% inbred individuals, and the group of 69 females had 75.36% inbred ones. The mean inbreeding coefficients (F_x) were 0.0717 and 0.0915 for all animals and for inbred individuals, respectively. The Tatra Shepherd males were more inbred than the Tatra Shepherd females (Table 1). Average inbreeding coefficients for inbred Tatra Shepherd animals ranged from 8.71% to 9.95%, depending on sex, and except 14 animals individual F_x values did not exceed the critical value of 12.5% (Falconer, 1996). The inbreeding values increased in time for active animals and for their ancestors but much more for the former (Figure 1).

The active Tatra Shepherd dog population included $[102 \times 101] / 2 = 5151$ pairs of animals, i.e. all pairs which could be made from 102 active animals (male-male, female-female and male-female), 76.26% of which were related. Among the pairs of males, there were 71.97% related pairs. Among the pairs of females, 78.13% related pairs were identified. For the mixed male-female pairs, 75.32% were related. The average relationship coefficients (R_{xy}) for all pairs and for related pairs were 0.1820 and 0.2387, respectively. Among related pairs, mixed pairs had the highest value of mean R_{xy} (Table 1). The relationship values increased in time both for all and for active animals in the population examined (Figure 1).

Table 1. Average inbreeding (F_x) and relationship (R_{xy}) coefficients for Tatra Shepherd dogs from branches of PKC in Zakopane and Nowy Targ

Item	Sex		
	male	female	
Number of animals in active population	33	69	
Number of animals in pedigrees	98	162	
Number of inbred animals	28	52	
Mean F_x – all animals	0.0826	0.0666	
Mean F_x – inbred animals	0.0995	0.0871	
Maximum F_x value	0.2312	0.1941	
	Pairs		
	male	female	mixed*
Number of pairs	528	2346	2277
Number of related pairs	380	1183	1715
Mean R_{xy} – all pairs	0.1777	0.1846	0.1803
Mean R_{xy} – related pairs	0.2469	0.2363	0.2394
Maximum R_{xy} value	0.6697	0.6489	0.6729

*Mixed = male × female pairs.

Figure 1. Trends in average relationship (R_{xy}) coefficients for all and active animals (above) and trends in mean inbreeding (F_x) coefficients for active animals and their ancestors (below) from examined Tatra Shepherd dog population

The group of 26 inbred Tatra Shepherd dogs from the active population had F_x value above 10%. The highest F_x value, reaching almost 24%, was found in one male. The next five animals had almost the same values of inbreeding coefficients, i.e. about 19%. There were four females and one male in this group, all from the same kennel. The F_x values for the remaining inbred Tatra Shepherd dogs from this group (in most cases young and very young animals) did not exceed 18%. In the whole group of inbred Tatra Shepherd dogs there were 26 animals from the aforementioned kennel: 19 females and 7 males. The next kennel had seven inbred animals (four males and three females); the most inbred dog in the examined population also originated from that kennel. The next four kennels had five inbred animals each. Thus, these six kennels produced the overwhelming majority of the inbred animals in the Tatra Shepherd dog population from Podhale region.

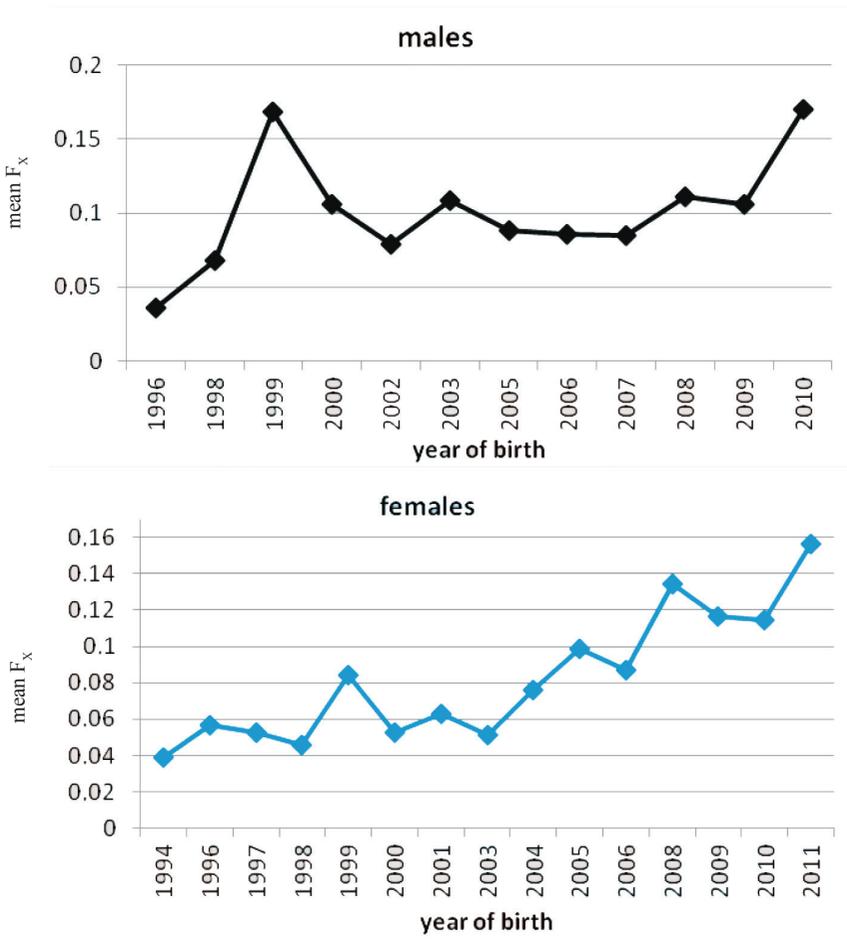


Figure 2. Trends in mean inbreeding (F_x) coefficients for inbred active males (top) and females (bottom) of Tatra Shepherds

Figure 2 shows the average inbreeding coefficients of inbred males and females born in different years. The percent of inbred Tatra Shepherd dogs increased from 29% of animals born before the year 2000 to 44% of young individuals born in the last 6 years (2006–2011) and the average inbreeding coefficient went up almost two times between those two periods. The number of inbred males between those two time intervals doubled, with the mean F_x increase from about 8% to more than 11%. The increase in the number of inbred females was not so intense as in the male group, but the value of inbreeding coefficient for the youngest female group was twice as big as for the oldest one. The inbreeding coefficient rose steadily in time for both male and female Tatra Shepherd dogs, but for the latter the trend was more significant (Figure 2).

Founder and ancestor contribution analysis

The total number of founders was almost twice as high as the total number of ancestors. The effective number of founders was exactly four times higher than the effective number of ancestors. The joint contribution of only four ancestors explained 50% of the gene pool of the reference population; however, the collective contribution of as many as 25 ancestors was necessary to explain 90% of the gene pool of the population (Table 2), because of intensive use of only a few sires. The equivalent number of complete generations known per animal in our study was low (Table 2), because in recent years some animals without pedigrees continue to be registered.

Table 2. Parameters of gene origin in the Tatra Shepherd dog population from Podhale region

Parameter	Value
Number of animals in reference population	102
Maximum number of generations traced	14
Equivalent number of complete generations known per animal	3.44
Total number of	
founders	88
ancestors	46
Effective number of	
founders (f_e)	44
ancestors (f_a)	11
Explaining 50% of the genetic pool:	
founders	16
ancestors	4
Explaining 90% of the genetic pool:	
founders	45
ancestors	25

Figure 3 shows the main founders, and Figure 4 the main ancestors, with more than 2% of gene contribution to the Tatra Shepherd dog population from Podhale region. There were 18 main founders and they contributed almost 55% to the gene pool (Figure 3). The contributions of 9 main ancestors explained about 69% of the genetic variability in the population (Figure 4).

Eleven animals were both main founders and main ancestors of the population. The remaining 10 animals (3 males and 7 females) from this group are not shown because of their low individual contributions both as founders and as ancestors.

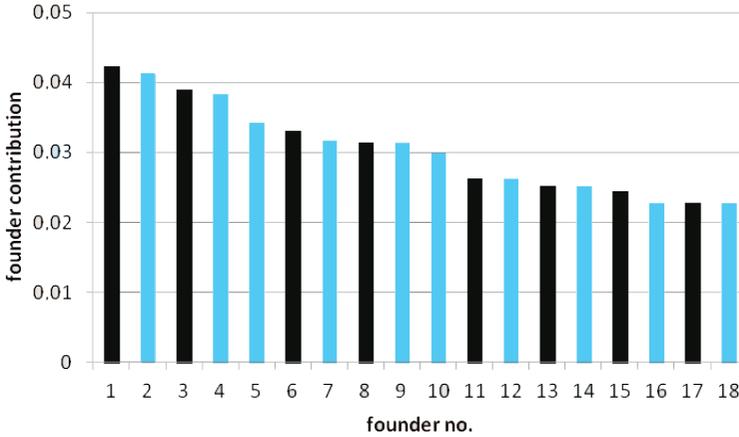


Figure 3. The 18 main founders with individual contribution of genes over 0.02 to the reference population of Tatra Shepherd dogs (black – male, grey – female)

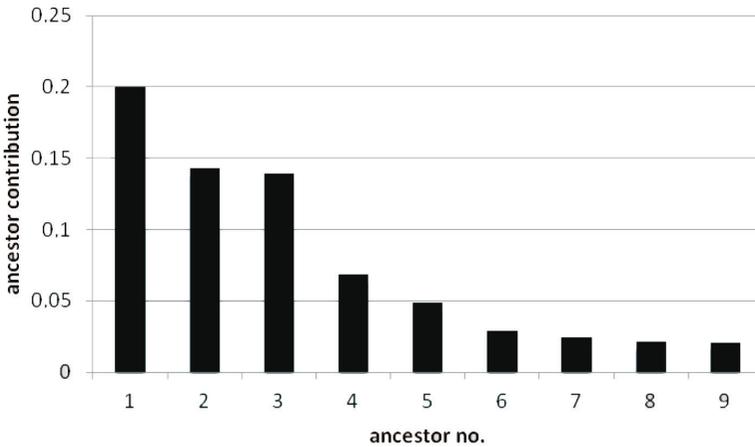


Figure 4. The 9 main ancestors with individual marginal contribution of genes more than 0.02 to the reference population of Tatra Shepherd dogs (black – male)

Discussion

Inbreeding and relationship coefficients

Table 3 shows inbreeding and relationship coefficients obtained for various dog breeds by other authors.

Table 3. Inbreeding (F_x) and relationship (R_{xy}) coefficients in different dog breeds obtained by other authors

Breed	F_x	R_{xy}	Source
German Shepherd dog	0–0.262	0.0016–0.253	(Cole et al., 2004)
Labrador Retriever	0–0.220	0.0015–0.155	(Cole et al., 2004)
German Shepherd dog	0.051–0.104	–	(Coutts and Harley, 2009)
German Shepherd dog	0.0023–0.0311	0.0034–0.0039	(Drozd and Karpiński, 1997)
Rottweiler	0.0112–0.0585	0.0072–0.0101	(Drozd and Karpiński, 1997)
German Boxer	0.0068–0.0426	0.0052–0.0268	(Drozd and Karpiński, 1997)
Great Dane	0.0061–0.0879	0.0056–0.0070	(Drozd and Karpiński, 1997)
Beagle	0.0068–0.0565	0.0095–0.0926	(Gierdziewicz et al., 2011)
Polish Hound	0.0710–0.3700	–	(Głazewska, 2008)
Tatra Shepherd dog	0.0106–0.0644	0.0453–0.1492	(Kalinowska et al., 2010)
German Shepherd dog	0.1178–0.1658	0.0353–0.0436	(Kania-Gierdziewicz et al., 2011 a)
Tatra Shepherd dog	0.042–0.058	0.110–0.154	(Kania-Gierdziewicz and Gierdziewicz, 2013)
French dog breeds	0–0.1600	–	(Leroy et al., 2006)
61 dog breeds in France	0.0020–0.0880	0.0040–0.0880	(Leroy et al., 2009)
Cimarrón Uruguayo dog	0.0300	0.0400	(Martinez et al., 2011)
Nova Scotia Duck Tolling Retriever	0.260	0.260	(Mäki, 2010)
Lancashire Heeler dog	0.100	0.080	(Mäki, 2010)
Icelandic Sheepdog	0.210	–	(Ólafsdóttir and Kristjánsson, 2008)
Icelandic Sheepdog	0–0.270	0–0.550	(Oliehoek et al., 2009)
Czech Dachshund	0.0132–0.0293	–	(Příbaňová et al., 2009)
Bavarian Mountain hound	0.0451	–	(Voges and Distl, 2009)
Hanoverian hound	0.0678	–	(Voges and Distl, 2009)
Tyrolean hound	0.0947	–	(Voges and Distl, 2009)
Hovawart dog	0.0021–0.0320	0.0061–0.0833	(Róžańska-Zawieja et al., 2013)

The F_x values for all and inbred animals in our study were in general similar or higher than those cited in Table 3. However, they were much lower than obtained for Labrador Retrievers (Cole et al., 2004), for German Shepherds (Cole et al., 2004; Kania-Gierdziewicz et al., 2011 a) and for Polish Hounds (Głazewska, 2008). Also Icelandic Sheepdog (Ólafsdóttir and Kristjánsson, 2008; Oliehoek et al., 2009) and Nova Scotia Duck Tolling Retriever (Mäki, 2010) populations were much more inbred than our Tatra Shepherd dogs. The relationship coefficients estimated for Tatra Shepherd dogs in our study were higher than most R_{xy} values cited in Table 3, except those for Icelandic Sheepdogs (Oliehoek et al., 2009), which were higher. Nova

Scotia Duck Tolling Retrievers (Mäki, 2010) and our Tatra Shepherd dog have both similar relationship coefficients (Table 3). The generation interval obtained in our study was in general similar to that estimated by others (Mäki, 2010; Voges and Distl, 2009; Leroy et al., 2009, 2006). The equivalent number of complete generations known per animal estimated in our study was similar or much lower than in other studies (Mäki, 2010; Voges and Distl, 2009; Leroy et al., 2009; 2006).

Founder and ancestor contribution analysis

Table 4 provides the effective number of founders and ancestors and the total number of animals in reference population obtained by other authors for a variety of dog breeds.

Table 4. Effective number of founders (f_e) and ancestors (f_a) and total number of animals in population (N) examined for different dog breeds obtained by other authors

Breed	N	f_e	f_a	Source
German Shepherd dog	4699	24–35	21–24	(Cole et al., 2004)
Labrador Retriever	3573	14–30	12–27	(Cole et al., 2004)
Tatra Shepherd dog	34	28	16	(Gierdziewicz et al., 2010)
Beagle	84	102	26	(Gierdziewicz et al., 2011)
German Shepherd dog	60	66	36	(Kania-Gierdziewicz et al., 2011 b)
Tatra Shepherd dog	31	28	14	(Kania-Gierdziewicz and Gierdziewicz, 2013)
Labrador Retriever	272	96	43	(Kania-Gierdziewicz et al., 2013)
Golden Retriever	192	52	33	(Kania-Gierdziewicz et al., 2013)
French dog breeds	307–10077	6.9–91.3	6.7–40.2	(Leroy et al., 2006)
61 dog breeds in France	112–8808	10–656	9–209	(Leroy et al., 2009)
Cimarrón Uruguayo dog	1455	37	31	(Martinez et al., 2011)
Nova Scotia Duck Tolling Retriever	7707	9.8	5.2	(Mäki, 2010)
Lancashire Heeler dog	1291	15.2	13.6	(Mäki, 2010)
Bavarian Mountain hound	3231	43.7	34.3	(Voges and Distl, 2009)
Hanoverian hound	1371	41.6	20.1	(Voges and Distl, 2009)
Tyrolean hound	1167	18.9	12.2	(Voges and Distl, 2009)
Hovawart dog	845	268	233	(Róžańska-Zawieja et al., 2013)

The estimates of the effective number of founders (f_e) and ancestors (f_a) of the Tatra Shepherd dog population, obtained in our study, were in most cases similar or even lower than those reported by other authors (Table 4). However, the number of animals in the reference population in our study was much smaller or similar (Table 4).

In the study conducted by Voges and Distl (2009), covering much larger reference populations, the number of founders and ancestors explaining 50% of Bavarian

Mountain, Hanoverian and Tyrolean hound population gene pools, were similar or markedly higher than our results. The numbers of founders and ancestors explaining 90% of the above mentioned dog population gene pools were in some cases higher than those obtained in our study.

In summary, the mean values of the inbreeding and relationship coefficients obtained in the Tatra Shepherd dog population from Podhale region were not very high, but these values steadily increased in the years between 2000 and 2011. Also the number of inbred animals in this time period went up. In addition, over 66% of all inbred animals were born in only six kennels and individual inbreeding coefficients for 26 of 80 inbred animals, in almost all cases born after 2000, exceeded 10%. Therefore, taking into account the large proportion of inbred animals (over 78%) and more than 76% related animal pairs in this population, it should be noted that in the investigated population the actual threat of inbreeding depression exists. The values of the effective number of founders and, in particular, the effective number of ancestors, which is reduced to one fourth of the former, indicate that the genetic pool of the examined population is steadily narrowing down. Such situation could cause more health and reproduction problems.

The population under study was a very important part of the Tatra Shepherd dog population, from which all Polish and foreign Tatra Shepherd dogs originate. Therefore, mating of related animals should be particularly avoided in order to prevent further increase of the inbreeding level, which could be difficult because of relatively small number of unrelated animals in this population – however, it is still possible because many relationship coefficients have small values. To maintain the examined population as a genetic reserve of this native breed it will be necessary to design and to introduce a special breeding scheme, which would include not only a replacement of males but also some females. And a mating system would be constructed with special focus on keeping the number of common ancestors in pedigrees of mated animals as low as possible and limiting their occurrence to not closer than 4 or 5 generations back.

Acknowledgements

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