Ann. Anim. Sci., Vol. 12, No. 4 (2012) 501–512, DOI: 10.2478/v10220-012-0042-2

GENETIC VARIABILITY OF FARMED AND FREE-LIVING POPULATIONS OF RED FOXES (*VULPES VULPES*)*

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Abstract

This study was designed to determine the degree of genetic distinctiveness between farmed and wild foxes (*Vulpes vulpes*). Analysis of polymorphism in 16 microsatellite sequences led to the conclusion that red foxes raised on Polish farms and wild foxes living in Poland are two groups of genetically distinct animals. Farmed Polish foxes are genetically more similar to the population of wild animals from North America than they are to the free-living population in Poland, as confirmed by the fact that the farmed animals are descended from animals raised in Canada. The small genetic distance between wild Canadian foxes (indicated as the progenitor of farmed Polish foxes) and farmed Polish foxes possibly suggests that the differences between the farmed and wild Polish populations may result from the fact that Canadian and Polish foxes took separate evolutionary paths.

Key words: *Vulpes vulpes*, wild and farmed animals, microsatellites, domestication

For many years, the domestication process has been the subject of study by researchers in both animal and human sciences. The first scientific definition of domestication was proposed in 1868 by Charles Darwin, who described morphological changes in domesticated animals. Over the years, the definition was repeatedly expanded and modified. It is now believed that domestication occurs after many generations of taming and captive reproduction under human control. These animals will develop new heritable characteristics that will distinguish them from their

* Research work financed from NCBiR funds, development project no. NR 12-0140-10.

wild ancestors. The only way these characteristics develop is through selection (Lasota-Moskalewska, 2005). The domestic dog (*Canis familiaris*) is a first example of a domesticated species. However, it remains unclear when and where the dog became a domesticated species encompassing today a number of phenotypically diverse breeds. Red fox (*Vulpes vulpes*) is one of the best studied wild animals worldwide (Wandeler and Funk, 2006). However, the domestication of the red fox has a short history. This species has been farmed worldwide since the 1890s. In Poland, first farms of silver foxes were established around 1924 in Upper Silesia and around 1927 near Gdańsk (Sławoń and Woliński, 1975). Experimental domestication process gave rise to a population whose behaviour showed the characteristics of the domestic dog, namely devotion, friendliness and a desire to form bonds with humans (Trut, 1999). There are also many morphological and physiological changes associated with domestication (Trut et al., 2004).

Molecular analyses provide insight into organismal variation at the most basic level, that of DNA. They can be used, among others, to examine phylogenetic relationships between different groups of animals. In case of fur-bearing animals this is supported by the results of molecular studies with both silver foxes (Statham et al., 2011) and other farmed species of *Canidae*, such as arctic foxes (Norén et al., 2009) and raccoon dogs (Ślaska et al., 2010).

The aim of the study was, based on microsatellite analysis, to determine genetic distances within and between farmed and wild populations of red foxes in Poland and North America.

Material and methods

A total of 178 red foxes (*Vulpes vulpes*), including 100 unrelated animals from a farm in southern Poland and 78 wild animals (31 from two parts of Poland and 47 from Canada) were used for the present study. Peripheral blood was collected from the saphenous vein of farmed animals into vacuum tubes containing EDTA. Soft tissues and pieces of skin served as a source of DNA for wild foxes from Poland and Canada, respectively. DNA from blood was isolated with a QIAamp DNA Blood Mini Kit, and from tissues with a QIAamp DNA Mini Kit (QIAGEN).

Based on the literature, 17 microsatellite markers from the domestic dog genome were chosen for the analysis: Ren01E05, Ren02K21, Ren06C11, Ren13J22, Ren37H09, Ren39L15, Ren41D20, Ren44K10, Ren67C18, Ren02C20, Ren02P03, Ren04M22 (Jouquand et al., 2000); INU005, INU013, INU014, INU019, and INU020 (Ichikawa et al., 2002).

PCR was performed using AmpliTaq Gold 360 DNA Polymerase in an MJ Research PTC 225 Tetrad thermal cycler. Optimization of the physical and chemical parameters of PCR made it possible to group the 15 microsatellites into 4 multiplexes. An individual PCR was performed for two markers. Composition of the reaction mixture, primer characteristics and the PCR temperature/time profiles are given in Tables 1 and 2. Each reaction consisted of 10 µl: 9 µl reaction mixture and 1 µl

DNA template. PCR product was determined by spectrophotometry and in agarose gel. PCR was followed by electrophoresis of DNA fragments using the capillary sequencer 3100 Avant Genetic Analyser (Applied Biosystems). The results were analysed by Gene Mapper Software v 3.5. Allele lengths were determined by comparison with GeneScan 500 Rox Size Standard markers.

Table 1. Composition of PCR reaction mixture for individual microsatellite sequences in 32 samples

Multiplex	Locus	AmpliTaq Gold 360 Buffer (µl)	$MgCl_2$ (µl)	360 G/C Enhancer (µl)	dNTP mix (µl)	Primer (µl for each)	AmpliTaq 360 DNA Polymerase (µl)
		Initial concentration					
		10x	25mM	-	10mM (2.5mM each)	100pM each	5U
M1	INU005	36	36	10	30	1.2	9
	INU013					2.2	
	INU014					2.2	
	INU19					3.0	
	INU20					3.0	
M2	Ren01E05	36	36	10	30	2.8	8
	Ren67C18					3.0	
	Ren02C20					1.2	
	Ren02P03					1.2	
	Ren04M22					1.2	
M3	Ren02K21	36	27	8	24	2.0	5
	Ren37H09					3.0	
	Ren39L15					1.6	
M4	Ren13J22	36	28	6	20	2.0	4
	Ren44K10					1.0	
Single amplification	Ren06C11	36	12	2	4	2.0	2
Single amplification	Ren41D20	36	12	2	6	2.5	2.5

Statistical analysis

For 16 microsatellite loci alleles specific for the farm-bred population and for the two wild populations were recorded. The results were analysed using the statistical software POPGENE v. 1.31, Cervus v. 3.0.3. and MEGA4 (Tamura et al., 2007). Within- and between-population variation was estimated based on polymorphic information content (PIC) (Botstein et al., 1980; Hearne et al. 1992), observed (Ho) and expected heterozygosity (He) (Nei, 1987), and Nei's (1978) genetic similarity and distance. A dendrogram was constructed by the neighbour-joining method (Saitou and Nei, 1987).

Table 2. Primer characteristics for canine microsatellite sequences and the PCR temperature profile optimized for *Vulpes vulpes*

Multi-plex	Locus	Chro-mo-some	Primer sequence F – Forward, R – Reverse	Primer annealing tempe-rature (°C)	Dye	Access number
M1	INU005	33	F:5'CTTTCTACCAGCAAGGTTAC3' R:5'TTCCCATTTAATTGCCTCT3'	60	VIC	AF421441.1*
	INU013	3	F:5'AGAGAAAAGCATCCAGTAAG3' R:5'AAATGGTCTTCCTGTATCCT3'		6-FAM	AF421449*
	INU014	3	F:5'ACATTTATCATAGTAAGTACCG AG3' R:5'AAAACCACAAAACCTAACCT3'		NED	AF421450*
	INU19	10	F:5'TGACAAATAGGGTGGATGAT3' R:5'GGTCTTTAGCAGGGACGAAT33		6-FAM	AF421455*
	INU20	21	F:5'TGAGTATGTTGATGGCTGTG3' R:5'TGAAAGGTATGCCAAGTC3'		NED	AF421456*
M2	Ren01E05	-	F:5'TCATCACTTCCTGCTCCATT3' R:5'TCTCATGCCACACGGAACCT3'	52	6-FAM	AJ391553#/ AJ391554#
	Ren67C18	37	F:5'TCTGTGCGTTTCCGTTTATG3' R:5'TTAGTACCTGTTTGTTATCC3'		VIC	AJ391665#
	Ren02C20	38	F:5'AGAAATTGCATCACTCACAT3' R:5'GCTGCTCCGAAAACTAACTT3'		VIC	AJ391538#
	Ren02P03	23	F:5'CATTCTTATCCTTCAGTGCTGA3' R:5'GGCTCAGTCAGTAGTTGTGCG A3'		6-FAM	AJ391542#
	Ren04M22	-	F:5'AGAGAAAAGCATCCAGTAAG3' R:5'AAATGGTCTTCCTGTATCCT3'		NED	AJ391581#
M3	Ren02K21	-	F:5'CTTAGTTTTCAGGCTTTCAG3' R:5'TGATAGGAAGTAAAGATGTT3'	50	NED	AJ391561#
	Ren37H09	6	F:5'ATTCCCTTGTATTGCTCA3' R:5'CCCCAAAAAATCCAACCA3'		VIC	AJ391610#
	Ren39L15	3	F:5'CTTGTTTTCTTTTGGATAGC3' R:5'CTGCCTTGAAGAATGATAAA3'		6-FAM	AJ391615#
M4	Ren13J22	-	F:5'TATTGCAACTGTCTTATGTA3' R:5'TGTCTTAGTGATGGCTCCTG3'	50	VIC	AJ391603#/ AJ391604#
	Ren44K10	X/Y	F:5'CATATTGGACCTTCACAT3' R:5'TTAACGCACAACTTCATC3'		NED	AJ391641#
Single ampli-fication	Ren06C11	15	F:5'GGGGGTGTCGGTGGAGTTCT3' R:5'TGCAGGGCAGAGGCTGGAGG3'	58	NED	AJ391592#
Single ampli-fication	Ren41D20	32	F:5'TGTCTATGTAATATCACAGG3' R:5'TTCTGGGTATTTATCTGAAG3'	50	6-FAM	AJ391618#

* – GeneBank; # – EMBL.

Results

Sixteen microsatellite loci could be analysed. Because no amplification product was obtained in foxes for the INU005 sequence, this marker was excluded from further analysis.

Table 3. Length and frequency of alleles found within the populations studied

Locus	Allele length (bp)	Allele frequency		
		Farmed foxes	Wild Polish foxes	Wild Canadian foxes
1	2	3	4	5
Ren44K10	198		0.0167	
	200		0.0667	0.0106
	202	0.1968	0.3000	0.1383
	204	0.2660	0.3833	0.3936
	206	0.4309	0.1500	0.1489
	208	0.0957	0.0167	0.2128
	210		0.0667	0.0319
	212			0.0319
	214	0.0106		0.0319
Ren67C18	158	1.0000	1.0000	1.0000
Ren02C20	292	0.0051	0.1500	0.0532
	294	0.2296	0.2500	0.1277
	296	0.0765	0.2667	0.0213
	298		0.0333	
	300		0.0333	0.1064
	302	0.4031	0.1333	0.1277
	304	0.0153		0.1489
	306	0.0051	0.1000	0.0213
	308	0.0204	0.0167	
	310	0.1786		0.2553
	312	0.0663		0.0532
	314		0.0167	0.0851
Ren01E05	394			0.0106
	396			0.0319
	398	0.0206		0.1277
	400	0.2165		0.1489
	402		0.1000	0.0957
	404	0.6649	0.2667	0.2340
	406	0.0052	0.1833	0.0532
	408		0.3833	0.1809
	410		0.0500	0.0851
	412	0.0103	0.0167	0.0319
	414	0.0670		

Table 3 – contd.

1	2	3	4	5
Ren02K21	280		0.0484	
	288		0.0645	0.0326
	290	0.0051		0.4348
	292	0.4040	0.1452	0.2174
	294	0.4343	0.1613	0.1304
	296	0.0909	0.3548	0.0652
	298	0.0202	0.1129	0.1087
	300	0.0253	0.0484	0.0109
	302	0.0202	0.0645	
Ren06C11	86	1.0000	1.0000	1.0000
Ren13J22	404			0.0109
	406			0.0217
	408	0.0109	0.1379	0.0109
	410	0.7609	0.4483	0.5978
	412	0.2283	0.3621	0.2174
	416			0.0217
	418		0.0517	0.0978
	422			0.0217
Ren37H09	196	1.0000	1.0000	1.0000
Ren39L15	214	0.0101		
	220		0.0323	
	226	0.0960		
	228	0.6869	0.0161	0.4468
	230	0.0253	0.0645	0.0957
	232	0.1515	0.1290	0.1915
	234		0.2258	0.0106
	236		0.4516	0.0319
	238		0.0484	0.0319
	240	0.0303	0.0161	0.1064
	242		0.0161	0.0638
	244			0.0106
	246			0.0106
Ren41D20	192	1.0000	1.0000	1.0000
Ren02P03	163	0.1212		0.2979
	165	0.0152	0.1667	
	167	0.8232	0.7500	0.7021
	171	0.0404	0.0167	
	173		0.0667	
Ren04M22	179		0.2167	0.0106
	181	0.3990	0.0833	0.1277
	183	0.3586	0.0500	0.4362
	185	0.0101	0.0500	0.0638
	187		0.1000	0.2234
	189	0.0051	0.4167	0.1064
	191	0.0455	0.0833	0.0213
	193	0.1818		0.0106

Table 3 – contd.

1	2	3	4	5
INU013	163		0.1034	
	167		0.1207	
	169		0.0517	
	173	0.2500	0.0862	0.3000
	175	0.7250	0.0517	0.6556
	177	0.0250	0.3276	0.0444
	179		0.0517	
	183		0.1552	
	185		0.0517	
INU014	158		0.2097	
	162		0.0323	
	164		0.0323	
	166	0.0464	0.2097	
	168	0.0773	0.0484	0.0909
	170		0.0806	
	174		0.0806	
	176		0.1290	
	178		0.0161	0.0455
	180	0.0309	0.0161	0.0795
	182	0.1598	0.0484	0.2045
	184	0.2113	0.0806	0.3295
	186	0.4742	0.0161	0.1818
	188			0.0341
	190			0.0341
INU019	262			0.0109
	266	0.3250	0.1167	0.5652
	268	0.6750	0.0333	0.2717
	270		0.0667	0.1413
	272		0.0333	0.0109
	274		0.3333	
	276		0.1667	
	278		0.0667	
	280		0.1833	
INU020	231		0.0179	
	233		0.0357	
	235	0.2250	0.0179	0.2273
	237	0.0050	0.1071	
	241	0.4650	0.2857	0.1705
	243	0.1350	0.0179	0.0114
	245		0.0179	0.0341
	247	0.0200	0.0714	0.3068
	249		0.0714	0.1250
	251	0.0200	0.1250	0.0114
	253	0.1150	0.1607	0.0795
	255	0.0150	0.0714	0.0227
	263			0.0114

The highest number of alleles (15) within all populations was seen for the INU014 locus. More than 10 alleles were found for Ren39L15 (13), INU020 (13), Ren02C20 (12) and Ren01E05 loci (11). The population of farmed foxes was characterized by the lowest number of unique alleles (Table 3). Most specific alleles were noted for the group of wild foxes from Poland. At the INU013 locus, 6 out of 9 alleles were specific to this group (163, 167, 169, 179, 183 and 185 bp). Likewise at the INU014 locus, 6 out of 15 alleles were only found in the wild Polish population. They were 158, 162, 164, 170, 174 and 176 bp in size. At the INU019 locus, 4 of all detected alleles were specific to this group of animals (274, 276, 278 and 280 bp). For the wild Canadian population at the Ren13J22 locus, 4 of 8 alleles were characteristic. These alleles were 404, 406, 416 and 422 bp in size. At the Ren44K10, Ren02C20, Ren01E05, Ren02K21, Ren02P03 and Ren04M22 loci, alleles common to the farmed Polish population and free-living Canadian population did not occur in the wild Polish population (Table 3).

The values of PIC, He and Ho are listed in Table 4. The highest PIC values were found in both wild populations. In the Polish population, only at the Ren02P03 locus PIC was lower than 0.5 (0.368). At the Ren13J22 locus, polymorphic information content was 0.579 and in the other loci it reached values around 0.7 or higher. The highest PIC value in this group of animals was found for the INU014 locus (0.855). In the Canadian population, the Ren02C20 locus had the highest PIC of 0.839. PIC values below 0.5 were noted for two loci: Ren02P03 (0.331) and INU013 (0.399). PIC was 0.541 for the Ren13J22 locus and 0.523 for the INU019 locus. For the other eight loci, PIC was close to or higher than 0.7. The lowest polymorphism at the analysed loci was observed in the group of farmed foxes. PIC exceeded 0.5 in only six loci, with the highest value of 0.706 at the Ren02C20 locus. Like in the other populations, the lowest polymorphic information content was noted at the Ren02P03 locus (0.283).

The analysed loci differed considerably for their observed heterozygosity. However, it can be observed that in all the populations studied, high observed heterozygosities were detected for INU020. They were 0.810 in farmed foxes, 0.821 in wild foxes from Poland, and 0.795 in the wild population from Canada. In addition, high Ho values were found at the INU014 locus for farmed foxes (0.866) and Canadian wild foxes (0.955). Meanwhile, in the Polish free-living population, high observed heterozygosity was characteristic of the INU013 (0.828) and Ren02K21 loci (0.871). The lowest observed heterozygosity was noted at the Ren02P03 locus in the population of wild Canadian foxes (0.213). An equally low Ho value at the same locus (0.232) was seen in farmed foxes. Low observed heterozygosity in all analysed groups was characteristic of Ren13J22. It was 0.283 in farmed foxes, 0.276 in the wild Polish population, and 0.304 in the wild Canadian population. In the last-mentioned population, low observed heterozygosity was also characteristic of INU013 (0.289).

Table 5 presents genetic similarities and distances among the populations studied. The farmed Polish population is genetically more similar to the population of wild animals from Canada (similarity of 0.9058) than it is to the wild population from Poland (similarity of 0.7667). Genetic similarity between the two wild popula-

tions was 0.8068. The genetic distance values are shown graphically in the dendrogram (Figure 1).

Table 4. Number of alleles, PIC, observed (Ho) and expected heterozygosity (He) for individual groups of animals at the analysed polymorphic loci

Locus	Farmed population				Wild Polish population				Wild Canadian population			
	N_a	H_o	H_e	PIC	N_a	H_o	H_e	PIC	N_a	H_o	H_e	PIC
Ren44K10	5	0.702	0.699	0.644	7	0.600	0.744	0.689	8	0.681	0.763	0.722
Ren02C20	9	0.694	0.746	0.706	9	0.600	0.827	0.788	10	0.723	0.864	0.839
Ren01E05	7	0.536	0.508	0.459	6	0.667	0.748	0.694	10	0.681	0.862	0.836
Ren02K21	7	0.636	0.642	0.570	8	0.871	0.814	0.779	7	0.717	0.737	0.695
Ren13J22	3	0.283	0.371	0.308	4	0.276	0.658	0.579	8	0.304	0.591	0.541
Ren39L15	6	0.576	0.497	0.462	9	0.742	0.732	0.686	10	0.660	0.745	0.709
Ren02P03	4	0.232	0.307	0.283	4	0.400	0.412	0.368	2	0.213	0.423	0.331
Ren04M22	6	0.566	0.680	0.616	7	0.567	0.763	0.721	8	0.617	0.735	0.692
INU013	3	0.450	0.413	0.345	9	0.828	0.840	0.807	3	0.289	0.484	0.399
INU014	6	0.866	0.699	0.657	13	0.806	0.883	0.855	8	0.955	0.807	0.771
INU019	2	0.375	0.442	0.342	8	0.700	0.816	0.778	5	0.457	0.593	0.523
INU020	8	0.810	0.704	0.661	12	0.821	0.863	0.832	10	0.795	0.810	0.774

Table 5. Nei's genetic similarity (above diagonal) and distance (below diagonal) between the farmed fox population and the wild populations from Poland and Canada

	Wild Polish foxes	Wild Canadian foxes	Farmed foxes
Wild Polish foxes	***	0.8068	0.7667
Wild Canadian foxes	0.2146	***	0.9058
Farmed foxes	0.2657	0.0990	***

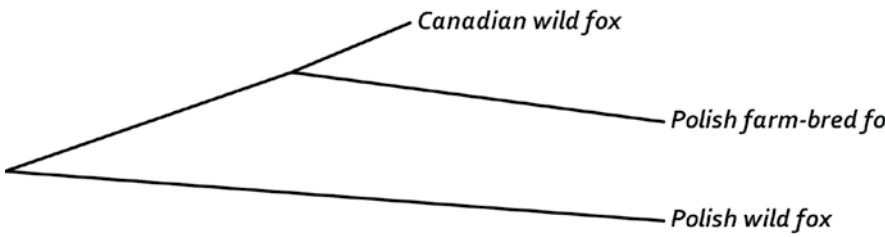

Figure 1. Neighbour-joining dendrogram based on Nei's genetic distance

Discussion

High genetic variation was found for the populations of free-living foxes, for which very high PIC values were observed for most of the analysed loci. These populations were also characterized by a considerable observed heterozygosity. In addition, wild Polish foxes were found to carry several alleles not found in the other populations studied. In the group of farmed animals, the pool of alleles at individual loci was distinctly smaller and the PIC values of the analysed loci were also much smaller for these animals. The limited number of alleles is probably the result of animal selection. Each year basic herd replacement is done but breeding programmes are practised at all farms. On the other hand, detection of specific alleles at microsatellite loci in the group of farmed fur bearing animals can be useful if it is associated with the occurrence of a specific value of production trait (Ślaska et al., 2008). Together with the information about genetic determination of these traits (Ślaska et al., 2007; Przysiecki et al., 2000), microsatellite markers might be a helpful tool in animal selection.

It is useful to determine differences between farmed and wild populations of fur animals in the context of escapes of farmed animals, their environmental adaptation, and the possibility of crossbreeding with wild members of their species. Using analysis of microsatellite sequences and mitochondrial DNA, Norén et al. (2005) investigated arctic foxes to assess differentiation within Scandinavian farm-bred and free-living populations, and to develop a method for distinguishing between these groups and identifying their hybrid progenies. At the microsatellite loci, the authors detected alleles specific for the farmed population and the wild animals. In both groups, the observed heterozygosity showed different values that were close to expected heterozygosity values. The genetic diversity indicated that the populations were highly different, although it did not allow for an unambiguous distinction between farmed and wild arctic foxes. However, mitochondrial haplotypes of the control region revealed clear differences between farmed and free-living animals.

Genetic differentiation within farmed and wild populations of another canid, the raccoon dog, was studied by Ślaska et al. (2010). They analysed animals raised on three farms from different provinces of Poland and a Polish population of wild animals. Nei's genetic distances between these groups were calculated based on random amplified polymorphic DNA (RAPD) profiles obtained using three primer sequences. The distances between the wild population and the 3 farmed populations were 0.211, 0.208 and 0.179, respectively. The genetic distance between animals from different farms was invariably lower at 0.067, 0.112 and 0.126. In our study with red foxes, the distance between the wild Polish population and the wild Canadian population was 0.2146. The largest distance was noted between farmed Polish animals and the group of free-living animals from Poland. Such a considerable genetic difference can be useful in detecting immigrating red foxes from these populations. The smallest genetic distance occurred between the farmed Polish population and the wild Canadian population, thus allowing the conclusion that the animals raised on Polish farms are descendants from red foxes brought from North America. This is in agreement with historical data (Piórkowska, 2010). Because of the small genetic

distance between wild Canadian foxes (indicated as the progenitor of farmed Polish foxes) and farmed Polish foxes, it can be concluded that the differences between the farmed and wild Polish populations reflect their different origin.

To determine the origin of the Russian populations of silver foxes, Statham et al. (2011) sequenced two regions of mitochondrial DNA of farmed foxes from Novosibirsk and of animals representing the native populations from Europe, Asia, Alaska, Eastern and Western Canada, and Western Mountains of the USA. The identification of haplotypes and their comparison between individual groups revealed the greatest similarity between the Russian farmed population and Eastern Canadian wild population, confirming the historically documented origin of the Russian farmed population through imports from Prince Edward Island, Canada.

The data relating to wild foxes might be useful to compare it with historical samples of wild foxes not only from Poland but also from other countries. It can be used in a wide range of ecological studies. Genetic characteristics of modern and ancient red foxes enabled Teacher et al. (2011) to investigate phylogeographical patterning of these species in relation to historical climate changes.

Not surprisingly, the data indicate that the wild populations are more diverse than farmed populations. The currently farmed foxes are genetically different from the wild members of their species. In addition, the genetic distance between the farmed and free-living Polish populations indicates a considerable phylogenetic distance between these groups. To gain a more accurate assessment of the genetic differences, the study will be continued using analysis of mitochondrial gene polymorphism.

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Accepted for printing 13 VI 2012

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Zróżnicowanie genetyczne populacji hodowlanej i wolno żyjącej lisów pospolitych (*Vulpes vulpes*)

STRESZCZENIE

Polimorfizm szesnastu sekwencji mikrosatelitarnych (Ren01E05, Ren02K21, Ren06C11, Ren13J22, Ren37H09, Ren39L15, Ren41D20, Ren44K10, Ren67C18, Ren02C20, Ren02P03, Ren04M22, INU013, INU014, INU019, INU020) badano w celu oceny zróżnicowania genetycznego polskiej populacji hodowlanej oraz dwóch populacji wolno żyjących (z Polski i Kanady) należących do gatunku *Vulpes vulpes*. Wyższymi wartościami indeksu stopnia polimorfizmu oraz heterozygotyczności obserwowanej i oczekiwanej charakteryzowały się obie grupy osobników dziko żyjących. Na podstawie frekwencji alleli ustalono dystans genetyczny dzielący badane populacje zwierząt. Stwierdzono, iż polskie lisy hodowlane wykazują większe podobieństwo genetyczne do populacji osobników dzikich z Ameryki Północnej niż do rodzimej populacji wolno żyjącej. Zatem lisy pospolite hodowane na polskich fermach i lisy dziko żyjące zamieszkujące tereny Polski stanowią dwie grupy zwierząt wysoce odrębne pod względem genetycznym.