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Genetic diversity and bottleneck analysis of the Red Steppe cattle based on microsatellite markers

A.S. Kramarenko[1], E.A. Gladyr[2], S.S. Kramarenko[1], T.V. Pidpala[1], L.A. Strikha[1], N.A. Zinovieva[2]

[1]Mykolayiv National Agrarian University, Georgiy Gongadze Str., 9, Mykolayiv, 54020, Ukraine
E-mail: kssnail0108@gmail.com
[2]Federal Science Center for Animal Husbandry named after Academy Member L.K. Ernst, Dubrovitsy, 60, Podolsk Municipal District, Moscow Region, 142132, Russia
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Thirty-nine dairy cows representing the Red Steppe (RS) cattle breed (the State Enterprise "Pedigree Reproducers "Stepove" Mykolayiv region, Ukraine) were included in the study. A set of 11 microsatellite markers recommended by International Society of Animal Genetics (ISAG) for cattle was used to study genetic diversity in the RS cattle population. All of the studied loci were highly informative and polymorphic. In total, 71 alleles were detected at 11 microsatellite loci, from which 16 (22.5%) had frequency lower than 5%. The number of detected alleles per locus (*TNA*) ranged from four to ten, with a mean value of 6.45±0.51. The mean effective number of alleles (*Ae*) was 3.77±0.37. The allele frequencies ranged from 0.013 to 0.714. The average values for observed (*Ho*) and expected (*He*) heterozygosities were 0.607±0.085 and 0.703±0.034, respectively. The within breed estimate F_{IS} indicates heterozygosity shortage of 0.179. The Hardy-Weinberg equilibrium test revealed that 2 out of 11 loci deviated from equilibrium. The RS cattle population is non-bottlenecked, i.e., it has not undergone any recent reduction in the effective population size and remained at mutation-drift equilibrium. The estimated mean *Ne* for the RS cattle population was 23.3 (95% *CI*s = 11-74) individuals. These low values emphasize the need of controlling the rate of increase of inbreeding in the RS cattle herds.
Key words: genetic diversity, allele pool, bottleneck-effect, microsatellites DNA, Red Steppe cattle, dairy cow

Introduction

Cattle is an important livestock species that have played a special role in the human history and culture, and had a considerable impact on human society. The worldwide population of cattle is estimated to 1.4 billion animals, of which 159 million (11%) are found in Europe and Central Asia (Felius et al., 2011).

Dairy industry requires the development of very standardized cattle herds to fulfill their commercial needs that reflects on selection practices in breeding programs. The genetic characterization of populations, breeds and species allows evaluation of genetic variability, a basic element in working out breeding strategies and genetic conservation plans. Molecular markers have revolutionized our ability to characterize genetic variation and rationalize genetic selection (Goddard and Hayes, 2007; Hayes et al., 2009). Microsatellites (highly polymorphic simple sequence repeats) are still remained the popular molecular markers, essentially owing to the option of blending their analysis with use of the polymerase chain reaction (PCR). The employment of microsatellite markers is one of the powerful means for studying the genetic diversity, calculation of genetic distances, detection of bottlenecks and admixture because of high degree of polymorphism, random distribution across the genome, co-dominance and neutrality with respect to selection (Putman and Carbone, 2014).

The Red Steppe (RS) cattle breed was created in the Ukraine and southern European Russia by crossing of Red East Friesian and Angeln breeds with Ukrainian Grey and later with Swiss Brown and East Friesian breeds during the time from 1789 to 1824 by Mennonites. The RS breed was the most widespread breed found in the former U.S.S.R., which was characterized by the highest milk yield comparing to other breeds used fir milk production in the country (Mason, 1996).

Considering the importance of cattle in Ukrainian agriculture, few efforts have been made to evaluate the genetic diversity and relationship in Ukrainian cattle breeds using microsatellite markers (Shkavro et al., 2014: Shelyov, 2015; Kramarenko et al., 2015; Shelyov et al., 2017). Thus, a deeper knowledge of the genetic diversity and population structure of Ukrainian cattle breeds can provide a rational basis for the need of conservation and possible use of native breeds as genetic resources to meet potential future demand of adaptation to changing environment or production needs.

The aim of the current study was to evaluate the genetic diversity among the Red Steppe (RS) cattle breed, in order to provide information for future breeding programmes and conservation management strategy of the breed.

Methods

Thirty-nine dairy cows representing the Red Steppe cattle breed (the State Enterprise "Pedigree Reproducers "Stepove" Mykolayiv region, Ukraine) were included in the study. The animals were unrelated and were randomly selected from herd. Genomic DNA was extracted from tissue samples using Nexttec column (Nexttec Biotechnology GmbH, Germany) following the manufacturer's instructions. The DNA concentration was estimated by measuring the absorbance at 260 nm and the DNA quality was checked by separation on agarose gels.

Eleven microsatellite markers (*BM1818, BM1824, BM2113, ETH3, ETH10, INRA023, TGLA53, TGLA122, TGLA126, TGLA227* and *SPS115*) were analyzed to estimate various parameters of genetic diversity. Microsatellites were amplified in two multiplex reactions. Electrophoresis was carried out using an ABI 3130xl Genetic Analyzer (Applied Biosystems, USA). Allele sizes of each microsatellite were determined using GeneMapper ver. 4.0 (Applied Biosystems).

GenAIEx v.6.5 software (Peakall and Smouse, 2012) was used to estimate basic population genetic descriptive statistics for each marker: allelic frequencies, observed total number of alleles (*TNA*), effective number of alleles (*Ae*), observed (*Ho*) and expected heterozygosity (*He*). The effective allele number (*Ae*) for each locus was calculated using the following formula: $Ae = 1 / (1 - He)$, where *He* corresponds to the expected heterozygosity. Allelic richness (A_R) for the RS cattle population (for 14 diploid individuals) was calculated to correct distortion by sample size difference using FSTAT v. 2.9.3.2. (Goudet, 2002).

Deviations from Hardy-Weinberg equilibrium (HWE) were tested for each locus using the Markov chain method implemented by Guo and Thompson (1992), using the software GENEPOP v.4.2 (Rousset, 2008) using Markov chain algorithm implemented according to authors recommendation (with 10,000 dememorizations, 200 batches and 5,000 interactions per batch).

The BOTTLENECK v.1.2.03 (Cornuet and Luikart, 1996) analysis was performed to find out whether this cattle population was exhibiting a significant number of loci with the excess of heterozygosity.

Genetic diversity was assessed by effective population size (*Ne*) and it was calculated by linkage disequilibrium (LD) method, as implemented in the software package NeESTIMATOR v. 2.01 (Do et al., 2014).

Results and discussion

All bovine microsatellite loci were highly polymorphic for the RS cattle population. The alleles, which were observed only once, were excluded for the analysis. The allelic frequencies of the 11 microsatellite loci in the RS cattle population are presented in Table 1.

Table 1. The allelic frequencies of the 11 microsatellite loci in the RS cattle population

Locus	Allele	Freq.	Locus	Allele	Freq.	Locus	Allele	Freq.
TGLA227	77	0.064	*ETH10*	213	0.077	*TGLA126*	115	0.432
	79	0.013		215	0.077		117	0.189
	81	0.282		217	0.346		119	0.108
	83	0.141		219	0.231		121	0.027
	89	0.179		221	0.167		123	0.081
	91	0.154		223	0.026		125	0.149
	93	0.026		225	0.077		127	0.014
	95	0.038	*SPS115*	248	0.628	*BM1818*	258	0.103
	97	0.090		252	0.064		260	0.013
	103	0.013		254	0.077		262	0.269
BM2113	125	0.038		256	0.077		264	0.064
	127	0.179		258	0.013		266	0.449
	131	0.013		260	0.141		268	0.103
	133	0.038	*TGLA122*	133	0.103	*ETH3*	109	0.097
	135	0.179		137	0.167		117	0.375
	137	0.295		139	0.064		119	0.167
	139	0.256		141	0.231		121	0.097
TGLA53	160	0.241		143	0.321		123	0.028
	166	0.537		145	0.115		125	0.097
	168	0.111	*INRA23*	206	0.071		127	0.125
	170	0.037		208	0.143		129	0.014
	172	0.056		212	0.714	*BM1824*	178	0.186
	174	0.019		214	0.071		180	0.086
							182	0.471
							188	0.257

In total, 71 alleles were detected, from which 16 (22.5%) had frequency lower than 5%. FAO has specified a minimum of four distinct alleles per locus for evaluation of genetic differences among domestic livestock breeds. By this criterion, all of 11 microsatellites applied in this study showed ample polymorphism for assessment genetic variation within the RS cattle population.

Allele ranges, number of alleles, heterozygosity per locus are summarized in Table 2. The *TNA* per locus ranged from four (*INRA023* and *BM1824*) to 10 (*TGLA227*), with a mean value of 6.45±0.51 alleles. The mean value of *Ho* across loci was 0.607±0.085, with estimates per locus ranged from 0.000 (*INRA023*) to 0.872 (*TGLA227*). For *He*, the mean value for all loci was 0.703±0.034 with variation between 0.459 (*INRA023*) and 0.830 (*TGLA227*). In general, genetic variation of this population is high according to the allele numbers and heterozygosity values of the microsatellite loci (Table 2). The mean observed number of alleles across all the microsatellite loci was lower than other Ukrainian local dairy cattle breeds – Ukrainian Black Pied (mean of *TNA* across loci was 9.2 with estimates per locus ranging from 6 to 14 alleles per locus) and Ukrainian Red-and-White (mean of *TNA* across loci was 9.5 with estimates per locus ranging from 7 to 13 alleles per locus) (Shelyov, 2015). Lower allelic diversity than studied populations has been reported in indigenous cattle – Ukrainian Grey breed (the mean value of *TNA* across loci was 5.1 with estimates per locus ranging from 3 to 8 alleles) (Shkavro et al., 2010).

Table 2. Measures of genetic variation in the RS cattle population

Locus	Size range, bp	Parameters						
		TNA	*Ae*	A_R	*Ho*	*He*	F_{IS}	HWE
TGLA227	77-103	10	5.88	7.91	0.872	0.830	-0.050	ns
BM2113	125-139	7	4.54	5.84	0.769	0.780	0.013	ns
TGLA53	160-174	6	2.75	5.18	0.185	0.636	0.709	*
ETH10	213-225	7	4.56	6.41	0.846	0.781	-0.084	ns
SPS115	248-260	6	2.32	5.13	0.462	0.569	0.189	ns
TGLA122	133-145	6	4.72	5.86	0.769	0.788	0.024	ns
INRA023	106-214	4	1.85	4.00	0.000	0.459	1.000	*
TGLA126	115-127	7	3.79	5.92	0.649	0.736	0.119	ns
BM1818	258-268	6	3.34	5.21	0.692	0.701	0.012	ns
ETH3	109-129	8	4.69	6.93	0.806	0.787	-0.024	ns
BM1824	178-188	4	3.03	3.96	0.629	0.670	0.062	ns
Mean		6.45	3.77	5.67	0.607	0.703	0.179	
SE		0.51	0.37	0.35	0.085	0.034	0.105	

bp – base pair; *TNA* – total number of alleles; *Ae* – effective number of alleles; A_R – allelic richness (for 14 diploid individuals); *Ho* – observed heterozygosity; *He* – expected heterozygosity; F_{IS} – heterozygote deficiency; HWE – Hardy-Weinberg equilibrium; ns – non significant *p*-value; * – $p < 0.05$; *SE* – standard error.

The RS cattle seem to harbour a good amount of genetic variation. The average observed heterozygosity in this study is lower than that shown in Ukrainian Black Pied (0.821) and Ukrainian Red-and-White breeds (0.784) (Shelyov, 2015). Overall heterozygosity values were comparable with those estimated in Ukrainian Grey cattle (0.680) (Shkavro et al., 2010). The RS cattle population displayed considerable levels of genetic diversity as estimated by expected heterozygosity (*He* = 0.703±0.034). Shelyov (2015) had found a value of *He* of 0.819 in Ukrainian Black Pied and 0.884 in Ukrainian Red-and-White breeds. The high values of allelic diversity, gene diversity and expected heterozygosity obtained in this study well confirm that RS cattle breed represent an important reservoir of genetic variability and it reflects the absence of selection or organized breeding programs for Ukrainian dairy cattle.

Two loci in the RS cattle breed (*TGLA53* and *INRA023*) have shown deviation from HWE. Thus, our results differed from those of Kramarenko et al. (2015) where the Southern Meat cattle breed gave a significant deviation from HWE for *TGLA227, TGLA53, ETH3, ETH225* and *SPS115* loci. This deficiency of heterozygotes among populations is an indicator of inbreeding among cattle breeds or the occurrence of population substructure.

The values of F_{IS} were positive at 8 loci that indicates the within population heterozygotes deficiency, whereas three loci were characterized by negative F_{IS} values. The F_{IS} estimates ranged between -0.084 (*ETH10*) and 1.000 (*INRA023*), with average value of 0.179±0.105. Thus, the studied RS population was characterized a substantial heterozygote deficiency (17.9%). Only two microsatellite loci (*TGLA53* and *INRA023*) significantly contributed to observed heterozygote deficiency in the RS cattle population.

Microsatellite data were also subjected to statistical analysis to test whether the population exhibits a significant number of loci with gene diversity excess. Three mutation models – the Infinite Allele Model (IAM), Two Phase Model of mutation (TPM) and Stepwise Mutation Model (SMM) – were selected for running the BOTTLENECK program to test for population bottlenecks. The probability values obtained under these three models using three different statistical tests are depicted in Table 3.

The expected numbers of loci with heterozygosity excess were 6.49, 6.52 and 6.56 in IAM, TPM and SMM, respectively. The null hypothesis was not rejected using the Sign test and the Wilcoxon test and not indicated a recent genetic bottleneck event. In case of standardized difference test, the hypothesis of mutation-drift equilibrium was rejected for TPM ($p = 0.015$) and SMM ($p < 0.001$) models; under IAM, the results displayed no genetic bottleneck effect. Mode-shift indicator test as a second test for potential bottleneck was used. The microsatellite alleles were organized into 8 frequency classes, which permit checking whether the distribution followed the normal L-shaped form, where alleles with low frequencies (0.01-0.10) are the most numerous (Figure 1).

Table 3. Heterozygosity excess/deficiency under different mutation models (Heterozygosity Method) in the RS cattle population

Models	Sign test	Standardized differences test	Wilcoxon test
IAM	Hee =6.49 Hd = 3 He = 8 p = 0.274 (ns)	T2 = -0.111 p = 0.456 (ns)	P (one tail for H deficiency): 0.768 P (one tail for H excess): 0.260 P (two tails for H excess and deficiency): 0.520
TPM	Hee = 6.52 Hd = 4 He = 7 p = 0.513 (ns)	T2 = -2.168 p = 0.015	P (one tail for H deficiency): 0.483 P (one tail for H excess): 0.551 P (two tails for H excess and deficiency): 0.966
SMM	Hee = 6.56 Hd = 7 He = 4 p = 0.104 (ns)	T2 = -5.847 p < 0.001	P (one tail for H deficiency): 0.139 P (one tail for H excess): 0.880 P (two tails for H excess and deficiency): 0.278

IAM – Infinite allele model; TPM – Two phase model; SMM – Stepwise mutation model. Parameters for T.P.M: Variance = 30.00. Proportion of SMM in TPM = 70.00%; Estimation based on 1,000 replications. Hee – heterozygosity excess expected; Hd – heterozygosity deficiency; He – heterozygosity excess; P – probability; ns – non significant *p*-value.

The observed distribution suggests that the RS cattle breed did not encounter a genetic bottleneck in the recent past. According to the Bottleneck analysis, Turkish native cattle breeds were revealed a normal L-shaped distribution indicating that these populations did not experience any recent potential risk of extinction (Özşensoy and Kurar, 2014). The qualitative test of mode shift analysis supported the conservative SMM model which indicated absence of genetic bottleneck in the recent past in Senegalese cattle populations (Ndiaye et al., 2015). Bottleneck was examined assuming all three mutation models which showed that the population has not experienced bottleneck in recent past for the Kherigarh cattle also (Pandey et al., 2006). On other hand, bottleneck has been reported in two sub strains of Japanese black cattle by Sasazaki et al. (2004).

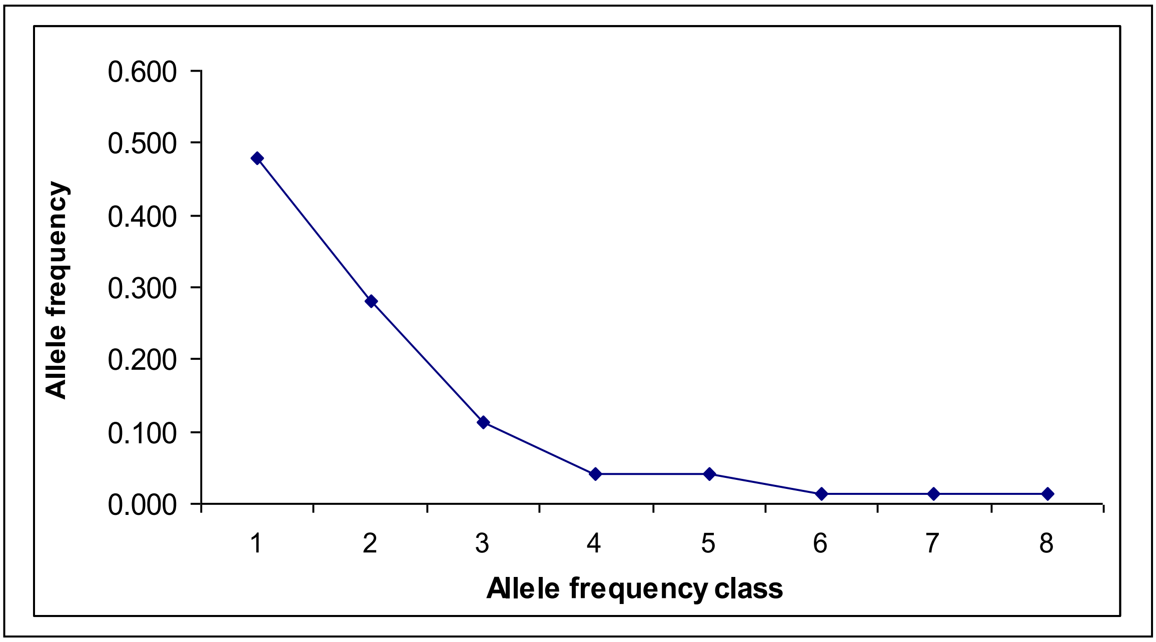

Figure 1. L-shaped mode-shift graph showing lack of recent genetic bottleneck in the RS cattle population

The estimated mean *Ne* for the RS cattle population was 23.3 (95% *CI*s = 11-74) individuals. Table 4 gives the estimates of effective population size for certain dairy cattle breeds. The effective population size obtained for the RS cattle in this study were in agreement with those reported data for the Reyna Creole cattle in Nicaragua (Corrales et al., 2010), Montbéliarde and Normande breeds in France (Leroy et al., 2013), Holstein in the USA (Weigel, 2001), Guernsey in South Africa, the USA and Canada (Melka et al., 2013). Generally, estimates of *Ne* in some modern breeds of dairy cattle (Ayrshire, Holstein, Jersey, etc.) are of the order of 100 or more.

From a consideration of the net genetic response in economic merit in dairy cattle breeding, Goddard and Smith (1990) suggested 40 as a minimum effective size. Another approach toward defining minimum effective size was considered by Meuwissen and Woolliams (1994), which balanced inbreeding depression and gain in fitness through natural selection. This resulted in recommendations of the order of 30 to 250. The current effective size of the RS cattle population is smaller than these critical values. Thus, the small *Ne* found in the RS cattle reflects the fact that breeding strategies followed in this breed have implied a very heavy use of few top sires.

Table 4. The estimates of effective population size (*Ne*) for certain dairy cattle breeds

Breed	Country	*Ne* (min-max)	Reference
Ayrshire	South Africa	148	Maiwashe et al., 2006
Brown Swiss	France	80 (55-98)	Leroy et al., 2013
Brown Swiss	South Africa	45-132	de Ponte Bouwer et al., 2013
Guernsey	South Africa	165	Maiwashe et al., 2006
Guernsey	South Africa	57	Melka et al., 2013
Guernsey	Canada	46	Melka et al., 2013
Guernsey	USA	46	Melka et al., 2013
Holstein	France	74 (49-93)	Leroy et al., 2013
Holstein	Spain	66-79	Rodríguez-Ramilo et al., 2015
Holstein	South Africa	137	Maiwashe et al., 2006
Holstein	Germany	103	Qanbari et al., 2010
Holstein	Canada	77 (33-114)	Stachowicz et al., 2011
Holstein	USA	39	Weigel, 2001
Holstein	Australian	150	Hayes et al., 2003
Holstein	Korea	122	Shin et al., 2013
Icelandic cattle	Iceland	111 (100-127)	Asbjarnardottir et al., 2010
Jersey	South Africa	108	Maiwashe et al., 2006
Jersey	Canada	114 (54-153)	Stachowicz et al., 2011
Montbéliarde	France	57 (30-82)	Leroy et al., 2013
Normande	France	64 (37-93)	Leroy et al., 2013
Red Steppe	Ukraine	23 (11-74)	present study
Reyna Creole cattle	Nicaragua	28-46	Corrales et al., 2010
Sahiwal	Kenya	270 (4-576)	Kamiti et al., 2016
Ukrainian Black Pied	Ukraine	397	Shelyov et al., 2017
Ukrainian Red-and-White	Ukraine	555	Shelyov et al., 2017

Conclusions

The study reports a first genetic within breed diversity estimate of the RS cattle population through microsatellite markers recommended by the ISAG. The *TNA, Ho* and *He* values observed in the present study is indicative of the fact that the markers used are highly informative for genetic characterization of the RS cattle and give reliable information on genetic diversity and population structure. Only two loci in the RS cattle breed (*TGLA53* and *INRA023*) have shown deviation from HWE. Our data suggest that the RS cattle population has not undergone any reduction at least in the recent past. Estimates of effective population size were ranged from about 11 to 74. These low values emphasize the need of controlling the rate of increase of inbreeding in the RS cattle herds.

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