



Full Length Article

Estimation of Effective Population Size of Korean Native Black Goat Using Genomic Information

Kwan-Woo Kim¹, Jinwook Lee¹, Sung-Soo Lee¹, Seungchang Kim¹, Hyun Tae Lim², Yousam Kim³ and Sang-Hoon Lee^{1*}

¹Animal Genetic Resources Research Center, National Institute of Animal Science, Rural Development Administration, Republic of Korea

²Division of Applied Life Science (BK21 plus), Gyeongsang National University, Republic of Korea

³TNT Research Co., Ltd., Anyang-si, Gyeonggi-do, Republic of Korea

*For correspondence: sanghoon@korea.kr

Received 15 September 2020; Accepted 23 November 2020; Published 25 January 2021

Abstract

The Korean native black goat (*Capra hircus coreanae*) is the only goat species to be officially registered in Korea under the Food and Agriculture Organization; however, no systematic research on their genetic diversity has been conducted. Decreased genetic diversity in Korean native black goat leads to an increase in the level of inbreeding across generations. In this study, the genetic parameters and effective population size of three strains of Korean native black goat—82 Dangjin, 87 Jangsu, and 118 Tongyeong individuals—were estimated using their genomic information. The average linkage disequilibrium (r^2) between single nucleotide polymorphism markers in the genome was 0.16, 0.14, and 0.13 for the Dangjin, Jangsu, and Tongyeong strains, respectively. The largest linkage disequilibrium was observed in the 14th and 26th chromosomes ($r^2 = 0.18$) of Dangjin individuals. Furthermore, an increase in physical distance between markers decreased the linkage disequilibrium. The effective population size of the three Korean native black goat strains showed a decreasing trend proportional to the decrease in generation. The effective population size was 47, 59 and 56 individuals for the Dangjin, Jangsu and Tongyeong strains, respectively, 13 generations ago. These values could be due to the high level of inbreeding for generating populations to preserve the Korean native black goat genetic resource. © 2021 Friends Science Publishers

Keywords: Korean native black goat strain; Genetic diversity; Inbreeding; Linkage disequilibrium

Introduction

Korean native black goat (*Capra hircus coreanae*) originated around 2000 years ago, and it exhibits a close genetic relationship with the native black goat of China and Vietnam. This suggests that Korean native black goat was introduced to the Korean Peninsula from East Asia (Kim *et al.* 2001). In the early 1990s, the Animal Genetic Resources Research Center in the National Institute of Animal Science of Rural Development Administration (Korea) collected Korean native black goats from Anmyeondo (Tae-an, Chungcheongnam-do), Yokjido (Tongyeong, Gyeongsangnam-do) and Beonam-myeon (Jangsu-gun, Jeollabuk-do) to preserve and manage these resources. The individuals were selected and categorized into Dangjin, Tongyeong, and Jangsu strains based on body shape, hair color, and hair length. These strains are managed as pure breeds and have been recently registered in the Domestic Animal Diversity Information System (DAD-IS, <http://dad.fao.org>) of the Food and Agriculture Organization (FAO) (Suh *et al.* 2012; Lee *et al.* 2019).

Goat meat has recently become popular among consumers, increasing its market demand, which has resulted in a continuous increase in the number of goat livestock. However, Korean native black goat is less productive than foreign goat strains, and therefore, many goat farmers are crossbreeding the native strains with foreign strains or dairy cattle to increase Korean native black goat productivity. This has led to a significant decrease in the number of pure native black goat individuals, and the Korean native black goat is currently at risk of being categorized as an endangered species (Lee *et al.* 2016, 2019).

Under these circumstances, maintaining the genetic diversity of Korean native black goat is important from both economical and biological perspectives (Amos and Balmford 2001). It has been reported that decreased genetic diversity reduces the potential of goat species to adapt to various environmental conditions and diseases, and it negatively affects traits related to survival and environment adaptability (Fernández *et al.* 2005). In particular, a decrease in genetic diversity in a small population such as

the Korean native black goat population can increase the coefficient of inbreeding across generations, which can lead to inbreeding deterioration, population reduction, and species extinction (Woolliams and Bijma 2000; Zenger *et al.* 2007). To prevent inbreeding, the FAO recommends maintaining the effective population size over 50 individuals (FAO 2000; Melka and Schenkel 2010). Therefore, in the present study, we estimated the genetic characteristics, effective population size, and linkage disequilibrium (LD) using single nucleotide polymorphism (SNP) information for each of the three Korean native black goat strains (Dangjin, Tongyeong, and Jangsu). We also collected basic information on the extent of genetic diversity in the three strains of native black goat to develop strategies that may improve the breeding of each strain.

Materials and Methods

Goat populations

All animal experiments were performed in accordance with the Guidelines for the Care and Use of Laboratory Animals (National Institute of Animal Science, Korea). From 1997 to 1998, the Animal Genetic Resources Research Center of the National Institute of Animal Science of Rural Development Administration, Korea, collected Korean native black goat individuals in Anmyeondo (Taeon, Chungcheongnam-do; Dangjin strain), Yokjido (Tongyeong, Gyeongsangnam-do; Tongyeong strain), and Beonam-myeon (Jangsu-gun, Jeollabuk-do; Jangsu strain) (Fig. 1). These individuals were not crossbred with other goat strains or lineages but were managed as a closed group of pure breeds. The study was conducted using 287 individuals, comprising 82 Dangjin, 87 Jangsu, and 118 Tongyeong individuals.

Single nucleotide polymorphism and quality control

The Illumina Goat SNP 50k panel (Illumina Inc., San Diego, C.A., U.S.A.) was used to generate genomic information of the three Korean native black goat strains, from which 50,618 SNP markers were obtained. Quality control (QC) of the genomic information obtained was conducted using PLINK software version 1.9 (Chang *et al.* 2015). The SNP markers of low quality with no mapping information and located on sex chromosomes, with a call rate of under 0.95, Hardy–Weinberg equilibrium (HWE) P-value of less than 10^{-6} and minor allele frequency (MAF) of less than 1%, were removed from the SNP analysis.

Estimation of linkage disequilibrium

The size of LD can be estimated using D' (Lewontin 1964), which is the standardized value of D and reflects the association and inheritance of two alleles located at different loci of the same chromosome, or r^2 (Hill and Robertson 1968). However, as the use of D' can lead to overestimation

due to population size and allele frequency (McRae *et al.* 2002; Hayes 2007), r^2 was used in this study. Linkage equilibrium of biallelic A and B loci located on the same chromosome was calculated as shown below:

$$r^2 = \frac{D^2}{p(A_1) \times p(A_2) \times p(B_1) \times p(B_2)} \quad r^2 = \frac{D^2}{p(A_1) \times p(A_2) \times p(B_1) \times p(B_2)} \quad (1)$$

Where $p(A_1)$, $p(A_2)$, $p(B_1)$ and $p(B_2)$ are the allele frequencies of marker loci A and B in the same population. D was calculated as shown below:

$$D = p(A_1B_1) \times p(A_2B_2) - p(A_1B_2) \times p(A_2B_1) \quad D = p(A_1B_1) \times p(A_2B_2) - p(A_1B_2) \times p(A_2B_1) \quad (2)$$

Where $p(A_1B_1)$, $p(A_2B_2)$, $p(A_1B_2)$ and $p(A_2B_1)$ are the frequencies of haplotypes consisting of the alleles in the A and B loci in the same population.

Estimation of effective population size

Linkage equilibrium occurs by mutation and recombination, in which a locus pair located further apart has a higher probability of recombination. The effective population size across generations can be estimated under the assumption that the distance between markers and linkage equilibrium value (r^2) is known and that there are no mutations (Sved 1971). In this study, 1 cM genetic distance and 1 Mb physical distance were assumed to be the same (Uimari and Tapio 2011) to estimate the effective population size, which was calculated as shown below (Corbin *et al.* 2012):

$$N_{T(t)} = \frac{1}{(4f(c_t))} \left(\frac{1}{E(r_{adj}^2[c_t])} - a \right) \quad N_{T(t)} = \frac{1}{(4f(c_t))} \left(\frac{1}{E(r_{adj}^2[c_t])} - a \right) \quad (3)$$

Where $N_{T(t)}$ is the effective population size t generations ago, estimated using $t = (2f(c_t)) - 1$ (Hayes *et al.* 2003), c_t is the recombination ratio defined by the physical distance between markers, r_{adj}^2 is the LD value adjusted to sample size, and $a = \{1, 2, 2.2\}$ is the correction value for mutation occurrence (Ohta and Kimura 1971). In this study, LD and effective population size were estimated using SNeP software version 1.1 (Barbato *et al.* 2015).

Results

Quality control

The QC results for the 50,618 SNP markers, excluding SNPs with a call rate of less than 0.95, MAF of 0.01, and HWE P-value of 10^{-6} , for each strain are shown in Table 1 and for each chromosome in each strain are shown in Table 2.

Linkage disequilibrium

The SNP marker information and LD value for each chromosome in each strain are shown in Table 3. In each strain, chromosome 1 was the longest and chromosome 25 was the shortest; the average distance among the SNP

Table 1: Quality control results for each strain

Strain	Individual call rate	SNP call rate	MAF	HWE	SNPs remaining
Dangjin	-	996	6369	77	43,176
Jangsu	-	1072	5446	83	44,017
Tongyeong	-	1095	7689	84	41,750

SNP, single nucleotide polymorphism; MAF, minor allele frequency; HWE, Hardy–Weinberg equilibrium

Table 2: Quality control results per chromosome (Chr) in each strain

Chr.	Dangjin			Jangsu			Tongyeong		
	Before	After	Removal percentage (%)	Before	After	Removal percentage (%)	Before	After	Removal percentage (%)
1	3269	2874	12.1	3269	2879	11.9	3269	2657	18.7
2	2830	2403	15.1	2830	2445	13.6	2830	2270	19.8
3	2430	2174	10.5	2430	2131	12.3	2430	2063	15.1
4	2484	2099	15.5	2484	2176	12.4	2484	2147	13.6
5	2286	1957	14.4	2286	1985	13.2	2286	1981	13.3
6	2482	2094	15.6	2482	2110	15.0	2482	1921	22.6
7	2221	1942	12.6	2221	1898	14.5	2221	1861	16.2
8	2347	2063	12.1	2347	2097	10.7	2347	2037	13.2
9	1898	1692	10.9	1898	1707	10.1	1898	1613	15.0
10	2114	1804	14.7	2114	1833	13.3	2114	1782	15.7
11	2146	1859	13.4	2146	1934	9.9	2146	1779	17.1
12	1800	1489	17.3	1800	1527	15.2	1800	1472	18.2
13	1671	1393	16.6	1671	1463	12.4	1671	1361	18.6
14	1940	1512	22.1	1940	1669	14.0	1940	1499	22.7
15	1684	1444	14.3	1684	1366	18.9	1684	1312	22.1
16	1608	1324	17.7	1608	1452	9.7	1608	1332	17.2
17	1447	1252	13.5	1447	1247	13.8	1447	1190	17.8
18	1390	1124	19.1	1390	1166	16.1	1390	1104	20.6
19	1234	1098	11.0	1234	1098	11.0	1234	1062	13.9
20	1496	1275	14.8	1496	1336	10.7	1496	1243	16.9
21	1477	1288	12.8	1477	1328	10.1	1477	1227	16.9
22	1171	1000	14.6	1171	1027	12.3	1171	976	16.7
23	1038	903	13.0	1038	901	13.2	1038	840	19.1
24	1328	1088	18.1	1328	1183	10.9	1328	1085	18.3
25	887	749	15.6	887	740	16.6	887	735	17.1
26	1060	848	20.0	1060	835	21.2	1060	883	16.7
27	934	823	11.9	934	770	17.6	934	735	21.3
28	929	763	17.9	929	832	10.4	929	761	18.1
29	1017	842	17.2	1017	882	13.3	1017	822	19.2
Total	50,618	43,176	14.7	50,618	44,017	13.0	50,618	41,750	17.5

Table 3: Linkage disequilibrium per chromosome (Chr) in each strain

Chr.	Dangjin				Jangsu				Tongyeong			
	C.L.	NSP	AVD	r ²	C.L.	NSP	AVD	r ²	C.L.	NSP	AVD	r ²
1	157.30	153,149	2.02	0.16	157.30	154,106	2.01	0.13	157.27	126,049	2.02	0.14
2	136.48	123,101	2.01	0.16	136.48	116,309	2.01	0.14	136.48	119,854	2.01	0.13
3	120.01	117,444	2.01	0.17	119.95	111,169	2.01	0.12	120.01	107,945	2.01	0.13
4	120.68	107,964	2.01	0.17	120.68	114,176	2.01	0.15	120.68	115,094	2.01	0.14
5	118.95	98,538	2.00	0.17	118.89	97,675	1.99	0.14	118.89	99,792	2.00	0.14
6	117.63	112,105	2.00	0.17	117.63	100,322	2.01	0.13	117.63	99,134	2.01	0.14
7	108.27	93,579	2.01	0.16	108.37	92,316	2.00	0.14	108.32	95,589	2.00	0.15
8	112.59	114,178	2.02	0.16	112.59	123,692	2.01	0.14	112.59	107,964	2.01	0.14
9	91.54	89,185	2.01	0.15	91.54	91,197	2.01	0.12	91.54	77,603	2.01	0.15
10	100.96	92,473	2.00	0.17	100.86	98,792	2.01	0.13	100.81	93,872	2.00	0.14
11	106.22	102,184	2.02	0.17	106.22	104,533	2.01	0.12	106.22	89,106	2.02	0.13
12	87.25	65,467	2.00	0.16	87.25	78,944	1.99	0.15	87.11	67,010	1.99	0.15
13	83.02	68,896	2.01	0.16	83.02	76,109	2.00	0.13	83.02	73,582	2.01	0.15
14	94.57	54,274	2.01	0.18	94.65	74,554	2.00	0.14	94.57	70,072	2.01	0.15
15	81.90	74,300	2.01	0.15	81.90	63,033	2.01	0.14	81.90	71,377	2.02	0.15
16	79.35	57,940	1.99	0.17	79.35	78,310	2.01	0.15	79.29	61,449	2.00	0.14
17	71.11	62,073	2.01	0.14	71.11	57,673	2.00	0.14	71.11	54,127	2.00	0.15
18	67.18	54,725	2.00	0.13	67.18	58,515	2.00	0.13	67.18	52,910	2.00	0.14
19	62.46	63,099	2.00	0.13	62.51	59,766	2.00	0.12	62.46	55,760	2.00	0.13
20	71.50	69,327	2.00	0.15	71.50	70,248	1.99	0.12	71.78	61,053	1.99	0.14
21	69.23	73,302	2.01	0.16	69.39	74,256	2.01	0.14	69.39	59,303	2.01	0.12
22	60.19	51,763	1.99	0.16	60.19	55,320	2.00	0.12	60.15	50,848	2.01	0.15
23	48.75	46,507	1.99	0.14	48.79	43,531	1.99	0.12	48.75	41,297	2.00	0.14
24	62.18	57,741	2.00	0.16	62.18	66,226	2.00	0.12	62.18	50,318	2.00	0.16
25	42.84	42,698	1.99	0.13	42.84	38,770	2.00	0.13	42.84	39,332	2.00	0.10
26	50.99	36,971	2.02	0.18	50.83	34,661	2.00	0.11	51.36	42,379	2.00	0.13
27	44.59	46,510	1.99	0.16	44.59	39,292	1.98	0.14	44.59	36,174	1.99	0.13
28	44.60	38,663	1.99	0.16	44.63	42,412	1.99	0.12	44.60	38,257	2.00	0.13
29	51.31	40,669	1.99	0.17	51.31	41,484	1.99	0.11	51.31	39,024	1.99	0.12
Overall	2463.64	2,208,825	2.00	0.16	2463.71	2,257,391	2.00	0.13	2464.00	2,096,274	2.00	0.14

Table 4: Effective population size (N_e) across generations of Korean native black goat strains

Generations ago	Dangjin				Jangsu				Tongyeong			
	N_e	Distance (Kb)	r^2	r^2 S.D.	N_e	Distance (Kb)	r^2	r^2 S.D.	N_e	Distance (Kb)	r^2	r^2 S.D.
13	47	3749.1	0.126	0.158	59	3749.1	0.103	0.136	56	3749.2	0.109	0.145
15	51	3273.3	0.131	0.164	64	3273.1	0.108	0.143	61	3273.0	0.113	0.150
17	56	2844.1	0.138	0.171	70	2844.4	0.113	0.148	66	2844.1	0.119	0.157
20	61	2459.8	0.144	0.177	77	2459.8	0.118	0.154	73	2459.9	0.124	0.162
23	68	2116.5	0.150	0.182	86	2116.5	0.122	0.159	81	2116.5	0.129	0.167
27	75	1811.3	0.156	0.190	96	1811.3	0.127	0.163	90	1811.3	0.134	0.173
32	85	1541.2	0.161	0.194	107	1541.2	0.132	0.169	100	1541.2	0.140	0.178
38	95	1303.5	0.168	0.200	121	1303.4	0.138	0.175	114	1303.4	0.145	0.182
45	108	1095.3	0.175	0.207	138	1095.4	0.143	0.180	129	1095.4	0.151	0.187
54	125	914.3	0.180	0.210	157	914.3	0.149	0.185	149	914.3	0.156	0.192
66	146	758.0	0.185	0.215	180	757.9	0.155	0.191	169	758.0	0.164	0.198
80	170	623.7	0.192	0.220	207	623.7	0.162	0.197	197	623.9	0.170	0.203
98	199	509.7	0.198	0.226	244	509.7	0.168	0.202	229	509.7	0.177	0.207
121	231	413.4	0.208	0.232	284	413.5	0.176	0.208	266	413.5	0.185	0.215
150	282	333.3	0.210	0.234	333	333.4	0.184	0.215	320	333.3	0.190	0.220
187	333	267.1	0.220	0.241	401	267.1	0.189	0.219	380	267.1	0.198	0.225
234	408	213.3	0.224	0.243	476	213.3	0.198	0.225	454	213.3	0.205	0.230
294	478	170.2	0.235	0.253	573	170.2	0.204	0.227	549	170.3	0.211	0.233
367	591	136.2	0.237	0.251	681	136.3	0.212	0.235	655	136.4	0.219	0.238
454	706	110.2	0.243	0.256	800	110.2	0.221	0.241	786	110.2	0.224	0.241
553	836	90.3	0.249	0.260	957	90.3	0.224	0.245	904	90.3	0.235	0.247
658	926	76.0	0.262	0.270	1048	76.0	0.239	0.251	1046	75.9	0.239	0.249

S.D., standard deviation



Fig. 1: Distribution of the Korean native black goat strains and the regions from which the genomic resources were collected. DJ, Dangjin strain; JS, Jangsu strain; TY, Tongyeong strain

markers was 2.0 Mb. The average LD was 0.16, 0.14 and 0.13 for the Dangjin, Jangsu, and Tongyeong strains, respectively.

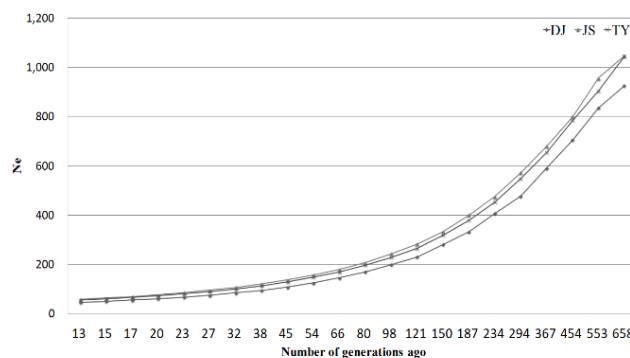


Fig. 2: Effective population size in each strain. DJ, Dangjin strain; JS, Jangsu strain; TY, Tongyeong strain

Effective population size

The effective population size for each generation in each strain is shown in Table 4 and Fig. 2. The effective population size was 47, 59, and 56 for the Dangjin, Jangsu, and Tongyeong strains, respectively. These differences could be due to inbreeding conducted to maintain the genetic resource at 20% of that approximately 100 generations ago. Only the effective population size of the Dangjin strain was smaller than 50, as established by the FAO (2002) for genetic diversity.

Discussion

To prevent inbreeding, the FAO recommends maintaining the effective population size over 50 individuals (FAO 2000; Melka and Schenkel 2010). Therefore, in the present

study, we estimated the genetic characteristics, effective population size, and linkage disequilibrium (LD) using single nucleotide polymorphism (SNP) information for each of the three Korean native black goat strains (Dangjin, Tongyeong and Jangsu). Visser *et al.* (2016), using the same Illumina Goat SNP 50k Chip, showed that the ratio of genes after QC in goat populations from South Africa, France, Argentina and Angora was 15.7, 12.4 and 11.8%, respectively. A similar trend was observed in the present study—the ratio of the removed genes was 14.7, 13.0 and 17.5% for the Dangjin, Jangsu and Tongyeong strains, respectively. The size of LD can reflect the evolutionary history of a population with its ancestor, selection pressures, and phylogenetic relationships. It can also measure genetic diversity within and between strains (McRae *et al.* 2002) and can be used for mapping quantitative trait loci (QTL) (fine mapping) that can increase the accuracy of genomic information (Hayes *et al.* 2003). These values are similar to those of Canada Alpine strains reported by Brito *et al.* (2015) but 0.11 higher than the LD size reported by Visser *et al.* (2016). This difference could be due to the breeding of goat strains with close blood relatives to preserve the genetic resource of Korean native black goat used in the present study. Effective population size can be used to identify the cause of genetic composition change. For example, inbreeding to maintain the characteristics of a breed can increase homozygosity, which eliminates one allele and decreases genetic diversity, thereby decreasing breeding capacity and survival rate (Thompson *et al.* 2000). Therefore, the effective population size represents the minimum size required to maintain a population. Therefore, the selection and breeding methods of Korean native black goat should be examined to enable the exchange of genetic resources between strains to preserve their genetic diversity and increase their productivity.

Conclusion

We estimated the LD value and effective population size of three strains of Korean native black goat, namely the Dangjin, Jangsu, and Tongyeong strains. The average LD of the three strains was 0.13 and their population size was close to that reported by the FAO for genetic diversity (*i.e.*, 50), and only Dangjin showed a value lower than 50. These values could be due to the high level of inbreeding for generating populations to preserve the Korean native black goat genetic resource. Minimum introduction of alien genes and reduced inbreeding, as well as the examination of selection and breeding methods for each strain, should be followed to preserve and improve the productivity of this species.

Acknowledgments

This work was supported by the Cooperative Research Program for Agriculture Science & Technology

Development [grant number PJ01431501] and the Fellowship Program of the National Institute of Animal Science, Rural Development Administration, Republic of Korea. The authors declare that there are no conflicts of interest.

Author Contributions

Kwan-Woo Kim, Jinwook Lee, Sung-Soo Lee, Seungchang Kim and Sang-Hoon Lee carried out the design and data analysis. Hyun Tae Lim and Yousam Kim conducted the experiments and literature search. Kwan-Woo Kim and Sang-Hoon Lee performed wrote the manuscript and review. All authors have read and approved the content of the manuscript.

References

- Amos W, A Balmford (2001). When does conservation genetics matter? *Heredity* 87:257–265
- Barbato M, P Orozco-terWengel, M Tapio, MW Bruford (2015). SNeP: A tool to estimate trends in recent effective population size trajectories using genome-wide SNP data. *Front Genet* 6; Article 109
- Brito LF, M Jafarikia, DA Grossi, JW Kijas, LR Porto-Neto, RV Ventura, M Salgorzaei, FS Schenkel (2015). Characterization of linkage disequilibrium, consistency of gametic phase and admixture in Australian and Canadian goats. *BMC Genet* 16; Article 67
- Chang CC, CC Chow, LC Tellier, S Vattikuti, SM Purcell, JJ Lee (2015). Second-generation PLINK: Rising to the challenge of larger and richer datasets. *GigaScience* 4; Article 7
- Corbin LJ, AY Li, SC Bishop, JA Woolliams (2012). Estimation of historical effective population size using linkage disequilibria with marker data. *J Anim Breed Genet* 129:257–270
- FAO-Food and Agriculture Organization of the United Nations (2000). *Secondary Guidelines for Development of Farm Animal Genetic Resources Management Plans*. Management of Small Populations at Risk. FAO, Rome, Italy
- Fernández J, B Villanueva, R Pong-Wong, MA Toro (2005). Efficiency of the use of pedigree and molecular marker information in conservation programs. *Genetics* 170:1313–1321
- Hayes BJ (2007). QTL mapping, MAS, and genomic selection. *In: A short-course organized by Animal Breeding & Genetics Department of Animal Science*. Iowa State University, 4–8 June, 2007. Available at <https://www.ans.iastate.edu/files/page/files/notes.pdf>
- Hayes BJ, PE Visscher, H McPartlan, ME Goddard (2003). Novel multilocus measure of linkage disequilibrium to estimate past effective population size. *Genomics Res* 13:635–643
- Hill WG, A Robertson (1968). Linkage disequilibrium in finite populations. *Theor Appl Genet* 38:226–231
- Kim JH, CY Cho, SB Choi, YM Cho, SH Yeon, BS Yang (2001). mtDNA diversity and phylogenetic analysis of Korean native goats. *J Life Sci* 21:1329–1335
- Lee SH, JW Lee, DY Jeon, S Kim, KW Kim (2019). Morphological characteristics and growth performance of Korean native black goats. *J Kor Acad Industr Cooperat Soc* 20:149–155
- Lee SS, SW Kim, KW Kim, HY Cho, CY Cho, SH Yeon, TJ Choi (2016). Growth curve parameters for body weight by sex in Korean native goat. *Ann Anim Resour Sci* 27:152–158
- Lewontin RC (1964). The interaction of selection and linkage. I. General considerations; heterotic models. *Genetics* 49:49–67
- McRae AF, JC McEwan, KG Dodds, T Wilson, AM Crawford, J Slate (2002). Linkage disequilibrium in domestic sheep. *Genetics* 160:1113–1122
- Melka MG, F Schenkel (2010). Analysis of genetic diversity in four Canadian swine breeds using pedigree data. *Can J Anim Sci* 90:331–340

- Ohta T, M Kimura (1971). Linkage disequilibrium between two segregating nucleotide sites under the steady flux of mutations in a finite population. *Genetics* 68:571–580
- Suh S, M Byun, YS Kim, MJ Kim, SB Choi, YG Ko, DH Kim, HT Lim, JH Kim (2012). Analysis of genetic diversity and relationships of Korean native goat populations by microsatellite markers. *J Life Sci* 22:1493–1499
- Sved JA (1971). Linkage disequilibrium and homozygosity of chromosome segments in finite populations. *Theor Pop Biol* 2:125–141
- Thompson JR, RW Everett, NL Hammerschmidt (2000). Effects of inbreeding on production and survival in Holsteins. *J Dairy Sci* 83:1856–1864
- Uimari P, M Tapio (2011). Extent of linkage disequilibrium and effective population size in Finnish Landrace and Finnish Yorkshire pig breeds. *J Anim Sci* 80:609–614
- Visser C, SF Lashmar, EV Marle-Köster, MA Poli, D Allain (2016). Genetic diversity and population structure in South African, French and Argentinian angora goats from genome-wide SNP data. *PLoS One* 11; Article e0154353
- Woolliams JA, J Bijma (2000). Predicting rates of inbreeding in populations undergoing selection. *Genetics* 154:1851–1864
- Zenger KR, MS Khatkar, JA Cavanagh, RJ Hawken, HW Raadsma (2007). Genome wide genetic diversity of Holstein Friesian cattle reveals new insights into Australian and global population variability, including impact of selection. *Anim Genet* 38:7–14