Dynamic comparison of genetic diversity in a Small Tail Han sheep population using meta-analysis

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ABSTRACT. The aim of this research was to identify the dynamic diversity of Small Tail Han sheep in its main producing areas between different years, and provide a basis for a breeding and genetic resources conservation strategy. For this purpose, 15 microsatellites were genotyped for Small Tail Han Sheep sampled in 2014 from Heze, China, and a comparative analysis of these data with those from a previous study was undertaken using meta-analysis. The results reveal that inbreeding has caused a reduction in diversity of Small Tail Han Sheep from 2008 to 2014. Overall,

our results are helpful in understanding the dynamic change in diversity, as well as providing information for a conservation strategy for this population.

Key words: Small Tail Han sheep; Diversity; Microsatellite; Inbreeding; Genetic resource conservation

INTRODUCTION

Sheep (*Ovis aries*) is a predominantly domestic animal, and it not only provides meat, but also milk, wool, and fur. Currently, a wide array of sheep breeds with abundant phenotypic diversity exists as a result of domestication and selection. However, commercial lines and industrialized livestock production systems have spread across continents, resulting in a decrease of large indigenous sheep populations in comparison to some commercial breeds. Therefore, it seems particularly important to build a complete monitoring system of conservation genetic resources for sheep. Small Tail Han sheep is an indigenous sheep genetic resource in the reaches of the Yellow River in China, where they live in an alpine climate (between 30 and 60 m). It is a commercially important domestic species, characterized with a middle to large body size and preeminent fecundity (China National Commission of Animal Genetic Resources, 2011).

In the past, many studies have investigated functional candidate genes in Small Tail Han Sheep, such as during prolificacy, including bone morphogenetic protein 15 (BMP15; Chu et al., 2005), BMP4 (Chu et al., 2008), blood protein (Yang and Luo, 2004), gonadotropin releasing hormone receptor (GnRHR; Sun et al., 2008), polymorphism of serum esterase (Yang and Li, 2009), Booroola (FecB), and Inverdale (FecXI) mutations (Davis et al., 2006). Furthermore, the association of FecB (Chu et al., 2007), insulin-like factor1 gene (IGF1; He et al., 2012), follicle-stimulating hormone receptor (FSHR; Chu et al., 2012a), luteinizing hormone receptor (LHR; Jia et al., 2007), inhibin βB (Chu et al., 2011) and Kisspeptin-1 (KISS-1) and G protein coupled receptor 54 (GPR54; Chu et al., 2012b) with litter size have been investigated. To date, with the development of biotechnology, a large number of studies of Small Tail Han sheep have been undertaken using next generation sequencing technology, such as transcriptome analysis between Small Tail Han sheep and the Surabaya fur sheep (Miao and Luo, 2013), and comparative muscle transcriptome (Zhang et al., 2013) or miRNA (Miao et al., 2015) in Dorper and Small Tail Han sheep using high-throughput RNA sequencing.

With regard to the estimated diversity of sheep, recently, a series of reports were published worldwide (e.g., Arora et al., 2011; Paiva et al., 2011; Crispim et al., 2013; Ferreira et al., 2014; Yilmaz et al., 2014; Pons et al., 2015), and particularly in China (e.g., Sun et al., 2007; Zhong et al., 2011). However, most studies focused on diversity estimation and population structure and no study concentrated on dynamic change or group status. It is meaningless and less or without contribution to genetic protection strategy for indigenous sheep. The aim of this research was to identify the dynamic development of diversity and provide a basis for a breeding and genetic resources conservation strategy in Small Tail Han sheep in its main producing areas.

MATERIAL AND METHODS

Sample collection and genotyping

We genotyped 32 unrelated Small Tail Han sheep individuals, which were sampled from the concordant region as previously reported by Zhong et al. (2011) in its main producing area

of Heze, China in September 2014. Individuals were genotyped at fifteen previously developed microsatellite loci (Kappes et al., 1997; Maddox et al., 2001; FAO, 2011), which have been suggested for biodiversity studies in sheep (Table 1). Approximately 1 to 2 µL PCR product was diluted with 10 µL of autoclaved distilled water for use in DNA genotyping. Diluted products (2 µL) were added to 7.75 µL Hi Di™ formamide and 0.25 µL Gene Scan-500 LIZ™. The mixtures were heated at 94°C for 5 min and then immediately chilled on ice for 2 min. Genotyping was performed on a Genetic Analyzer 3130 xl (AB Applied Biosystems).

Table 1. Microsatellite primers used to genotype Small Tail Han sheep.

Name	Direction	Primer sequence (5' to 3')
HSC	Forward	CTGCCAATGCAGAGACACAAGA
	Reverse	GTCTGTCTCCTGTCTTGTCATC
McM42	Forward	CATCTTTCAAAAGAACTCCGAAAGTG
	Reverse	CTTGGAATCCTTCCTAACTTTCGG
MCM527	Forward	GTCCATTGCCTCAAATCAATTC
	Reverse	AAACCACTTGACTACTCCCCAA
OarAE129	Forward	AATCCAGTGTGTGAAAGACTAATCCAG
	Reverse	GTAGATCAAGATATAGAATATTTTTCAACACC
OarFCB11	Forward	GCAAGCAGGTTCTTTACCACTAGCACC
	Reverse	GGACTGAACTCACAAGTTGATATATCTATCAC
ILSTS005	Forward	GGAAGCAATGAAATCTATAGCC
	Reverse	TGTTCTGTGAGTTTGTAAGC
OarFCB129	Forward	GCGACTTAGCAGCAGCAGCATCC
	Reverse	CATCAAGAGATGAATGAGTAAAGAAGATG
OarFCB20	Forward	AAATGTGTTTAAGATTCCATACAGTG
	Reverse	GGAAAACCCCCATATATACCTATAC
MAF209	Forward	GATCACAAAAAGTTGGATACAACCGTG
	Reverse	TCATGCACTTAAGTATGTAGGATGCTG
OarFCB304	Forward	CCCTAGGAGCTTTCAATAAAGAAI,CGG
	Reverse	CGCTGCTGTCAACTGGGTCAGGG
OarJMP29	Forward	GTATACACGTGGACACCGCTTTGTAC
	Reverse	GAAGTGGCAAGATTCAGAGGGGAAG
ILSTS44	Forward	AGTCACCCAAAAGTAACTGG
	Reverse	ACATGTTGTATTCCAAGTGC
MAF65	Forward	AAAGGCCAGAGTATGCAATTAGGAG
	Reverse	CCACTCCTCCTGAGAATATAACATG
ILSTS49	Forward	CAATTTTCTTGTCTCTCCCC
	Reverse	GCTGAATCTTGTCAAACAGG
TGLA53	Forward	GCTTTCAGAAATAGTTTGCATTCA
	Reverse	ATCTTCACATGATATTACAGCAGA

Data from a previous study of Small Tail Han sheep

The genotypes of 48 individuals of Small Tail Han sheep based on 19 microsatellite loci and collected in 2008 was offered by Dr. Zhong (Farm Animal Genetic Resources Exploration and Innovation Key Laboratory of Sichuan province, Sichuan Agricultural University, Chengdu, Sichuan 625014, China; Zhong et al., 2011).

Meta dataset

Of the microsatellite loci used in this study and the previous study (Zhong et al., 2011), there were six markers uniform to both studies (MCM527, ILSTS005, MAF209, OarJMP29, OarAE129, and OarFCB304). Twenty random samples from those collected in 2008 were re-genotyped with the 32 new individuals from 2014 using the six uniform microsatellites to provide insight on the consistency between the two datasets from 2008 and 2014.

Statistical and data analysis

Expected (H_E) and observed (H_O) heterozygosity, mean number of alleles (N_A), and polymorphism information content (PIC) were estimated from the allele frequencies using the Microsatellite Toolkit (Park, 2001). For each locus-population combination of the global data set and population groupings, we used Fisher's exact test with Bonferroni correction to test for possible deviations from Hardy-Weinberg equilibrium (HWE) using GENEPOP 3.4 (Raymond and Rousset, 1995) and Arlequin software 3.5.1.3 (Excoffier and Lischer, 2010).

RESULTS

Estimation of diversity in the 2014 Small Tail Han sheep

In total, 217 alleles were found in the 2014 Small Tail Han sheep population across the 15 microsatellite loci. Across individuals, an average of 14.47 alleles per locus was observed, ranging from 9 in MCM527, ILSTS005, and MAF65 to 22 in ILSTS44.

Across individuals, mean H_O and H_E for all loci across the population were 0.603 (0.281 to 0.844) and 0.851 (0.751 to 0.927), respectively (Table 2). The average PIC across loci was 0.821 and ranged from 0.713 (ILSTS005) to 0.907 (OarFCB129). Across loci, N_A was 14.467 ± 4.291, H_O was 0.601 ± 0.023, and H_E was 0.851 ± 0.016.

Most loci in the 2014 Small Tail Han sheep population, except MCM527, deviated from HWE (Table 2). The inbreeding coefficient (F_{IS}) for the 2014 population was also found to be significant (F_{IS} = 0.295, P = 0.0033, Fisher's test).

Table 2. Diversity and polymorphism information content (PIC) of the 2014 Small Tail Han sheep population based on fifteen microsatellite loci.

Locus	H_O	H_E	PIC	F_{IS}	P value (F_{IS})
HSC#	0.3333	0.9271	0.9051	0.644	0.0033*
McM42#	0.75	0.811	0.7727	0.076	0.2467
MCM527#	0.5909	0.8594	0.8208	0.318	0.0100
OarAE129#	0.500	0.7881	0.7557	0.370	0.0033*
OarFCB11#	0.6875	0.9077	0.8846	0.246	0.0033*
ILSTS005#	0.3462	0.7511	0.7134	0.544	0.0033*
OarFCB129#	0.7813	0.9271	0.9066	0.159	0.0067
OarFCB20#	0.7188	0.9112	0.8882	0.214	0.0133
MAF209#	0.6452	0.7779	0.7335	0.173	0.0267
OarFCB304#	0.4516	0.825	0.799	0.457	0.0033*
OarJMP29#	0.75	0.8259	0.8015	0.093	0.0900
ILSTS44#	0.7188	0.9142	0.8925	0.216	0.0033*
MAF65#	0.2813	0.8041	0.7617	0.654	0.0033*
ILSTS49#	0.6452	0.8038	0.7707	0.200	0.0133
TGLA53	0.8438	0.9256	0.9049	0.090	0.0600
mean	0.603	0.851	0.821	0.295	0.0033*

Indicative adjusted nominal level (5%) for the table is 0.00333; *denotes significant difference; #indicates which loci deviated from Hardy-Weinberg equilibrium; H_O, observed heterozygosity; H_E, expected heterozygosity; F_{IS}, inbreeding coefficient.

Re-estimation of diversity in 2008 Small Tail Han sheep

In total, 157 alleles were observed in the 2008 Small Tail Han sheep population across 15 microsatellite loci. Across individuals, an average of 8.26 alleles per locus was observed, ranging

from 4 in SRCRSP5 to 16 in DYMS1.

Across individuals, mean H_O and H_E for all loci across the population were 0.664 (0.381 to 0.917) and 0.702 (0.489 to 0.866), respectively (Table 3). PIC across loci was 0.821 and ranged from 0.456 (OarCP38) to 0.842 (DYMS1). Across loci, N_A was 8.26 ± 3.36, H_O was 0.664 ± 0.016, and H_E was 0.702 ± 0.026. Only three loci deviated from HWE in the 2008 population, OarCP38, SRCRSP5, and OarAE129. F_{IS} for the 2008 population was 0.054 and was not significant (Table 3).

Table 3. Diversity and polymorphism information content (PIC) of the 2008 Small Tail Han sheep population based on fifteen microsatellite loci.

Locus	H_O	H_E	PIC	F_{IS}	P value (F_{IS})
OarCP38#	0.4167	0.490	0.4561	0.150	0.0737
SRCRSP9	0.6222	0.574	0.5224	-0.085	0.8316
MAF214	0.8511	0.828	0.7975	-0.028	0.7658
OarCP34	0.7708	0.745	0.6955	-0.035	0.7211
OarVH72	0.6875	0.721	0.681	0.047	0.3000
OarFCB128	0.6667	0.757	0.7213	0.120	0.0421
OarHH47	0.8298	0.850	0.8249	0.024	0.4237
MCM527	0.6875	0.762	0.7162	0.099	0.1237
ILSTS5	0.5625	0.537	0.4972	-0.049	0.7421
SRCRSP5#	0.381	0.605	0.5196	0.373	0.0079
MAF209	0.8947	0.8547	0.8257	-0.047	0.8289
OarJMP29	0.6364	0.7074	0.6676	0.101	0.1421
OarFCB226	0.8511	0.7193	0.6678	-0.186	0.9921
ILSTS28#	0.5227	0.7827	0.7469	0.335	0.0026*
BM8125	0.4524	0.5364	0.4939	0.158	0.0974
DYMS1	0.9167	0.8658	0.8422	-0.059	0.9211
ILSTS11	0.6250	0.6612	0.616	0.055	0.2868
OarAE129#	0.4783	0.6061	0.5589	0.213	0.0237
OarFCB304	0.766	0.7282	0.7002	-0.052	0.8605
mean	0.664	0.702	0.661	0.054	0.0053

Indicative adjusted nominal level (5%) for one table is 0.00263; *denotes significant difference; #indicates which loci deviated from Hardy-Weinberg equilibrium; H_O, observed heterozygosity; H_E, expected heterozygosity; F_{IS}, inbreeding coefficient.

Comparison of the dynamic change and group status of Small Tail Han sheep between 2008 and 2014 using six microsatellite loci

In total, 49 and 50 alleles were found in the 2014 and 2008 Small Tail Han sheep populations across 6 microsatellite loci, respectively. For the 2014 population, an average of 8.2 alleles per locus was observed, ranging from 6 in OarAE129 to 10 in OarJMP29. For the 2008 population, an average of 8.3 alleles per locus was observed, ranging from 5 in OarAE129 to 14 in OarFCB304.

Across individuals, the mean H_O and H_E for all loci across the population was 0.651 (0.537 to 0.855) and 0.669 (0.533 to 0.784) for the 2014 population and 0.671 (0.478 to 0.895) and 0.700 (0.537 to 0.855) for the 2008 population, respectively (Table 4). In addition, across loci, N_A = 8.17 ± 1.47, H_O = 0.651 ± 0.034, and H_E = 0.700 ± 0.038 for the 2014 population, and N_A = 8.33 ± 3.27, H_O = 0.671 ± 0.028, and H_E = 0.699 ± 0.046 for the 2008 population. F_{IS} was 0.071 and 0.041 for the 2014 and 2008 populations, respectively, and was not significant (Table 5).

Table 4. Diversity and polymorphism information content (PIC) of the 2008 and 2014 populations of Small Han sheep based on six uniform microsatellite loci.

Locus	H_E		H_O		PIC	
	2014	2008	2014	2008	2014	2008
MCM527	0.765	0.762	0.813	0.688	0.730	0.716
ILSTS005	0.701	0.537	0.656	0.563	0.647	0.497
MAF209	0.754	0.855	0.688	0.895	0.704	0.826
OarJMP29	0.784	0.707	0.719	0.636	0.741	0.668
OarAE129	0.533	0.606	0.531	0.478	0.485	0.559
OarFCB304	0.664	0.728	0.500	0.766	0.616	0.700

H_O, observed heterozygosity; H_E, expected heterozygosity.

Table 5. Comparative diversity between the 2008 and 2014 populations of Small Tail Han sheep based on six microsatellite loci.

Sampled Year	Code	Sample Size	H_O	H_E	N_A	F_{IS}	P value (F_{IS})
2014	SIH	32	0.651 ± 0.034	0.700 ± 0.038	8.17 ± 1.47	0.071	0.0333
2008	SBW	48	0.671 ± 0.029	0.699 ± 0.046	8.33 ± 3.27	0.041	0.0708

Indicative adjusted nominal level (5%) for the table is 0.00417; *denotes significant difference; #indicates which loci deviated from Hardy-Weinberg equilibrium; H_O, observed heterozygosity; H_E, expected heterozygosity; N_A, mean number of alleles; F_{IS}, inbreeding coefficient.

DISCUSSION

The majority of the results obtained in the current study are consistent with those from the previous study of Small Tail Han sheep undertaken in 2008 (H_O = 0.661 ± 0.014, H_E = 0.703 ± 0.024, and N_A = 7.82 ± 2.85; Zhong et al., 2011). However, there are a number of differences. First, the 2008 population has a greater number of alleles than the 2014 population, and this is evident from looking at the results for each locus, e.g., OarFCB304 has 14 alleles in the 2008 population but only 8 alleles in the 2014 population. Second, only three loci (OarCP38, SRCRSP5, and OarAE129) deviated from HWE in the 2008 population, and there was only a small difference between H_E and H_O for each locus in this population, which means the Small Tail Han sheep in Heze, China was in a neutral and good risk status in 2008. However, in the Small Tail Han sheep population sampled in 2014, nearly all microsatellite loci deviated from HWE, except TGLA53. Thirdly, only one locus (ILSTS28) had a significant inbreeding coefficient in the 2008 population; however, in the 2014 population, more than half (8) of the microsatellite loci had significant and high F_{IS} values. Finally, comparing the diversity in Small Tail Han sheep between 2008 and 2014 using six uniform loci revealed a smaller divergence between H_E and H_O in the 2008 population, and a larger difference between H_E and H_O in the 2014 population. These results indicate a decrease in diversity in the Small Tail Han sheep population from Heze between 2008 and 2014.

In short, from the comparative results of this study, it evident that inbreeding is reducing the diversity in the Small Tail Han sheep population at this moment in time. In addition, inbreeding results in homozygosity and this can increase the chances of offspring being affected by recessive or deleterious traits (Nabulsi et al., 2003). This generally leads to decreased biological fitness of a population (inbreeding depression) (Jiménez et al., 1994), which is its ability to survive and reproduce. Therefore, the conservation status of the genetic resources of the Small Tail Han sheep population from Heze is not optimistic.

Conflicts of interest

The authors declare no conflict of interest.

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