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Dominant-genotype Frequency Analysis of Economic Traits Related to SNP Candidate Markers in Three Yak Populations

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ABSTRACT

Background: Yak as a unique domestic animal that has extremely important social value and influence on the local culture and economy in the Qinghai-Tibet Plateau. The current study aimed to evaluate the genotype distribution of a series of economic traits (growth, meat quality and lactation) related to single nucleotide polymorphisms (SNP) in three Tibetan yak populations.

Methods: A total of 238 yaks from three populations [Sibu (SB), Chawula (CWL) and Jiali (JL) yaks] including 34 SB, 104 JL and 100 CWL yak individuals were collected. All samples were genotyped for 12 SNP markers by using SNaPshot technology.

Result: All loci had abundant polymorphisms in the three populations, except for the Hesx1_G618C locus. The dominant growth-related genotype was MyoD1_C1710T (C/T), which had the highest frequency in the three Tibetan yak populations. However, the growth-related dominant genotypes at UCP2_T1499C (C/T) and CYP4A11_G4806A (G/A) loci were rare genotypes in the three Tibetan yak populations. Results of Hardy-Weinberg equilibrium (HWE) analysis showed that all sites did not deviate from the HWE within the population. This finding indicated that these populations belonged to a natural one without having been subjected to artificial selection on economic traits. Overall, this study provided valuable reference for the future molecular breeding of yak based on the genotype distribution of economic-trait candidate markers in three yak populations in Tibet.

Key words: Economic traits, Genotype, SNP, Tibet yak.

INTRODUCTION

Domestic yak (*Bos grunniens*) has perfect plateau adaptability and is one of the mammals living in the Qinghai-Tibet Plateau, which has the highest altitude (>3000 m) in the world. This animal provides milk, meat, wool, labor, fuel and other daily necessities for local herdsmen and is thus an important life and economic resource (Nie *et al*., 2020).

The molecular markers (MMs) of economic traits in cattle and buffalo have been largely identified to be related to their growth traits and milk production (Ujan *et al*., 2011; Lyu *et al*., 2020; El-Komy *et al*., 2021). Conversely, only a few candidate genes related to the economic traits of yak have been reported. For example, a single nucleotide polymorphism (SNP; G1069C) from MC4R is significantly (P<0.01) correlated with the body weight of 18-month-old Maiwa yak (Cai *et al*., 2015). A new SNP (C19913T) in exon 7 of the LPL gene is reportedly responsible for the Phe-to-Ser substitution of amino acids, which have significant effects on the body weight (P<0.01), carcass body weight (P<0.05), eye area and visceral fat weight of yak (Ding *et al*., 2012).

At present, the yak population in the Tibet Plateau of China subsists mostly on extensive grazing and breeding methods. Considering the slow technological development in the region, the production level of yak breeding is low. Therefore, screening the frequency of dominant genotypes of economic-trait-related markers in Tibetan yak populations is needed to assess the breeding potential of these populations for future Tibetan yak breeding. In the present study, we aimed to identify the dominant-genotype distribution of 12 previously known MMs in three Tibetan yak populations and to evaluate the breeding potential for genetic improvement.

MATERIALS AND METHODS

Animals and samples

A total of 238 yak individuals from three populations were collected, including 34 Sibu (SB), 104 Jiali (JL) and 100 Cawula (CWL) yak individuals (Table 1). Venous blood (5 mL) was collected from each animal and genomic DNA was

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extracted using a PureLink Genomic DNA Mini Kit (Shanghai, China). Nano Drop 2000 was used to determine DNA concentration and quality.

Primers and PCR amplification

PCR amplification primers were designed using Primer3Plus (http://www.primer3plus.com/) according to the sequence information and previous reports of 12 SNP markers (Table 2).

The 10 μL PCR amplification system included 5 μL of 2×Taq PCR Mix, 1 μL of Primer Mix, 1 μL of DNA (20 ng/μL) and 3 μL of ddH_2O. The PCR amplification-reaction program was as follows: 95°C pre-denaturation for 5 min; 40 cycles each of 94°C denaturation for 30 s, 52°C annealing for 30 s and 72°C extension for 80 s and 72°C extension for 10 min. The PCR product genotyped using SNaPshot technology was referenced as conducted in previous studies (Wang *et al*., 2021; Cheng *et al*., 2020).

Data analysis

A Microsatellite Toolkit (Park, 2012) was used to analyze genotype frequency and genetic-diversity parameters, such as observed heterozygosity (H_O), expected heterozygosity (H_E) and polymorphism information content (PIC). Arlequin 3.5 software (Excoffier and Lischer, 2010) was used for Hardy-Weinberg equilibrium (HWE) analysis.

RESULTS AND DISCUSSION

Results of genetic-diversity parameter analysis (Table 3) showed that the distribution of H_E in the CWL population was 0.000 (Hesx1-G618C and OXGR1-A347G) to 0.4984 (MyoD1-C1710T) and that of H_O ranged from 0.0000 (Hesx1-G618C and OXGR1-A347G) to 0.5400 (CAPN_G-1222A). The PIC of the MyoD1_C1710T locus was the highest (0.373). In the JL population, CAPN_G-1222A had the highest H_E (0.5023) and H_O (0.5098) and CAPN_G-1222A (0.3749) and GHSR_T1387C (0.3731) had the highest PICs. In the SB population, the highest H_E was found in GHSR_T1387C (0.5035) and MyoD1_C1710T (0.4965). MyoD1_C1710T and CAPN_G-1222A had the highest H_O and five sites, namely, ACSL1_A2079T, GHSR-T1387C, MyoD1_C1710T, CAPN_G-1222A and TMEM-18_C1267T, were medium polymorphic (0.25<PIC<0.5). The HWE results further revealed that no loci considerably deviated from the HWE within the population. This finding implied that the genetic diversity of the three yak populations was well maintained and that the three populations had not undergone artificial selection for economic traits.

Table 4 shows the genotype frequencies of 12 SNPs in the three yak populations. The Hesxl gene is known to indirectly affect the growth and development of animals (Kaminski *et al*., 2008). A previous report has found that Hesxl_G-618C and Hesxl_T226C are significantly correlated (P<0.05) with the weight and height of 12-month-old hornless yak (Zhang *et al*., 2019). The present study showed that the Hesxl_G-618C locus was a homozygous G/G type in the three populations and more than 90% of individuals carried the T/T type of the Hesxl_T226C locus. Thus, whether these two markers can be used for the molecular breeding of these three Tibet yaks requires further research.

Myogenic differentiation 1 (MyoD1) from the muscle regulatory factor (MyoD) family is an important transcription factor that regulates skeletal-muscle production (Talbot *et al*., 2016). It can activate muscle-gene transcription, transform non-muscle cells into muscle cells, regulate muscle-cell fusion and promote the differentiation of myoblasts into myotubes, subsequently fusing them into muscle fibers and thus regulating embryonic muscle development (Hodge *et al*., 2019). A large number of genetic variations distributed in the MyoD1 gene region are remarkably related to the growth and meat quality of domestic animals (Liu *et al*., 2008; Ujan *et al*., 2011). Specifically, a SNP (MyoD1_C1710T) on exon 3 of the MyoD1 gene has been identified to be significantly correlated with body-size traits (P<0.05) in Shenzha yak and C/T is the dominant genotype (Huang *et al*., 2019). Herein, we found that the C/T genotype of MyoD1_C1710T had the highest frequency (51.00%-67.64%) within all three yak populations.

Cytochrome P450 4A11 (CYP4A11) can be used to diagnose renal cell carcinoma (Kim *et al*., 2020) and is related to the occurrence of non-alcoholic fatty liver and coronary artery disease (Gao *et al*., 2020). In particular, a recently discovered SNP marker of the CYP4A11 gene (CYP4A11_G4806A) is significantly correlated with weight and tube circumference in Maiwa yak and G/A genotype is significantly higher in these phenotypes than that of individuals with G/G (P<0.05) (Guan *et al*., 2019). In the current study, we found that the CYP4A11_G4806A locus had a high frequency of the G/G genotype (73.53%-85.58%) in the three yak populations, the G/A genotype had a certain proportion of distribution, ranging from 14.42% (JL) to 26.47% (SB). Whether the two SNPs of CYP4A11 can be extensively used as MMs of yak growth traits requires further clarification.

Transmembrane protein 18 (TMEM18) participates in the migration and regulation of neural stem cells *in vivo* and *in vitro* (Jurvansuu *et al*., 2008) and regulates adipocyte differentiation through the nervous system to affect obesity (Gutierrez-Aguilar *et al*., 2011). In previous studies, some

Table 1: Geographic location and sample information of three Tibetan yak populations.

Population	Code	Sample size	Altitude (m)	East longitude (E) and north latitude (N)	Location
Jiali Yak	JL	104	~4500	E 93.23253, N 30.64081	Nagqu Jiali County, Tibet
Sibu Yak	SB	34	~4300	E 91.811043, N 29.674002	Muzugongga County, Tibet
Chawula Yak	CWL	100	~4700	E 92.30327, N32.10784	Neirong County, Tibet

Table 2: PCR amplification and genotyping primers for 12 SNP markers related to the economic traits of yak.

Type	Marker ID	Primer ID	Sequence of primer (5′-3′)
Amplification primers	ACSL1_A2079T	ACSL1_A2079T-F	TTG ATC AGG TGG CAG AGA AC
		ACSL1_A2079T-R	CAA GGC TGA TGA CCA TCA AC
	ACSL1_G2409A	ACSL1_G2409A-F	CGA GCT GTT CCA GTA CTT TC
		ACSL1_G2409A-R	TGC TTG GGA TTG TGA TCC TG
	CAPN_G-1222A	CAPN4_G-1222A-F	GTC CCA AGA CAA GTA TCA GG
		CAPN4_G-1222A-R	TAA GAC TGC GCA TGT GCT TG
	CYP4A11_G4806A	CYP4A11_G4806A-F	GCT ATG GAC AGA CAT ACT GG
		CYP4A11_G4806A-R	ACA AGT GAT GGA CTC TCC AG
	GHSR_T1387C	GHSR_T1387C-F	TTG AGC TAC AAC GTT GTC CC
		GHSR_T1387C-R	GTA GGG CAT ATG CTG TGT AG
	Hesx1_G618C	Hesx1_G618C-F	TAG AGG AGG ACA GAA TCC AG
		Hesx1_G618C-R	CTC AGA TTA AAC ACA GAA AAC
	Hesx1_T226C	Hesx1_T226C-F	CTG TGT TCC ATC GAC GAA AC
		Hesx1_T226C-R	CTC ATG GGT GCA CTT CAT AC
	MyoD1_C1710T	MyoD1_C1710T-F	ACC CCT GCA TAC TAA CCT AC
		MyoD1_C1710T-R	TCA GAG CAC CTG GTA AAT CG
	OXGR1_A347G	OXGR1_A347G-F	ACA TCT TCA AAA TGC GGC CC
		OXGR1_A347G-R	ATG GCC CAT CGC TTT TTG TG
	TMEM_18-C1267T	TMEM_18-C1267T-F	CTG TCT TCT CTC CCA GAA TG
		TMEM_18-C1267T-R	GGA CAC ACA GCA GAA ACA AG
	TMEM_18-C4447T	TMEM_18-C4447T-F	TGG ACA AAC AGC AGT GCA GG
		TMEM_18-C4447T-R	TCC TTC CTG AAA GCA ACA CC
	UCP_T1499C	UCP_T1499C-F	GGC AGA GTT CAT GTA TCT CG
		UCP_T1499C-R	TTG AAG CCA TGC ACC TTG AG
Genotyping primers for single base extension	ACSL1_A2079T	ACSL1_A2079T-E	AGC AAG AAT TCT GAG TGG CT
	ACSL1_G2409A	ACSL1_G2409A-R-E	GAC TGC CAG AGC TGC TTG ACT TCC GGC A
	CAPN_G-1222A	CAPN4_	CTG ACT AGT GTC GAT TTT CGC CCG AAA G
	CYP4A11_G4806A	CYP4A11_G4806A-E	GAC TGA CTG ACT ATC CGC CGG TGC TGG AAC CA
	GHSR_T1387C	GHSR_T1387C-E	ACT GAC TGA CTG ACT GCC CCC TTT ACC AGC TCC CCC
	Hesx1_G618C	Hesx1_G618C-E	ACT GAC TGA CTG ACT ACT AAA CAT GTG GAA TTA TCT TCC A
	Hesx1_T226C	Hesx1_T226C-E	ACT GAC TGA CTG ACT GAC TGA CTA CAC CTG CGG CTC TTC AGG TA
	MyoD1_C1710T	MyoD1_C1710T-E	TGA CTG ACT GAC TGA CTG ACT GAC TGA CTC GAC ACC GCA GCG CTC TTC CC
	OXGR1_A347G	OXGR1_A347G-E	ACT GAC TGA CTG ACT GAC TGA CTG ACT GAC TAT GAC AAA GTA GCG GAA GAT G
	TMEM_18-C1267T	TMEM-18_C1267T-E	CTG ACT GAC TGA CTG ACT GAC TGA CTG ACT GAC TGA CTT TCA CAT GCC GTC TTC TCT GC
	TMEM_18-C4447T	TMEM-18_C4447T-E	TGA CTG ACT GAC TGA CTG ACT GAC TGA CTG ACT GAC TGA CTG GGT GGT GGG TCT GCC CAG GC
	UCP_T1499C	UCP_T1499C-E	CTG ACT GAC TGA CTG ACT GAC TGA CTG ACT GAC TGA CTG ACT TCT GAG TCG TTT TGC CCA TGT AG

Table 3: Genetic diversity parameters and Hardy Weinberg equilibrium analysis of 12 SNP markers in three Tibetan yak populations.

Marker	CWL				JL				SB			
	H_E	H_O	PIC	*P*-value	H_E	H_O	PIC	*P*-value	H_E	H_O	PIC	*P*-value
ACSL1-A2079T	0.2420	0.2400	0.2118	1.00000	0.2748	0.2885	0.2361	1.00000	0.3139	0.3235	0.2614	1.00000
ACSL1-G2409A	0.3449	0.3600	0.2843	0.77561	0.2939	0.3173	0.2497	0.51911	0.1383	0.1471	0.127	1.00000
CAPN_G-1222A	0.4782	0.5400	0.3626	0.21031	0.5023	0.5098	0.3749	1.00000	0.4860	0.5000	0.3642	1.00000
CYP4A11-G4806A	0.1646	0.1800	0.1504	1.00000	0.1345	0.1442	0.1249	1.00000	0.2331	0.2647	0.2033	1.00000
GHSR-T1387C	0.4374	0.4600	0.3405	0.65136	0.4987	0.4327	0.3731	0.23505	0.5035	0.2647	0.373	0.00687
Hesx1-G618C	0.0000	0.0000	0.0000	-	0.0000	0.0000	0.0000	-	0.0000	0.0000	0.0000	-
Hesx1-T226C	0.0955	0.0800	0.0905	0.21068	0.0654	0.0673	0.0629	1.00000	0.0579	0.0588	0.0555	1.00000
MyoD1-C1710T	0.4984	0.5100	0.373	0.84236	0.489	0.5096	0.3682	0.69024	0.4965	0.6765	0.3695	0.0408
OXGR1-A347G	0.0000	0.0000	0.0000	-	0.0000	0.0000	0.0000	-	0.0000	0.0000	0.0000	-.
TMEM-18-C1267T	0.2492	0.2300	0.2172	0.42411	0.2411	0.2788	0.2112	0.20965	0.3490	0.2059	0.2847	0.02999
TMEM-18-C4447T	0.2633	0.2900	0.2276	0.45361	0.2411	0.2019	0.2112	0.10502	0.2950	0.2941	0.2484	1.00000
UCP-T1499C	0.2123	0.2000	0.1889	0.62731	0.1093	0.0962	0.1028	0.28541	0.0856	0.0882	0.0808	1.00000

mutations from TMEM18 gene have been confirmed to be related to appetite in humans (Larder *et al*., 2017) and growth traits in cattle (Crispim *et al*., 2015). Another study has suggested that the TMEM18_C1267T and TMEM18_C4447T loci are significantly associated with body height and slaughter rate (*P*<0.05) in Tianzhu yak (Zhang *et al*., 2017) and that T/T and C/T are the dominant genotype of these loci, respectively. However, the current study found that the two loci from the TMEM-18 gene (C1267T and C4447T) carried the highest frequency of the C/C genotype in the three populations, whereas T/T in TMEM18_C1267T was rare.

Calpain 4 (CAPN4) is extensively known to be associated with beef quality traits (Colle *et al*., 2017). An SNP (CAPN_G-1222A) in the CAPN4 gene's promoter region is significantly related (P<0.05) to multiple meat quality and growth traits of Gannan yak, including cooking rate and water-loss rate (Niu *et al*., 2015). This study found that the CAPN_G-1222A locus had abundant polymorphisms in the three populations. Thus, this locus had potential in the molecular breeding of meat-quality traits in the three yak populations.

Growth hormone (GH), growth hormone receptor (GHR) and growth hormone secretagogue receptor (GHSR) are important regulatory genes for body growth and development (Wegmann *et al*., 2017; Wang *et al*., 2020). GHSR can stimulate the release and secretion of GH and thus participate in the body's growth and energy metabolism (Zhang *et al*., 2017; Lv *et al*., 2018). Particularly, an SNP (T1387C) at the 52 UTR of the GHRS gene is confirmed as significantly related to the body weight in Maiwa yak (*P*<0.05) (Hai *et al*., 2017) and the dominant gene has a C/C genotype. In the present study, the frequency of the C/C genotype of GHRS_SNP (T1387C) in the three Tibetan yak populations was 32.69%-45.00%. This finding indicated that the three yak populations carried abundant dominant genotypes in this locus.

Uncoupling proteins (UCPs), as an anion carrier member of the inner mitochondrial membrane, maintain energy metabolism and homeostasis in vivo (Krauss *et al*., 2005). Some studies have shown that UCP2 is associated with body weight in humans and domestic animals (Oliveira *et al*., 2017; Oguzkan-Balci *et al*., 2013). Coincidentally, an SNP (UCP2_T1499C) of UCP2 gene is related to the weight of Maiwa yak and individuals with the C/T genotype have significantly higher weight (*P*<0.05) than those with the T/T genotype (Hao *et al*., 2019). In the current work, we found that the dominant genotype C/T was a rare genotype in the three Tibetan yak populations.

A series of studies has shown that long-chain acyl-CoA synthetase 1 (ACSL1) is the most important quantitative-trait locus and functional candidate gene that affects fatty acid composition in pork. Moreover, the polymorphism of the ACSL1 gene is significantly related (*P*<0.05) to the composition and ratio of fatty acid in the skeletal muscle of

Table 4: Genotypic frequency distribution of 12 SNP markers related to the economic traits of three Tibetan yak populations.

SNP marker	CWL		JL		SB	
	NOS	FG	NOS	FG	NOS	FG
ACSL1_A2079T	A/A (74)	74.00%	72	69.24%	22	64.71%
	T/T (2)	2.00%	2	1.92%	1	2.94%
	A/T (24)	24.00%	30	28.85%	11	32.35%
ACSL1_G2409A	G/G (60)	60.00%	69	66.35%	29	85.29%
	A/A (4)	4.00%	2	1.92%	0	0.00%
	G/A (36)	36.00%	33	31.73%	5	14.71%
CAPN4_G-1222A	G/G (34)	34.00%	26	25.49%	12	35.29%
	A/A (12)	12.00%	24	23.53%	5	14.71%
	G/A (54)	54.00%	52	50.98%	17	50.00%
CYP4A11_G4806A	G/G (82)	82.00%	89	85.58%	25	73.53%
	G/A (18)	18.00%	15	14.42%	9	26.47%
GHSR_T1387C	T/T (9)	9.00%	25	24.04%	11	32.35%
	C/C (45)	45.00%	34	32.69%	14	41.18%
	T/C (46)	46.00%	45	43.27%	9	26.47%
Hesx1_G618C	G/G (100)	100.00%	104	100.00%	34	100.00%
Hesx1_T226C	T/T (91)	91.00%	97	93.27%	32	94.12%
	C/C (1)	1.00%	0	0.00%	0	0.00%
	T/C (8)	8.00%	7	6.73%	2	5.88%
MyoD1_C1710T	C/C (29)	29.00%	34	32.69%	3	8.82%
	T/T (20)	20.00%	17	16.35%	8	23.53%
	C/T (51)	51.00%	53	50.96%	23	67.65%
OXGR1_A347G	G/G (100)	100.00%	104	100.00%	0	0.00%
	A/A (0)	0.00%	0	0.00%	34	100.00%
TMEM-18_C1267T	C/C (74)	74.00%	75	72.12%	23	67.65%
	T/T (3)	3.00%	0	0.00%	4	11.76%
	C/T (23)	23.00%	29	27.88%	7	20.59%
TMEM-18_C4447T	C/C (70)	70.00%	79	75.96%	23	67.65%
	T/T (1)	1.00%	4	3.85%	1	2.94%
	C/T (29)	29.00%	21	20.19%	10	29.41%
UCP_T1499C	T/T (78)	78.00%	93	89.42%	31	91.18%
	C/C (2)	2.00%	1	0.96%	0	0.00%
	T/C (20)	20.00%	10	9.62%	3	8.82%

Note: NOS: Number of observed genotypes; FG: Frequency of genotypes.

cattle (Widmann *et al.*, 2011). Some genetic variations in ACSL1 are also substantially related to the milk-production traits of Holstein cows (Liang *et al.*, 2020). In Gannan yaks, the two SNPs (ACSL1_A2079T and ACSL1_G2409A) in the promoter region of the ACSL1 gene are significantly related (P<0.05) to the protein rate and milk-fat rate (Zhao *et al.*, 2019). The present study found that these two loci were rich in polymorphisms in three Tibetan yak populations.

CONCLUSION

This study analyzed the genotype distribution of 12 candidate SNP genetic markers related to the economic traits of yak in three Tibetan yak populations. Some of them may have value in the breeding selection of Tibet yaks in the future, although extensive and in-depth research is required.

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