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RESEARCH ARTICLE

Potential emigration of Siberian cattle germplasm on Chirikof Island, Alaska

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Abstract

Feral cattle residing in Chirikof Island, Alaska, are relatively distinct from breeds used in commercial production in North America. However, preliminary evidence suggested that they exhibit substantial genetic relationship with cattle from Yakutian region of Siberia. Thus, our objective was to further elucidate quantify the origins, admixture and divergence of the Chirikof Island cattle relative to cattle from Siberia and USA. Subject animals were genotyped at 15 microsatellite loci. Compared with Turano–Mongolian and North American cattle, Chirikof Island cattle had similar variation, with slightly less observed heterozygosity, fewer alleles per locus and a positive fixation index. Analysis of the genetic distances revealed two primary clusters; one that contained the North American breeds and the Kazakh White head, and a second that contained the Yakutian and Kalmyk breeds, and the Chirikof population. Thus, it is suggested that Chirikof Island cattle may be a composite of British breeds emanating from North America and Turano–Mongolian cattle. A potential founder effect, consistent with historical records of the Russian–American period, may contribute to the adaptation of the Chirikof Island cattle to their harsh high-latitude environment. Further study of adaptive mechanisms manifest by these cattle is warranted.

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Introduction

The spread of domestic animals through time is one of the topics studied by archaeologists to assess human trade and migration (Lidia Colominas *et al.* 2015). Economically motivated emigration from Russia to Alaska necessitated sourcing foodstuffs for the colonists. During the Russian–American period, cattle husbandry was common in lush grassland of the ‘big bend’ of the Lena River of eastern

Russia proximate to Yakutsk and cattle were driven from there to the port at Okhotsk from which ships carried provisions to the Russian colonies (Gibson 1976). In 1798, a Russian outpost was established on Chirikof Island (Long 1975). Cost and desires for beef, milk and butter led to a very general importation of Siberian cattle to every post in Alaska and efforts were undertaken to produce cattle in Alaska (Bancroft 1886; Elliott 1886). Lands of the Aleutian Islands were found particularly well suited for cattle breeding due to lush grass in summer and limited snowfall in winter, allowing for grazing year-round (Gibson 1976). Thus, it is

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plausible that cattle of Yakutian origin were brought to isolated Chirikof Island in the Gulf of Alaska and persisted even in the absence of local husbandry.

Enterprising producers have brought cattle originating from USA to Chirikof Island since the mid 1880s (Long 1975). According to reports in the popular press, these more recent immigration events have included Hereford, Angus, Highland, Shorthorn and perhaps other breeds (Fields 2000; d'Oro 2003, 2005). However, apart from these sporadic immigration events, contemporary cattle on Chirikof Island are isolated in the North Pacific Ocean, thought to descend from many generations of feral stock, and persist without husbandry (McKnight 1964). Four-hundred cattle were tallied on Chirikof Island in 1927 (USDA 1929) and today there are estimated 2024 head in residence (Sonnen 2014).

Feral livestock are populations of formerly domesticated animals that now live independent of man. The cattle that presently reside on Chirikof Island represent one such population. Genetic variation of commercial, scientific, historical or esthetic value may be derived from feral livestock as they potentially have alleles that are rare or missing from domestic animal populations (Van Vuren and Hedrick 1989). This genetic variability may arise due to founder effects, drift and mutation with subsequent natural selection favouring those alleles that confer improved adaptation to prevailing environmental conditions. Rational decision making relative to conservation, genetic and phenotypic evaluation can be facilitated by knowledge of this genetic diversity (FAO 1997, 2004). Substituting for adapted breeds with 'improved' counterparts also may be counterproductive in harsh environments (Drucker et al. 2001).

The cattle that reside on Chirikof Island have been found to be both genetically variable and relatively unique when compared to Angus, Charolais, Hereford, Highland, Limousin, Red Angus, Salers, Shorthorn, Simmental, Tarentaise and Texas Longhorn breeds (MacNeil et al. 2006, 2007). Recently, SNP genotypes for a limited number of cattle from Chirikof Island were analysed in concert with a worldwide survey of breed diversity (Decker et al. 2014). Results of that study suggest potential for Yakutian ancestry of the Chirikof Island cattle (Decker et al. 2016). *Bos taurus* cattle breeds from a wide range of geographical origins in Eurasia, mostly its northern territory have also been recently characterized using microsatellites (Li et al. 2005; Li and Kantanen 2010). Thus, our objective was to more definitively quantify the origins, admixture and divergence of the Chirikof Island cattle relative to cattle from Siberia and USA.

Materials and methods

All DNA used in this study originated in separate investigations that examined: the genetic structure of Eurasian cattle (Li et al. 2005; Li and Kantanen 2010); and the relationship of cattle on Chirikof Island to commercial breeds that are commonly used in North American beef production (MacNeil et al. 2007). Here, Turano–Mongolian breeds

(Yakut ($N = 60$), Kalmyk ($N = 28$), and Kazakh White head ($N = 40$)); North American breeds (Charolais ($N = 17$), Limousin ($N = 15$), Simmental ($N = 19$), Tarentaise ($N = 9$), Angus ($N = 22$), Hereford ($N = 22$), Highland ($N = 18$), Red Angus ($N = 16$), Shorthorn ($N = 12$), Texas Longhorn ($N = 9$) and Criollo ($N = 30$)); and cattle from Chirikof Island ($N = 23$) (Li et al. 2005; Granberg et al. 2006) were genotyped using 15 common microsatellites (*ETH10*, *ETH3*, *INRA032*, *HEL-5*, *HEL-1*, *ETH185*, *TGLA126*, *INRA005*, *ILSTS005*, *ETH225*, *TGLA227*, *BM1818*, *ILSTS006*, *INRA037* and *INRA063*) selected from those recommended for collaborative genetic diversity studies (<http://www.bbsrc.ac.uk/>). DNA was extracted by phenol–chloroform precipitation. Standard polymerase chain reactions (PCR) were performed and samples from North America were genotyped using a Licor DNA Analyzer 4200 (LI-COR Biosciences, Lincoln, USA). Samples from Russia were genotyped using a MegaBACE™500 DNA sequencer (Amersham Biosciences, Uppsala, Sweden). Three Simmentals were genotyped using both platforms to ensure consistency in the scoring of genotypes.

Measures of genotypic diversity and differentiation were analysed and displayed using several complementary approaches. Microsatellite DNA variation among and within breeds was initially quantified by analysis of molecular variance with R-statistics (Excoffier et al. 1992) as implemented in the GenAIEx add-in (Peakall and Smouse 2006, 2012) for the Excel spreadsheet software (Microsoft, Redmond, USA). Within breed, variation was further dissected by counting private alleles and calculating average number of alleles per locus (A), observed heterozygosity (H_o), unbiased expected heterozygosity ($H_e = 1 - \sum p_i^2$, where p_i is the frequency of the i th allele) and fixation index (F_{is} : Wright 1921). Allelic richness (Foulley and Ollivier 2006), accounting for the influence of sample size on the number of alleles detected was calculated using FSTAT (Goudet 2001). Principal coordinates analysis (Gower 1998; Peakall and Smouse 2006, 2012) was conducted using the genetic distance covariance matrix with data standardization. Genetic distances (D_s) among individual breeds and three groups of breeds (Siberian, North American and Chirikof Island) were quantified (Nei 1972) and illustrated with neighbour-joining cluster analysis (Saitou and Nei 1987). Differences in average genetic distances among groups were tested using two-tailed z -tests and declared significant at $P \leq 0.05$.

Results and discussion

As partitioned by the analysis of molecular variance, ~25% of total genetic variance was between breeds and 75% existed within breeds. Thus, there was ~11% more genetic diversity than was previously observed for the Chirikof Island cattle and 11 US beef breeds (10 of which are also represented in this study) previously examined (MacNeil et al. 2007). Thus, using Turano–Mongolian cattle in this study significantly

added to the diversity among breeds relative to the previous investigation.

Measures of heterozygosity indicating the degree to which individuals in a population are either observed or expected to be heterozygous given the allele frequencies are commonly used to characterize the genetic diversity of populations (Toro *et al.* 2009). Thus, these measures are sensitive to allele frequencies as opposed to the number of alleles. Decreased heterozygosity may be correlated with reduced fitness (MacNeil *et al.* 1989; Reed and Frankham 2003) and thus may have ecological consequences (Greenbaum *et al.* 2014). Further, decreased allelic richness may indicate reduced potential for adaptation to environmental changes, since this diversity provides the basis for evolution by natural selection (Greenbaum *et al.* 2014). Here, the Turano–Mongolian and North American cattle breeds exhibit similar levels of genetic variation (table 1) with averages observed and expected heterozygosity between 0.6 and 0.7, number of alleles per locus between 5.0 and 6.0, allelic richness between 2.4 and 2.5 and negative fixation indexes. Compared to the averages of the Turano–Mongolian and North American cattle, the Chirikof Island cattle had similar variation with slightly less observed heterozygosity (0.59), a fewer alleles per locus (4.1) and a positive fixation index. Thirty-one private alleles were observed at 12 of the 15 loci genotyped. Of the breeds/populations studied, only Limousin and Chirikof Island cattle did not have any private alleles. Lack of private alleles in the cattle of Chirikof Island is consistent with their being an admixed population. While inconsistent with best practices of industrial cattle production, the low cow-to-bull ratio observed on Chirikof Island (Sonnen 2014) has likely aided in maintenance of genetic diversity

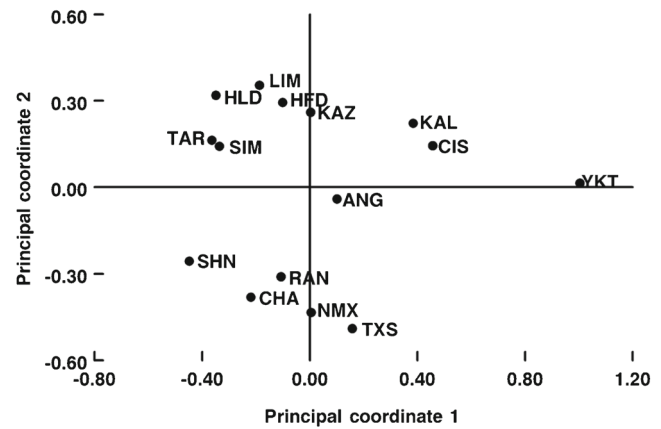


Figure 1. Plot of principle coordinates 1 and 2 which explain 40% of the variation in relationship among Angus (ANG), Charolais (CHA), Chirikof Island cattle (CIS), Criollo cattle (NMX), Hereford (HFD), Highland (HLD), Kalmyk (KAL), Kazakh White head (KAZ), Limousin (LIM), Red Angus (RAN), Shorthorn (SHN), Simmental (SIM), Tarentaise (TAR), Texas Longhorn (TXS) and Yakut (YKT) breeds of cattle as derived from 15 microsatellite loci.

through an increased number of breeding males and reduced variance of family size relative to managed populations.

Analysis of the microsatellite genotypes, as illustrated from the first two principle coordinates, cast the Chirikof Island cattle as being most similar to the Kalmyk breed (figure 1). However, the historical evidence documents supply of the Russian–American colonies in Alaska through the Yakutian region (Gibson 1976). Moving Kalmyk cattle from the far more distant Republic of Kalmykia to Alaska seems far less feasible or likely. In addition, the indigenous Kalmyk cattle were crossed (circa 1900) with Simmental to

Table 1. Measures of genetic variation in 10 North American breeds, three Turano–Mongolian breeds, and the Chirikof Island population of cattle.

Breed/population	<i>N</i>	<i>N_a</i>	<i>A_R</i>	<i>H_o</i>	<i>H_e</i>	<i>F_{is}</i>
Angus	35.1	5.33	2.50	0.658	0.662	−0.021
Charolais	16.9	6.00	2.62	0.725	0.689	−0.071
Chirikof Island	22.9	4.13	2.37	0.588	0.615	0.018
Criollo	29.8	7.20	2.76	0.716	0.736	0.007
Hereford	19.9	5.27	2.50	0.624	0.656	0.003
Highland	16.7	4.27	2.23	0.569	0.566	−0.039
Kalmyk	28.0	5.73	2.43	0.650	0.626	−0.064
Kazakh White head	40.0	6.67	2.51	0.675	0.662	−0.038
Limousin	12.9	4.53	2.49	0.667	0.660	−0.067
Shorthorn	11.0	4.13	2.39	0.652	0.626	−0.095
Simmental	18.7	4.80	2.38	0.641	0.624	−0.060
Texas Longhorn	8.7	4.80	2.69	0.677	0.723	0.004
Tarentaise	8.4	4.27	2.54	0.663	0.670	−0.070
Yakut	60.0	4.47	2.28	0.576	0.591	0.019
Average value						
Turano–Mongolian		5.62	2.41	0.634	0.626	−0.028
North American*		5.06	2.51	0.659	0.661	−0.041
All populations		5.11	2.48	0.649	0.651	−0.034

N, average sample size for 15 loci; *N_a*, no. of alleles; *A_R*, allelic richness; *H_o*, observed heterozygosity; *H_e*, expected heterozygosity (corrected for sample size); *F_{is}*, fixation index.

*Excluding Chirikof Island population.

Table 2. Genetic distances within and between groups of North American and Turano–Mongolian cattle.

Population	Mean	SD	95% CI
All	0.283	0.093	0.264–0.302
Within North American*	0.271	0.073	0.249–0.293
Within Turano–Mongolian	0.261	0.066	0.096–0.426
North American* versus Turano–Mongolian	0.305	0.127	0.258–0.352
Chirikof Island versus all others	0.279	0.065	0.240–0.318
Chirikof Island versus Turano–Mongolian	0.209	0.050	0.086–0.332
Chirikof Island versus North American*	0.301	0.054	0.262–0.340
Yakut versus North American*	0.440	0.079	0.384–0.496

*Excluding Chirikof Island cattle; SD, standard deviation; CI, confidence interval.

obtain larger animals and with Shorthorn to improve their beef qualities (Baimukanov *et al.* 1989). Thus, the collocation of Chirikof Island and Kalmyk cattle as intermediates between some North American breeds and Yakut is consistent with the interpretation that these two populations may be admixtures of these breeds and Yakut or ones that are similar (McVean 2009).

Average D_s (table 2) among breeds are not significantly different either within North America (average $D_s = 0.27$) or within Turano–Mongolian (average $D_s = 0.26$). The average genetic distance between North American and Turano–Mongolian breeds (average $D_s = 0.30$) is neither significantly different from the average distance among North American breeds nor from the average distance among Turano–Mongolian breeds. However, genetic distances between Yakut and North American breeds (average $D_s = 0.44$) are greater ($P < 0.01$) than the average distances among the North American breeds. Further, the genetic distance between the Chirikof Island population and the Turano–Mongolian breeds (average $D_s = 0.21$) is significantly less ($P < 0.05$) than the genetic distance between Chirikof and the North America breeds (average $D_s = 0.30$).

Integration of relationships among the genetic distances is illustrated in a neighbour-joining tree (figure 2). There are two primary clusters; one contains the North American breeds and the Kazakh White head which is known to have been influenced by Hereford (Buchanan and Lenstra 2015). The second primary cluster contains the Yakutian and Kalmyk breeds and the Chirikof population, reflecting the relatively small genetic distance between Chirikof and these latter breeds (0.22 and 0.19, respectively).

The available evidence suggests Chirikof Island cattle may be a composite of British breeds emanating from North America and Turano–Mongolian cattle. This composite appears to be at least as distinct as other recognized breeds of cattle. Further, the mixture of germplasm to form the Chirikof Island population is relatively unique compared to contemporary North American breeds. Yakut cattle are well adapted to the extreme conditions of the subarctic region (Granberg *et al.* 2006) and may provide an important founder effect that contributes to the fitness of the Chirikof Island population. Further, the extent to which natural selection in the relatively harsh environment of Chirikof Island has impacted their genetic architecture has not been quantified. Chirikof Island cattle may be an economically important

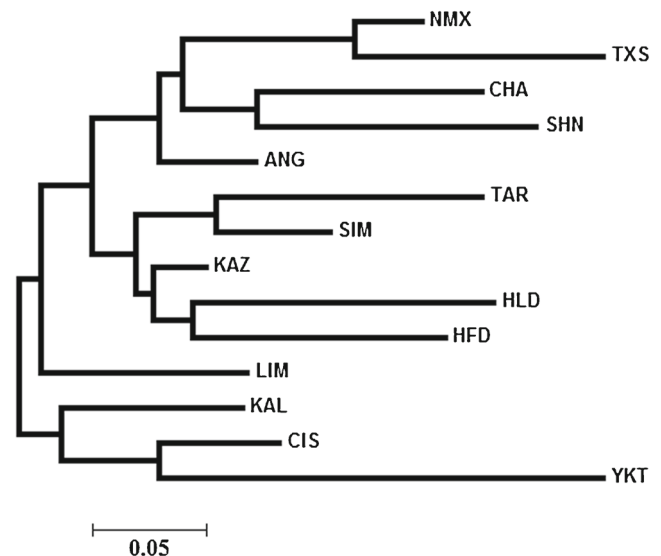


Figure 2. Neighbour-joining tree that illustrates genetic distances of Angus (ANG), Charolais (CHA), Chirikof Island cattle (CIS), Criollo cattle (NMX), Hereford (HFD), Highland (HLD), Kalmyk (KAL), Kazakh White head (KAZ), Limousin (LIM), Red Angus (RAN), Shorthorn (SHN), Simmental (SIM), Tarentaise (TAR), Texas Longhorn (TXS) and Yakut (YKT) breeds of cattle.

resource if they harbour genetic variation that contributes to adaptation as a feral population in the harsh high latitude environment of Chirikof Island. These circumstances lead to the recommendation that germplasm representative of the Chirikof Island cattle be conserved for further study. The ‘unfavorable’ state of the Yakutian population is probably caused by inbreeding depression due to a long-term isolation and a small number of animals (Li *et al.* 2005; Ruzina *et al.* 2010) provide further impetus for this recommendation. Further investigation into the uniqueness of Chirikof Island cattle may be facilitated through semen and ovary collections followed by monogamous mate assignment, *in vitro* fertilization and embryo transfer at a mainland-based research facility.

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