

Impact of genetic drift on access and benefit sharing under the Nagoya Protocol: The case of the Meishan pig¹

H. D. Blackburn,^{*2} Y. Plante,[†] G. Rohrer,[‡] E. W. Welch,[§] and S. R. Paiva[#]

*National Animal Germplasm Program, National Center for Genetic Resources Preservation ARS-USDA, Fort Collins, CO 80521; †Saskatoon Research Center, Agriculture and Agri-Food Canada, Saskatoon, SK, Canada; ‡U.S. Meat Animal Research Center, ARS-USDA, Clay Center, NE 68935; §University of Illinois, Chicago 60607; and #EMBRAPA Secretaria de Relações Internacionais (Secretariat of International Affairs), Brasilia, Brazil

ABSTRACT: Genetic drift (GD) randomly impacts small breeds and imported populations. Therefore, it can impact policies that affect conservation of animal genetic resources. This paper evaluates GD for a population of Meishan pigs imported into the United States and explores the ramifications of GD on access and benefit sharing of genetic resources under the Nagoya Protocol (NP) of the United Nations' Convention on Biological Diversity. The NP was motivated by concerns about fair and equitable benefit sharing of genetic resources across life forms. In this experiment, 35 microsatellite markers were used to quantify the level of GD that occurred between Meishan pigs (Meishan-China; n = 22) imported into the United States in the late 1980s and contemporary Meishan (Meishan-US; n = 42), which have been randomly bred since importation. The Meishan-US consisted of 2 subpopulations (Meishan-MARC and Meishan-ISU). Five other breeds were also included in the analysis to serve as reference populations: Fengjing and Minzhu, which were imported with Meishan-China, and Duroc, Berk-

shire, and Yorkshire from the United States. Mean shift in allele frequency was 0.11 (SE = 0.019) due to GD for Meishan-US vs. Meishan-China with some loci having changed allele frequencies by greater than 0.20. Principle coordinate analysis confirmed divergence among the Meishan populations. Model-based clustering tended to place the U.S. and Chinese breeds into 2 distinct clusters, likely due to differences in allele frequencies between U.S. and Chinese breeds. Contemporary Meishan-US has become differentiated from the original imported animals due to GD. Attributing future performance of Meishan-US to Meishan-China, as set forth by NP, is problematic due to GD. As an imported breed becomes established there will be an increasing number of breeders who may have different selection goals and private treaty contracts will govern the exchange of stock between them. Therefore, considering biological phenomena and social dynamics simultaneously draws into question whether a rigorous access and benefit sharing protocol as envisioned in the NP will be operational.

Key words: genetic diversity, genetic drift, Meishan, Nagoya protocol, *Sus scrofa*

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INTRODUCTION

Genetic drift (**GD**) in small populations causes random changes in allele frequencies across generations with

no tendency to revert back to the original frequencies (Falconer and MacKay, 1996). Since importation into the United States, Meishan pigs have been maintained at public institutions and randomly mated. Semen samples from the original importations were cryobanked. Therefore, this breed makes a good case study to assess the impact of GD on populations imported into a new country. Because GD impacts management of genetic diversity in breeds and imported populations with small effective population size, there is a need for breeders and policies concerning conservation and use of genetic resources to take GD into account.

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²Corresponding author: Harvey.blackburn@ars.usda.gov
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International policy discussions are underway to implement a global access and benefit sharing (ABS) policy as specified in the Nagoya Protocol (NP; UN CBD, 2011) of the Convention on Biological Diversity (CBD). The NP is designed to address concerns about fair and equitable benefit sharing of genetic resources across life forms. It requires ratification by 50 countries to come into force. The NP calls for all signatory countries to establish governmental mechanisms to authorize and monitor genetic resource exchange and use. However, the NP does not address how genetic mechanisms impact varying life forms. For example, GD in livestock is likely to limit the ability of the NP to effectively assign post facto ownership. Also, the NP does not specifically consider the existing norms of the livestock sector wherein private contracts between buyer and seller are well established. Ineffective consideration of the market system and GD in the NP has potentially negative consequences for the livestock sector including increased transaction costs and reduced gene flow and innovation (Welch et al., 2013).

The objective of this study was to evaluate the impact of GD on an imported Meishan pig population, as a means of informing policy development under the NP.

MATERIALS AND METHODS

Breeds

Meishan, Fengjing, and Minzhu were first imported into the United States from the People's Republic of China in 1989 in an effort to increase litter size of commercial pig populations. Meishan and Fengjing originate from the Taihu basin (near Shanghai) and Minzhu originated in northeast China (Li and Enfield, 1989). The original Meishan importation consisted of 66 gilts and 33 boars (Young, 1992). After quarantine, the population was equally subdivided into 3 subpopulations, with all families represented in each of the 3 subpopulations. They were established at the U.S. Meat Animal Research Center (MARC; Meishan-MARC), University of Illinois, and Iowa State University (ISU; Meishan-ISU). At these institutions the herds were maintained as randomly bred populations. No research populations of Fengjing or Minzhu are known to have been maintained. Duroc, Yorkshire, and Berkshire were included in this study to evaluate genetic differences between commercially important U.S. and Chinese breeds.

Animals

Data originated from 7 pig populations: Meishan-China ($n = 22$), Meishan-US ($n = 42$), Fengjing ($n = 22$), Minzhu ($n = 20$), Duroc ($n = 26$), Berkshire ($n = 26$), and Yorkshire ($n = 21$). The Meishan-China samples were from the original importation. Samples

of Meishan-US were recently collected from MARC ($n = 18$) and ISU ($n = 24$) herds. Duroc, Yorkshire, and Berkshire samples were representative of the current breeding populations and were selected from samples maintained by the USDA National Animal Germplasm Program.

Deoxyribonucleic acid from all animals was derived from semen samples. After extraction, the DNA was shipped to Agriculture and Agri-Food Canada (Saskatoon Research Centre, Saskatoon, Canada) for genotyping. Twenty-nine Food and Agriculture Organization of the United Nations (FAO) recommended swine microsatellites (FAO, 2011) and 6 additional microsatellite markers (CGA on chromosome 1, S0215 on chromosome 13, S0227 on chromosome 4, S0225 on chromosome 8, SW951 on chromosome 10, and S0386 on chromosome 11) were used (see Supplementary Table 1 for loci sequences, multiplexes, and annealing temperatures). Fluorescently labeled pig marker primers (Applied Biosystems Inc., Foster City, CA) were used to derive amplification products by PCR using the Qiagen Multiplex PCR Kit (Qiagen Inc., Burlington, CA). The amplicons were diluted and loaded onto a Genetic Analyzer 3130xl and genotypes determined using GeneMapper version 3.0 (Applied Biosystems Inc.).

Data Analysis

Allele frequencies, Hardy-Weinberg equilibrium, and Nei's genetic distance (standard and unbiased) were computed with GENALEX (Peakall and Smouse, 2006) and the fixation index (F_{st}) was calculated using MolKin (Gutierrez et al., 2005). STRUCTURE 2.1 (Pritchard et al., 2000) was used to infer admixture and to assign individuals to inferred clusters. Parameter settings for STRUCTURE were: number of *a priori* assumed populations $K = 2$ to 10, a burn-in period of 50,000 iterations and 100,000 Markov chain Monte Carlo (reaching equilibrium) samples, and 10 replicates. Structure Harvester (Earl, 2009) was used to estimate the optimal number of clusters using the approach of Evanno et al. (2005). CLUMPP version 1.1.2 (Jakobsson and Rosenberg, 2007) and DISTRUCT version 1.1 (Rosenberg, 2004) were used to cluster results from the 10 replicates into a single figure.

TempoFs (www.zoologi.su.se/~ryman/) was used to estimate GD for the Meishan-US and Meishan-China populations. In this program, Jorde and Ryman (2007) expanded both Nei and Tajima (1981) and Pollak (1983) approaches and developed an unbiased estimator of GD specifically for small microsatellite panels. This approach addresses bias that may be present with small sample sizes, as is the case in this study. For TempoFs, the population size parameter was set to 99 head based on Young (1992)

Table 1. Nei (below diagonal) and unbiased Nei (above diagonal) genetic distances for Chinese and U.S. pig breeds

	Meishan-US	Meishan-China	Fengjing	Minzhu	Yorkshire	Berkshire	Duroc
Meishan-US		0.850	0.787	0.857	1.341	1.227	1.312
Meishan-China	0.113		0.803	0.790	1.492	1.522	1.374
Fengjing	0.810	0.837		0.695	1.202	1.252	1.338
Minzhu	0.901	0.845	0.745		0.580	0.571	0.664
Yorkshire	1.367	1.528	1.234	0.633		0.328	0.471
Berkshire	1.247	1.552	1.278	0.617	0.357		0.452
Duroc	1.332	1.405	1.364	0.711	0.500	0.475	

and it was assumed that 8 generations (2.5 yr/generation) had elapsed since the herds were placed at each institution. The assumed number of generations was increased and decreased (± 2) and the results were found to be insensitive. For this study, GD and changes in allele frequency were compared between Meishan-China vs. Meishan-MARC, and Meishan-ISU.

To evaluate how selection might augment GD in increasing genetic differences, we hypothetically assumed selection had effectively changed the Meishan-US genotypes for the microsatellite IGF-1 to the same genotypes observed in Duroc and Yorkshire. Statistics indicative of genetic differentiation were recalculated for this hypothetical situation.

RESULTS

Comparisons of the Chinese and U.S. breeds served as a basis for evaluating differences between Meishan-China and Meishan-US. Both Nei and unbiased Nei distances between the breeds of Chinese origin and Duroc, Yorkshire, and Berkshire were large (>0.50). Between Meishan-China and Meishan-US these distance measures ranged from 0.08 to 0.11 (Table 1). In the scenario where the Meishan-US genotypes for IGF-1 were modified to the genotypes of Duroc and Yorkshire, Nei's and Nei's unbiased genetic distances between Meishan-US and Meishan-China were increased by 8 and 11%, respectively. Among the Meishan populations F_{st} was 0.05.

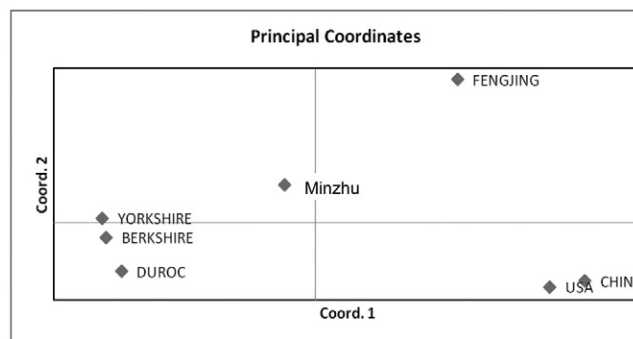
Approximately 75% of the variation among breeds was explained by the first and second principal coordinates and the breeds were distinct from one another (Fig. 1a). The principal coordinate analysis grouped Duroc, Berkshire, and Yorkshire in close proximity and distinct from Meishan. However, inspection of the genetic distance measures suggests the U.S. breeds were also distinct from one another with genetic distances greater than 0.36 (Table 1). Among Meishan populations more than 99% of the variation was explained by the first and second principal coordinates (Fig. 1b). The Meishan-US-ISU and Meishan-US-MARC were distinct from Meishan-China and each other.

Results from the STRUCTURE analysis indicated 2 major clusters (Fig. 2) for this set of breeds. The Meis-

han and Fengjing were in 1 cluster and the 3 U.S. breeds in the second. The Minzhu/Ming was found to be about equally admixed between the 2 clusters.

All loci were polymorphic for all breeds except Meishan-US and Berkshire, which were monomorphic at 1 locus each. At the polymorphic loci, the number of alleles ranged from 4.25 to 6.63 with Meishan-US and Minzhu populations at the minimum and maximum, respectively (Table 2). Observed and expected heterozygosity were least in Duroc and Berkshire and greatest in Minzhu (Table 2). While Meishan-China had greater levels of observed and expected heterozygosity than Meishan-US, the differences were small and the SE overlapped. Across breeds a majority of loci were in Hardy-Weinberg equilibrium (Table 2). However Meishan-US had only 65.4% of the loci in Hardy-Weinberg equilibrium.

a.



b.

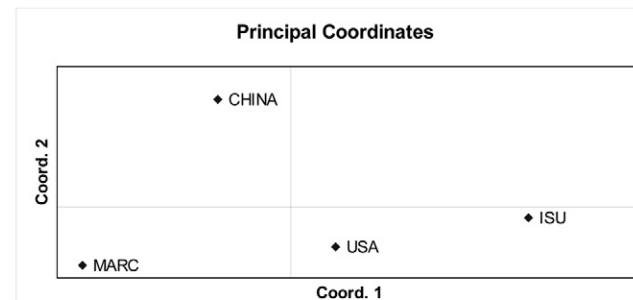


Figure 1. Principal coordinate (Coord.) analysis (PCA) for U.S. and Chinese pig breeds (a) and the PCA for the Meishan population (b). MARC = U.S. Meat Animal Research Center; ISU = Iowa State University; USA = United States.

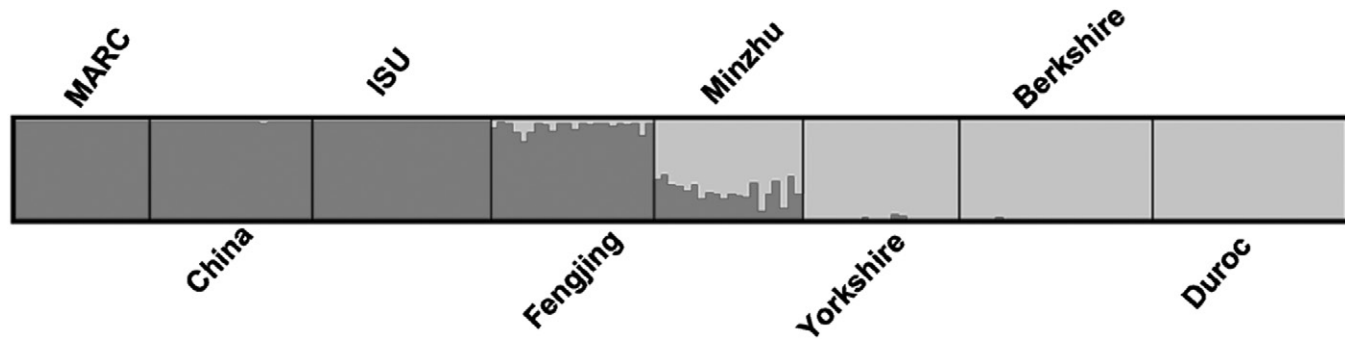


Figure 2. STRUCTURE analysis of pig breeds when $K = 2$. MARC = Meishan-MARC; China = Meishan-China; ISU = Meishan-ISU.

Private alleles within the Meishan-MARC and Meishan-ISU populations were found at 8 loci. The frequency for 2 of the private alleles exceeded 15%, and loci were less than 5% at the remaining loci (data not shown). It is assumed that these alleles are not new mutations but rather alleles that originated from animals not represented in the Meishan-China samples. This assumption would seem valid since the S0097 allele 231 in the Meishan-US population was not present in the Meishan-China population.

Mean change in allele frequency due to GD was 0.11 (Table 3) when comparing the Meishan-China and Meishan-US populations. Shifts in allele frequencies of the Meishan-ISU and Meishan-MARC populations from the Meishan-China population were greater than 50% larger than Meishan-US and Meishan-China comparison. Shifts in allele frequency per locus were also evaluated (Fig. 3). For Meishan-US, 7 loci had changes in allele frequency of more than 0.20 due to GD. Both Meishan-ISU and Meishan-MARC had loci with a high allele frequency suggesting they were trending towards fixation.

DISCUSSION

These data empirically suggest GD has separated the Meishan-US (and its subpopulations) from the imported Meishan-China population in a relatively short period of time. The departure of Meishan-ISU from Meishan-China may be greater than that of Meishan-MARC. Also, as expected with small isolated populations, there was an apparent but not statistically significant loss of genetic diversity (Table 2).

In addition to the direct estimates of GD, F_{st} can be used as an indicator of how subpopulations have diverged. The F_{st} values for populations within breed and country have been shown to be slight (Chikhi et al., 2004; Kijas et al., 2012). Table 4 provides F_{st} estimates for breeds within country or pairing breeds to the country of origin or to another importing country. The F_{st} found in this study were within the range of values in Table 4. While the Meishan F_{st} may be similar to other imported breeds, we recognize that the values in Table 4 arise from populations with much different histories of importation, numbers imported, potential reimportations, and selec-

Table 2. Mean and SE for number of animals (n), number of alleles per locus (N_a), number of effective alleles per locus (N_e), observed heterozygosity (H_o), expected heterozygosity (H_e), and percent loci in Hardy-Weinberg equilibrium (HWE) for each population

Population		n	N_a	N_e	H_o	H_e	% loci in HWE
Meishan-US	Mean	42.000	4.257	2.722	0.516	0.581	65.4
	SE	0.000	0.222	0.156	0.035	0.029	–
Meishan-China	Mean	22.000	4.543	2.934	0.588	0.618	85.7
	SE	0.000	0.226	0.151	0.038	0.026	–
Fengjing	Mean	21.943	4.429	2.613	0.577	0.551	80.0
	SE	0.040	0.233	0.162	0.042	0.035	–
Minzhu	Mean	19.943	6.629	4.023	0.713	0.726	77.1
	SE	0.040	0.336	0.212	0.036	0.015	–
Yorkshire	Mean	20.943	4.971	2.812	0.572	0.584	85.7
	SE	0.040	0.297	0.197	0.035	0.030	–
Berkshire	Mean	25.800	4.686	2.555	0.496	0.533	77.1
	SE	0.080	0.354	0.168	0.038	0.037	–
Duroc	Mean	25.914	4.686	2.566	0.503	0.539	80.0
	SE	0.063	0.327	0.206	0.034	0.031	–

tion practices over different time periods. These differences confound our ability to explain the observed F_{st} values. In this study, the F_{st} estimate is a function of GD with no major effects due to selection or reimportation and therefore suggests that this random process is capable of causing an imported population to differentiate itself from the parental population in a relatively short period of time and to potentially perform differently.

As with all imported livestock breeds, founder effects due to sampling determine the initial allelic composition of the imported population. Here the Meishan-China population, which was a sample of Meishan in China, was subject to this effect. In the context of trade, founder effects add complexity. Therefore, it would seem a combination of GD, selection, and founder effects all have potential to contribute to increasing the genetic distance between an imported and parent population and increase the difficulty in monitoring the exchange and use of genetic resources under the NP.

In CBD and ABS discussions held to date, there has been a lack of data and/or approaches that facilitate incorporating biological information in policy formulation (Laike, 2010). This void and lack of awareness of practices across sectors make the implementation of coherent policies difficult. Additionally, such a void makes a cause and effect mechanism difficult to track. Both Welch (2012) and Yun (2010) have stated that these types of sector-specific complexities are a shortcoming of the NP. The Meishan importation into the United States can be considered a “failed” importation in that the breed has not made a direct contribu-

Table 3. Observed change in mean allele frequency and SE attributed to genetic drift for the U.S., U.S. Meat Animal Research Center (MARC), and Iowa State University (ISU) Meishan herds when jackknifed over 35 loci

Meishan population	F_s ' ¹ mean (SE)	Upper and lower F_s ' 95% confidence interval
MARC	0.169 (0.034)	0.236 to 0.103
ISU	0.214 (0.036)	0.284 to 0.143
United States	0.111 (0.019)	0.150 to 0.072

¹ F_s ' = estimated drift.

tion to increasing production efficiency in U.S. commercial pig production due to its lack of growth and carcass quality attributes (Young, 1992; Lan et al., 1993; Blackburn and Gollin, 2009). However, Meishan-US has proved useful as a research model (e.g., Rohrer et al., 2001). This unintended use further illustrates the difficulty of developing ABS agreements that include a prior informed consent clause in the transfer of genetic resources, as suggested in the NP.

Genetic drift and selection that alter allele frequencies and crossbreeding make tracking the contribution of any imported population difficult over the long term. Therefore, any long-term and multigeneration benefit streams will be difficult to capture. Furthermore, as use of a “successful” imported breed grows, tracking the total number of producers using the resource becomes problematic, especially at a national level. These attributes of the livestock sector suggest the current industry practice of using private contracts between buyer

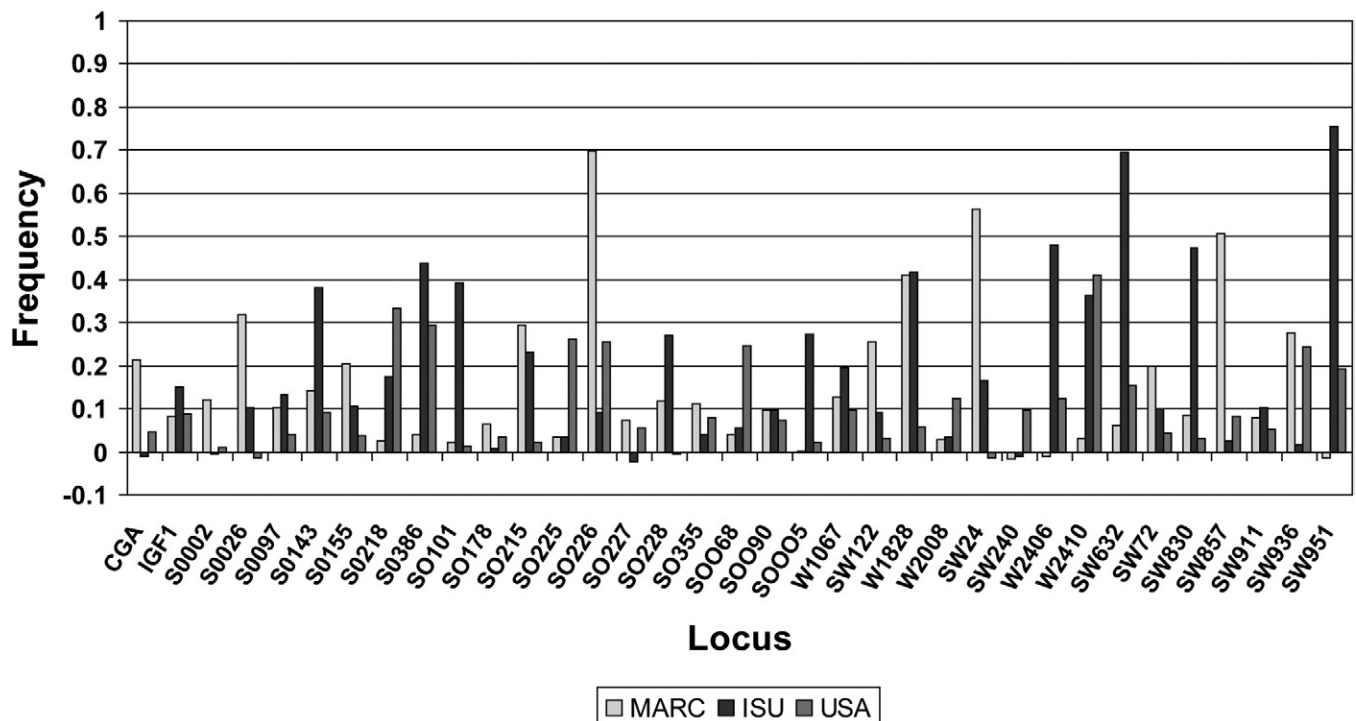


Figure 3. Estimated drift (F_s 's) corrected for expected contribution from sampling per locus over 8 generations for U.S. Meat Animal Research Center (MARC), Iowa State University (ISU), and U.S. populations

Table 4. Comparison of the fixation index (F_{st}) for breeds within country or between countries after importation

Status/species	Breed	Year of importation	F_{st}	Exporting and importing countries	Importing countries only	Reference
Within country						
Cattle	Jersey	–	0.015	Jersey Island	–	Chikhi et al., 2004
Sheep	Merino	1796	0.017	–	Australia	Kijas et al., 2012
Imported						
Sheep	Hampshire	1840	0.030	–	United States – Brazil	Paiva et al., 2011
Sheep	Dorset	1885	0.080	–	United States – Australia	Kijas et al., 2009
Sheep	Texel	1990	0.030	–	United States – New Zealand	Kijas et al., 2009
Sheep	Dorper	1990	0.090	–	United States – Brazil	Paiva et al. 2011
Sheep	Dorper	1990	0.050	S. Africa – United States	–	Kijas et al., 2009
Sheep	Suffolk	1888	0.060	United Kingdom – United States	–	Kijas et al., 2009
Goat	Boer	1993	0.030	–	United States – Brazil	H. D. Blackburn, unpublished data

and seller is the most direct and effective method to facilitate ABS. Since the 1700s private contracts that include exclusive or partial breeding rights have been used by livestock breeders (Wood and Orel, 2001).

A pragmatic approach to address the current concerns over the flow of benefits between buyer and seller would be to provide more market information so that both entities can make better decisions concerning the sale or purchase of breeding animals. The FAO Commission on Genetic Resources for Food and Agriculture could play an influential role in providing such market information through preexisting programs dealing with animal genetic resources used for food and agriculture by expanding the FAO's information system, Domestic Animal Diversity Information System. Such an action could also help build the profile of underutilized genetic resources, thereby increasing conservation of animal genetic resources and being in harmony with the perceived intentions of the NP.

Conclusion

The results inform policy development by illustrating how allele frequency changes over time for small imported populations. The Meishan importation was not commercially viable to increase production efficiency in the United States. However, it has been useful from a research perspective. In this study, GD played a primary role in changing allele frequencies of the imported population in a relatively short span of time. In commercial livestock populations, GD plus artificial and natural selection will affect allele frequencies and increase genetic divergence to a greater degree than was observed here. Multiple forces are acting simultaneously to change allele frequencies and therefore call into question the feasibility of a rigorous ABS protocol.

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