



ORIGINAL ARTICLE

## Prioritization based on neutral genetic diversity may fail to conserve important characteristics in cattle breeds

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### Introduction

Shortly after the potential of human blood groups to reveal aspects of human history and diversity was appreciated, similar approaches were applied to farmed cattle. Neutral genetic markers became appreciated as relevant to determine the evolutionary distinctiveness of breeds (Bruford 2004). In parallel, concern was growing about the endangered status of very many breeds of the major farmed species, culminating in the explicit recognition of animal genetic resources in the 1992 Convention on Biological Diversity (FAO 2007). A paradigm developed for assessing the priorities of breeds for conser-

### Summary

Conservation of the intraspecific genetic diversity of livestock species requires protocols that assess between-breed genetic variability and also take into account differences among individuals within breeds. Here, we focus on variation between breeds. Conservation of neutral genetic variation has been seen as promoting, through linkage processes, the retention of useful and potentially useful variation. Using public information on beef cattle breeds, with a total of 165 data sets each relating to a breed comparison of a performance variable, we have tested this paradigm by calculating the correlations between pairwise breed differences in performance and pairwise genetic distances deduced from biochemical and immunological polymorphisms, microsatellites and single-nucleotide polymorphisms. As already observed in floral and faunal biodiversity, significant positive correlations ( $n = 54$ ) were found, but many correlations were non-significant ( $n = 100$ ) or significantly negative ( $n = 11$ ). This implies that maximizing conserved neutral genetic variation with current techniques may conserve breed-level genetic variation in some traits but not in others and supports the view that genetic distance measurements based on neutral genetic variation are not sufficient as a determinant of conservation priority among breeds.

vation on the basis of distinct evolutionary histories. The paradigm has been conservation of breeds in such a way that neutral genetic variation is maximally retained, on the basis that functional and performance traits, both those currently known and those not yet documented or not yet valued, will be conserved because of linkage. This maximization has been on the basis of assigning the most genetically distinct breeds the highest conservation priority.

An influential paper warned against excessive dependence on genetic distances and emphasized the role of other criteria in conservation prioritization (Ruane 1999), and indeed, few if any national conservation programmes for livestock biodiversity

have actually been based on genetic distances (Bottcher *et al.* 2010). Instead, conservation priority has usually been assigned primarily on the basis of population size and other measures of endangerment, together with non-genetic considerations such as cultural significance. However, prioritization protocols remain a very important area of research especially as they can be expected to relate to the maintenance of within-breed variation in numerically strong breeds (Taberlet *et al.* 2008), and we might predict a shift in research focus towards methods of identifying individuals within these breeds for representation in genetic resource collections or other conservation procedures.

Interest has been growing in whether maximal conservation of neutral variation, assessed by genetic distance, is in fact the best paradigm for retaining adaptability of livestock into the future. Issues raised include the biological reality of genetic distances as currently assessed (Toro 2006) and the relative importance of within-breed variation as a component of the overall genetic diversity of livestock (Bruford 2004; European Cattle Genetic Diversity Consortium 2006; Meuwissen 2009).

Genetic distance between breeds, as measured using neutral variation, would be expected to be positively correlated with phenotypic distance for a wide range of traits as breeds have been selected to fill different functions in society (Hall & Ruane 1993). In non-livestock species, such correlations are often weak. Burstin & Charcosset (1997), using maize varieties, showed theoretically and experimentally that while low marker distances are usually associated with low phenotypic distances, the relationship between high marker distances and phenotypic distances depended on how many loci are involved in determining the phenotype. Reed & Frankham (2001) found that in 71 data sets from captive and wild non-livestock and non-crop animal and plant species, overall, the mean correlation between molecular (predominantly allozymes) and quantitative measures of variation was weak, but significantly greater than zero. There has not yet been a counterpart study in livestock.

We have investigated the relationship between genetic distances between pairs of breeds of cattle used in beef production and the differences between them in performance traits. Our hypothesis is that this relationship takes the form of a positive correlation. If this proves to be the case, then prioritization for conservation according to genetic distances is to some extent supported, bearing in mind the reservations noted above.

## Methods

Following Roughsedge *et al.* (2001), suitable published breed comparison studies were selected, in which relatively large numbers of breeds were compared statistically to yield what are effectively contemporary, common-garden comparisons. Traits were grouped as puberty and fertility traits, preweaning traits, postweaning traits and milk yield, and morphology and carcass traits. Published data were rearranged into pairwise comparisons. Each of these studies was matched with a genetic distance study, although performance studies because of their long-term nature cannot necessarily be considered as contemporary with the genetic distance measurements. For each performance trait, and following Reed & Frankham (2001), the Pearson correlation coefficient was calculated between the absolute difference between the values for each pair of breeds and the genetic distance between those breeds.

Performance data came from studies that ranged widely in methodologies and locations, and in when they were conducted. All had in common the use of a relatively large number of breeds and the presentation of corrected breed means or least-square means. Genetic data came from UK-based evaluations of genetic distances based on immunological and biochemical polymorphisms (Blott *et al.* 1998), from the European database of microsatellites (European Cattle Genetic Diversity Consortium 2006; Edwards *et al.* 2011) and from single-nucleotide polymorphisms (SNPs) studied in US populations of so-called British and continental breeds (Kuehn *et al.* 2008) and in a range of European breeds (Gautier *et al.* 2010). Only taurine cattle were considered. While the breeds considered include extreme dairy types like the Holstein and the Jersey, the data are all from studies in which these functioned as components of beef cattle systems rather than as dairy cattle.

For microsatellites, standard Nei genetic distances  $D_s$  and Reynolds distances  $D_r$  were calculated.  $D_s$  for immunological and biochemical polymorphisms were as reported in the respective publications. For SNPs, which were visualized using the Illumina Bovine SNP50 chip, Kuehn *et al.* (2008) reported  $D_s$  while Gautier *et al.* (2010) adopted the  $F_{ST}$  measure. Preliminary studies using Reynolds distances  $D_r$  yielded similar results and are not presented here.

## Results

The main body of the results comprises the 165 correlations calculated using genetic distance as

measured by  $D_s$  (Table 1). Sixty-four of these were significant ( $p < 0.05$ ) of which 53 were positive, with negative correlations being prominent among

preweaning traits (Tables 2–5). Overviews of the correlations are given in Figure 1. Numbers of correlations calculated using each genetic system were as

**Table 1** Breeds and traits analysed. Each column represents the pairing of a performance study with genetic distance data, with the names of the breeds considered

Reference to performance data	1	1	1	5	10	9	8	6	7	11	1	
Reference to genetic data	2	4	3	4	4	3	4	4	4	4	12	
Number of correlations calculated, with $D_s$ pairwise genetic distances												Totals
Puberty and fertility traits	5	5	5	1	0	0	0	0	1	0	5	22
Preweaning traits	10	10	10	0	0	2	3	8	3	2	10	58
Postweaning traits and milk yield	4	4	4	6	3	1	6	12	12	5	4	61
Morphological and carcass traits	0	0	0	15	0	0	9	0	0	0	0	24
Totals	19	19	19	22	3	3	18	20	16	7	19	165
Breeds covered in each study <sup>a</sup>												
Aberdeen Angus and Angus	+	+	+	+	+	+	+	+	+	+	+	11
Asturiana de las montañas				+								1
Asturiana de los valles				+								1
Avileña				+								1
Ayrshire					+							1
Belgian Blue	+	+					+	+				4
Blonde d'Aquitaine		+						+		+	+	4
Braunvieh		+	+			+			+			4
Brown Swiss	+											1
Charolais	+	+	+	+	+	+		+	+	+	+	10
Chianina	+	+	+									3
Danish Red				+								1
Dexter					+							1
Friesian (UK)	+	+										2
Galloway	+	+			+			+				4
Gascon								+				1
Gelbvieh	+	+	+			+			+			5
Guernsey					+							1
Hereford	+	+	+		+	+	+	+	+	+	+	10
Highland				+	+			+				3
Holstein	+	+		+	+						+	5
Jersey	+	+		+	+		+				+	6
Limousin	+	+	+	+		+	+	+	+	+	+	10
Longhorn	+	+			+							3
Maine Anjou	+	+	+			+					+	5
Piedmont	+	+		+				+		+	+	6
Pinzgauer		+							+			2
Poll Hereford	+											1
Pyrenean				+								1
Red Angus			+			+						2
Salers	+	+	+			+		+			+	6
Shorthorn	+	+	+			+						4
Simmental	+	+	+	+		+		+	+	+		8
South Devon	+	+		+	+		+					5
Tarentaise		+										1
Total number of breeds per study	20	22	12	14	12	11	6	12	8	7	10	

<sup>a</sup>For many breeds, synonyms are often used in commercial practice, although caution is needed when using these in international studies. Those most relevant here are Asturiana de las montañas (Casina), Asturiana de los valles (Carreña), Longhorn (English Longhorn), Piedmont (Piemontese), Tarentaise (Tarina), Pyrenean (Pirenaica) and Highland (Scottish Highland). For Brown Swiss and Braunvieh, the population being referred to must be inferred from the original publication.

References to sources: 1, Roughsedge *et al.* 2001; 2, Blott *et al.* 1998; 3, L. Kuehn, personal communication; Kuehn *et al.* 2008; 4, European Cattle Genetic Diversity Consortium 2006, Edwards *et al.* 2011; 5, Albertí *et al.* 2008; 6, Pribyl *et al.* 2003; 7, Jenkins & Ferrell 2002; 8, Afolayan *et al.* 2007; 9, Kuehn & Thallman 2010; 10, Taylor *et al.* 1986; 11, Jakubec *et al.* 2003; 12, Gautier *et al.* 2010.

**Table 2** Significant correlations (Pearson's *r*) between pairwise genetic distances ( $D_s$ ) and phenotypic differences: puberty and fertility traits. *p* is the significance level and relates to the number of breed comparisons  $[(n^2-n)/2]$ 

	<i>r</i>		n breeds	<i>p</i>	Animal data	Genetic system	References
	Positive	Negative					
Age at puberty	0.202		17	<0.05	M,X	B and I	1,2
Age at puberty	0.293		11	<0.05	M,X	SNP	1,3
Age at puberty	0.449		11	<0.001	M,X	SNP	1,12
Weight at puberty	0.301		17	<0.01	M,X	B and I	1,2
Weight at puberty	0.243		20	<0.001	M,X	MS	1,4
Pelvis width 365 days	0.251		14	<0.05	P	MS	4,5
Cow fertility	0.409		12	<0.01	M,X	B and I	1,2
Cow fertility	0.270		15	<0.01	M,X	MS	1,4

M, analysis of literature data 1976–1996; P, purebred design; X, cross-breeding design, analysed to provide information on parental breeds; B and I, biochemical and immunological variants; SNP, single-nucleotide polymorphisms; MS, microsatellites.

References: See caption to Table 1

**Table 3** Significant correlations (Pearson's *r*) between pairwise genetic distances ( $D_s$ ) and phenotypic differences: preweaning traits. 'Direct' and 'maternal' refer to direct and maternal effects, respectively. *p*: see caption for Table 2

	<i>r</i>		n breeds	<i>p</i>	Animal data	Genetic system	References
	Positive	Negative					
Gestation length maternal		-0.465	7	<0.05	M,X	SNP	1,3
Gestation length maternal	0.553		11	<0.001	M,X	SNP	1,12
Calving ease direct		-0.378	11	<0.01	BC,P	MS	4,6
Calving ease maternal		-0.250	13	<0.05	M,X	B and I	1,2
Calving ease maternal		-0.173	17	<0.05	M,X	MS	1,4
Birth weight direct	0.273		18	<0.01	M,X	B and I	1,2
Birth weight direct	0.267		11	<0.05	M,X	SNP	1,12
Birth weight maternal		-0.198	19	<0.05	M,X	MS	1,4
Birth weight	0.503		8	<0.01	P	MS	4,7
Birth weight direct	0.547		12	<0.001	BB,P	MS	4,6
Birth weight direct	0.469		11	<0.001	BC,P	MS	4,6
Survival to weaning maternal		-0.272	14	<0.01	M,X	B and I	1,2
Survival to weaning maternal		-0.269	15	<0.01	M,X	MS	1,4
Survival to weaning maternal		-0.532	11	<0.001	M,X	SNP	1,12
Preweaning growth rate direct		-0.443	11	<0.001	M,X	SNP	1,3
Preweaning growth rate direct	0.588		11	<0.001	M,X	SNP	1,12
Preweaning growth rate maternal	0.498		11	<0.001	M,X	SNP	1,12
Weaning weight	0.627		6	<0.05	L,X	MS	4,8
Weaning weight	0.391		8	<0.05	P	MS	4,7

M, analysis of literature data 1976–1996; P, purebred design; X, cross-breeding design, analysed to provide information on parental breeds; BB, estimations of breeding values – bulls; BC, estimations of breeding values – cows; L, Least-squares means; B and I, biochemical and immunological variants; SNP, single-nucleotide polymorphisms; MS, microsatellites.

References: See caption to Table 1.

follows: immunological and biochemical polymorphisms 19 (of which six were significant positive, two significant negative), microsatellites 105 (40 significant positive, five significant negative) and SNPs 41 (seven significant positive, four significant negative).

Generally, significances of correlations were higher for postweaning traits and milk yield.

A lower proportion (11 of 41) of the SNP correlations were significant than of the microsatellite correlations (45 of 105); this difference is significant ( $\chi^2 = 7.14$ ,  $p < 0.01$ , 1 d.f.).

There were three cases in which pairwise differences in trait showed significant positive correlation with genetic distance in one study and significant negative correlation in another. In all of these, the

**Table 4** Significant correlations (Pearson's *r*) between pairwise genetic distances ( $D_g$ ) and phenotypic differences: postweaning traits and milk yield. 'Direct' and 'maternal' refer to direct and maternal effects, respectively. *p*: see caption for Table 2

	<i>r</i>		n breeds	<i>p</i>	Animal data	Genetic system	References
	Positive	Negative					
Postweaning growth rate	0.446		22	<0.001	M,X	MS	1,4
Postweaning growth rate	0.392		19	<0.001	M,X	B and I	1,2
Calf voluntary feed intake (early)	0.347		12	<0.001	U	MS	4,10
Weight 120 days direct	0.537		12	<0.01	BB,P	MS	4,6
Weight 210 days direct	0.532		12	<0.01	BB,P	MS	4,6
Weight 120 days maternal	0.455		12	<0.01	BB,P	MS	4,6
Weight 210 days maternal	0.284		12	<0.05	BB,P	MS	4,6
Weight 120 days direct	0.579		11	<0.001	BC,P	MS	4,6
Weight 210 days direct	0.564		11	<0.001	BC,P	MS	4,6
Weight 120 days maternal	0.466		11	<0.001	BC,P	MS	4,6
Weight 210 days maternal	0.485		11	<0.001	BC,P	MS	4,6
Live weight 365 days	0.237		14	<0.05	P	MS	4,5
Weight 400 days	0.661		6	<0.01	L,X	MS	4,8
Weight 365 days direct	0.520		12	<0.001	BB,P	MS	4,6
Weight 365 days maternal	0.428		12	<0.001	BB,P	MS	4,6
Weight 365 days direct	0.556		11	<0.001	BC,P	MS	4,6
Weight 365 days maternal	0.495		11	<0.001	BC,P	MS	4,6
Withers height 365 days	0.433		14	<0.001	P	MS	4,5
Average daily gain	0.284		14	<0.01	P	MS	4,5
Maintenance efficiency <sup>a</sup>		-0.397	8	<0.05	P	MS	4,7
Maintenance efficiency <sup>b</sup>	0.395		8	<0.05	P	MS	4,7
Slaughter weight	0.240		14	<0.05	P	MS	4,5
Slaughter age	0.389		14	<0.001	P	MS	4,5
Mature weight	0.193		16	<0.05	M,X	MS	1,4
Weight 600 days	0.594		6	<0.05	L,X	MS	4,8
Milk yield	0.469		10	<0.001	M,X	B and I	1,2
Milk yield	0.353		13	<0.01	M,X	MS	1,4
Milk yield		-0.583	10	<0.001	M,X	SNP	1,3
Milk yield	0.756		11	<0.001	M,X	SNP	1,12
Milk fat%	0.635		8	<0.01	P	MS	4,7

<sup>a</sup>On feeding rate 58 g dry matter/kg<sup>0.75</sup>.

<sup>b</sup>76 g dry matter/kg<sup>0.75</sup>.

M, analysis of literature data 1976–1996; P, purebred design; X, cross-breeding design, analysed to provide information on parental breeds; BB, estimations of breeding values – bulls; BC, estimations of breeding values – cows; L, Least-squares means; U, multibreed design; B and I, biochemical and immunological variants; SNP, single-nucleotide polymorphisms; MS, microsatellites.

References: See caption to Table 1.

genetic distance had been measured using SNPs (Tables 3 and 4).

## Discussion

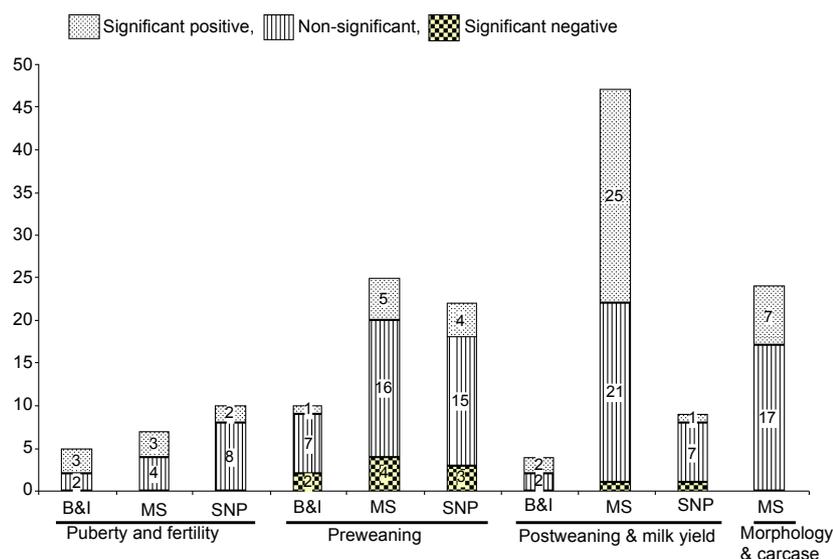
The use of neutral genetic variation in prioritization protocols presumes that maximizing it, through conserving genetically distant breeds, will achieve genetic conservation in relation to adaptive traits. This presumption has been examined. For most of the traits we have studied, there are correlations of pairwise genetic distance with pairwise trait difference. However, for many preweaning traits, there

are negative correlations. While this could in principle be due to convergent evolution in preweaning traits (which might be more subject to a form of natural selection than to artificial selection), it could also be due to differences in genetic architecture (patterns of interaction among loci) between preweaning and postweaning traits. Many productive traits are determined by the additive action of genes at several loci, but other architectures are possible, involving non-additive interactions among loci (Carlborg & Haley 2004). In wild and laboratory populations, traits related to fitness are often of this latter kind (Barker 2000). Formal studies in livestock are

**Table 5** Significant correlations (Pearson's  $r$ ) between pairwise genetic distances ( $D_s$ ) and phenotypic differences: morphological and carcass traits.  $p$ : see caption for Table 2

	$r$		n breeds	$p$	Animal data	Genetic system	References
	Positive	Negative					
Girth at weaning	0.661		6	<0.01	L,X	MS	4,8
Girth 400 days	0.725		6	<0.01	L,X	MS	4,8
Girth 600 days	0.593		6	<0.05	L,X	MS	4,8
Carcass weight	0.270		14	<0.01	P	MS	4,5
Length of hind limb	0.298		14	<0.01	P	MS	4,5
Blockiness index	0.244		14	<0.05	P	MS	4,5
Muscularity at weaning	0.512		6	0.05	L,X	MS	4,8

P, purebred design; X, cross-breeding design, analysed to provide information on parental breeds; L, Least-squares means; MS, microsatellites. References: See caption to Table 1.

**Figure 1** Numbers of correlations obtained for each group of traits, with the genetic distancing methods tabulated on the x-axis. ■■■, significant positive; ■■■■, non-significant; ■■■, significant negative.

lacking, but the general finding that reproduction and fitness traits in cattle are more susceptible than production traits to inbreeding depression (Carrillo & Siewerdt 2010) may be consistent with differences in genetic architecture.

Our findings suggest that while genetic distances may correlate with phenotypic distance for traits relating to puberty and fertility, postweaning and milk yield, and morphology and carcass, they often do not for preweaning traits. Perhaps, the preweaning traits we consider here are more likely to have a non-additive element to their genetic architectures and do not have a clear-cut relationship with neutral genetic variation.

This difficulty facing the use of microsatellites in breed prioritization is additional to the well-established

problem that microsatellite allele frequencies characteristic of breeds are believed to be largely determined by inbreeding and other demographic processes (Bruford 2004) that prevent them acting as unbiased indicators of numbers of generations since divergence of breeds. Thus, protocols based on microsatellite genetic distance may identify, as meriting conservation, breeds that are distinctive primarily because they have rare alleles at many loci through being inbred, rather than breeds that possess a high proportion of the genetic variation within a species (European Cattle Genetic Diversity Consortium 2006) and the value of microsatellites as a component of a protocol for between-breed prioritization continues to be challenged (Medugorac *et al.* 2009).

SNPs may also be handicapped in this respect because of the limited numbers of breeds used in development of chips. In our study, the strongest positive and negative correlations were both obtained for milk yield (+0.756 for French breeds; Gautier *et al.* 2010; and -0.583 for those reviewed by Roughsedge *et al.* 2001), and as both these used genetic distances derived from SNPs, the possibility of a form of ascertainment bias cannot be discounted. It is also clear that SNP-based methods only explain a proportion of the genetic variance in many quantitative traits (Maher 2008).

Recent papers have proposed other approaches – conservation of ‘adaptive variation’ (Toro 2006), continued representation of rare Y chromosome haplotypes (Kantanen *et al.* 2009), prioritization of breeds with high effective population size (Medugorac *et al.* 2009) and optimization of mean kinships (Eding & Meuwissen 2001). The continuing lack of adoption of science-based approaches to breed prioritization (Boettcher *et al.* 2010) shows that biologists are not yet delivering tools that can be used by policy makers in spite of the acknowledged urgency of the situation.

It may be necessary to develop two types of prioritization, one for within-breed prioritization, to enable individuals to be chosen for participation in breeding programmes or representation in gene banks, and the other for between-breed prioritization. These would apply, respectively, though not exclusively, to breeds that may be very strong numerically but of low effective population size (Taberlet *et al.* 2008) and to rarer, locally adapted breeds with generally low productivity. For prioritizing individuals, SNP-based methods or whole-genome sequencing might be appropriate, because genetic architectures may be similar within breeds, while ascertainment bias will not be an issue. For assessing the rarer breeds, molecular data can only contribute if they would reveal which breeds possess specific traits or are particularly rich in the genetic variation that is necessary to meet currently unknown future commercial opportunities, societal needs or environmental challenges. We suggest that neutral markers, whether microsatellites or SNPs, cannot necessarily be relied upon to do this for all traits. It seems highly likely that a molecular conservation measure can only be one of the criteria in prioritization.

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## Appendix

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