

Marker-assisted conservation of European cattle breeds: an evaluation

European Cattle Genetic Diversity Consortium*

Summary

Two methods have been developed for the assessment of conservation priorities on the basis of molecular markers. According to the Weitzman approach, contributions to genetic diversity are derived from genetic distances between populations. Alternatively, diversity within and across populations is optimized by minimizing marker-estimated kinships. We have applied, for the first time, both methods to a comprehensive data set of 69 European cattle breeds, including all cosmopolitan breeds and several local breeds, for which genotypes of 30 microsatellite markers in 25–50 animals per breed have been obtained. Both methods were used to calculate the gain in diversity if a breed was added to a set of nine non-endangered breeds. Weitzman-derived diversities were confounded by genetic drift in isolated populations, which dominates the genetic distances but does not necessarily increase the conservation value of a breed. Marker-estimated kinships across populations were less disturbed by genetic drift than the Weitzman diversities and assigned high conservation values to Mediterranean breeds, which indeed have genetic histories that differ from the non-endangered breeds. Prospects and limitations of marker-assisted decisions on conservation priorities are discussed.

Keywords cattle, conservation, genetic diversity, kinship, microsatellite, Weitzman.

Introduction

Most of the productive dairy and beef cattle breeds kept worldwide are of European origin, and breeds have been shaped by adaptation and selective breeding. Since the second half of the 20th century, breeding became considerably more effective by the introduction of artificial insemination and embryo transfer (Hall 2004). Highly selected breeds and intensively managed breeds such as the dairy Holstein Friesian cattle have now grown in numbers at the expense of local cattle breeds, which have become endangered or extinct. According to estimates of the FAO (2000), 30% of all livestock breeds are at risk of extinction. At the same time, the selection of top sires meeting the breeding objectives has made breeds more uniform and has decreased the effective population size. These developments lead to the loss of genetic variation and adaptations to local conditions or extensive management (Barker 1999).

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Loss of genetic variability and inbreeding in small populations is the main focus of attention in conservation genetics (Hall 2004). In most studies, differences between breeds or populations are quantified as genetic distances, which are calculated on the basis of allele frequencies. In order to translate distances in rational decisions about conservation, several publications (Thaon d'Arnoldi *et al.* 1998; Laval *et al.* 2000; Cañón *et al.* 2001; Reist-Marti *et al.* 2003; Garcia *et al.* 2005) have used the algorithm of Weitzman (1992, 1998) for ranking breeds according to their contribution to total diversity. However, this method ignores the genetic variability within breeds (Garcia *et al.* 2005) as well as the effect of inbreeding on genetic distances. For instance, founder effects and strict genetic isolation increase genetic drift, levels of homozygosity and genetic distances to other breeds, but do not normally lead to unique features (Eding & Meuwissen 2001; Caballero & Toro 2002). On the other hand, a breed with a high level of diversity harbours a relatively high proportion of the total diversity of the species, but generally contributes less to genetic distances than more inbred breeds.

Eding & Meuwissen (2001) developed an alternative method to rank populations according to their contribution to the overall genetic diversity. In this method, molecular markers are used to estimate the mean kinship coefficients

between and within populations (MEK, marker-estimated kinship). This approach weighs markers according to their probability of being alike in state (AIS) without being identical by descent (IBD), so that it reflects the genetic diversity relative to the diversity in a hypothetical founder population. Breeds can be compared via the genetic diversity gained by adding each breed separately to a 'safe set' of breeds that are not at risk (Eding *et al.* 2002).

Recent studies have assessed population structure and genetic uniqueness of cattle breeds (MacHugh *et al.* 1998; Peelman *et al.* 1998; Martin-Burriel *et al.* 1999; Kantanen *et al.* 2000; Cañón *et al.* 2001; Del Bo *et al.* 2001; Maudet *et al.* 2002; Wiener *et al.* 2004). Contributions of breeds to genetic diversity were assessed according to Weitzman criteria (Cañón *et al.* 2001; Reist-Marti *et al.* 2003; Garcia *et al.* 2005), the MEK approach (Mateus *et al.* 2004; Bennewitz *et al.* 2006) or both (Tapio *et al.* in press). However, these studies were on a national or regional scale and did not include genetic resources from other areas.

A recent international study resulted in a data set of genotypes from 69 European cattle breeds across Europe, all containing highly productive breeds as well as several local breeds with different levels of inbreeding (Lenstra & the European Cattle Genetic Diversity Consortium 2004). In this paper, this data set has been analysed using MEKs and different implementations of the Weitzman method.

Materials and methods

Data set

All breeds were genotyped for 30 microsatellite loci recommended for genetic diversity studies by the FAO (<http://www.projects.roslin.ac.uk/cdiv/markers.html>). DNA was isolated from blood or sperm samples collected by the laboratories participating in or collaborating with the Resgen project CT98-118 'Towards a strategy for the conservation of the genetic diversity of European cattle'. Interlaboratory standardization was achieved by typing three reference animals. Consistency of results across laboratories was checked and found to be satisfactory on the basis of the following:

- 1 One hundred per cent agreement with the same samples from Danish and Nordic breeds analysed by Labogena (Jouy-en-Josas) and by the Nordic consortium (Kantanen *et al.* 2000) respectively.
- 2 Breeds that were sampled and typed independently by two or more laboratories were always assigned to the same cluster by model-based clustering (unpublished data of the Consortium) and had standard Nei distances (D_s) of about 0.02, while normal values were in the range of 0.2–0.3.
- 3 Allele frequencies were consistent with the major alleles shared by most of the breeds.
- 4 Laboratory-dependent clustering of breeds was not observed.

A total of 2816 animals representing 69 European breeds with 25–50 animals per breed were typed. The sampling and genotyping of French (Moazami-Goudarzi *et al.* 1997; Cañón *et al.* 2001), Belgian (Peelman *et al.* 1998), Spanish (Martin-Burriel *et al.* 1999; Cañón *et al.* 2001), Swiss (Schmid *et al.* 1999), Nordic (Kantanen *et al.* 2000), North-Italian (Del Bo *et al.* 2001) and British (Wiener *et al.* 2004) breeds have been described previously in more detail. Additional sampling has been carried out by the laboratories in Utrecht, Piacenza, Viterbo, Campobasso, Giessen and Hannover. As a rule, sampled individuals were not directly related. Equal numbers of males and females were sampled with the exception of Dutch breeds, for which only males were used. Model-based clustering (results not shown) led to the differentiation of two Betizu populations sampled at different locations, Betizu1 from one location with an extremely high level of inbreeding (observed heterozygosity $H_o = 0.43$) and Betizu2 from two other locations with a normal level of heterozygosity ($H_o = 0.70$).

Observed heterozygosity and the mean number of alleles were calculated with the Excel microsatellite toolkit (S.D.E. Park, <http://animalgenomics.ucd.ie/sdeparck/ms-toolkit/>). Allelic richness based on minimum sample size of 11 individuals was calculated with the program *ESTAT* (J. Goudet, http://www.unil.ch/dee/page6767_en.html) and averaged over the markers.

Diversity analysis

The Weitzman diversity method was applied on the basis of F_{ST} distances as described previously (Cañón *et al.* 2001). The recommended Average Square Distance (FAO 1995; Goldstein *et al.* 1995) gave almost uniform contributions to the diversity (data not shown). Because the complete data set of 69 breeds was too large to be handled, we first calculated marginal diversities, extinction probabilities and conservation potential for a data set of 49 breeds or combinations of breeds (results not shown) and found that these parameters were highly correlated. For a direct comparison with the results of 69 separate breeds, we then followed two approaches. First, the data set of 69 breeds was split into subsets of 27 and 40 breeds without the highly inbred Betizu1 and Mallorquina, which confounded the analysis due to their large genetic distances to other breeds. For the set of 27 breeds, exact diversities were calculated. Because of computer time constraints, diversities for the 40 breeds were approximated as described (Garcia *et al.* 2005). Partial contributions of breeds to the diversity of the 27- and 40-breed subsets were then calculated as $1 - D(S - i)/D(S)$, where $D(S - i)$ is the diversity of the subset minus breed i . Secondly, we calculated the diversity of a safe set of nine non-endangered breeds with head counts of least 500 000 animals (Holstein Friesian, Belgian Blue, Nor-

mand, Charolais, Limousin, Montbéliard, German Simmental, Simmental and Swiss Brown) and the diversities of 60 safe + 1 sets of the nine safe breeds plus one of the 60 other breeds. Additional diversities are then calculated as $D(\text{safe} + 1)/D(\text{safe}) - 1$.

Diversity calculations on the basis of MEKs have been carried out using a weighed log-linear model as described by Eding & Meuwissen (2003). In short, a set of equations was solved that relate markers and kinships to molecular similarity, assuming that kinship is constant for any pair of individuals or populations across markers and that the probability of being AIS but not IBD is constant for a marker across pairs of individuals or populations. Next, the total genetic diversity $\text{Div}(M)$ was maximized by calculation of a value for the vector of contributions (c) of each breed to the total set that minimized the mean kinship within the set, thus eliminating genetic overlap of breeds. For prioritization of conservation, the c vector and the additional diversity $\text{Div}(M)$ for the same safe set of nine breeds and 60 safe + 1 sets as used for the Weitzman diversity were calculated (Eding *et al.* 2002). Markers *ETH152*, *INRA23* and *TGLA53* were not used because of missing data in several breeds. Calculations were implemented in a Fortran 95 computer program.

Results

Cattle breeds

An overview of the cattle breeds studied is given in Table S1 with the values for intrabreed diversity parameters. These values varied considerably within Europe, with the expected heterozygosity ranging from 0.41 in the isolated Betizu1 population and 0.50 in the Mallorquina island breed to 0.74 in the Podolica. Expected heterozygosities agreed well with other diversity parameters (Table S1), with the highest correlation for allelic richness ($r = 0.945$). Within breeds, most MEKs were in the range of 0.28–0.35, while the extreme value of 0.485 within Betizu1 (Table S1) approached full-sib kinship. Within-breed MEKs also correlated with other diversity parameters ($r = -0.702$ to -0.872).

Table 1 Correlation coefficients (r) of within-breed diversity parameters for 69 European cattle breeds.

Parameter 1	Parameter 2	r
Number of alleles	Allelic richness	0.792
Number of alleles	Expected heterozygosity	0.702
Allelic richness	Expected heterozygosity	0.946
Expected heterozygosity	MEK within breed	-0.828
Observed heterozygosity	MEK within breed	-0.702
Number of alleles	MEK within breed	-0.872
Allelic richness	MEK within breed	-0.810

Weitzman diversity criteria

Weitzman partial contributions to diversity were calculated on the basis of F_{ST} distances for two separate sets of 27 north-western and 40 central or Mediterranean breeds. As shown in Fig. 1, partial contributions are up to 6% for central and Mediterranean breeds (40-breed data set) and up to 9% for north-western breeds (27-breed data set). For the complete data set of 69 breeds, we also calculated the additional diversity by adding a breed to the safe set of nine non-endangered breeds. These additional diversities relative to the safe set were up to 39% for the Betizu1 and 30% for the Mallorquina and correlated well with the partial contributions in the 27- and 40-breed data sets (Fig. 1; $r = 0.89$ and 0.83 respectively).

Significant contributions to Weitzman diversity were also assigned to other relatively homozygous breeds like Danish Red, Jersey, Groningen White-Headed and Highland. The overall correlation of the safe + 1 extra diversity with the expected heterozygosity was -0.85 (0.79 without Betizu1 and Mallorquina, Fig. 2a). Similar trends were observed with marginal diversities and conservation potentials (data not shown).

Marker-estimated kinships

MEKs across breeds (data not shown) were relatively high for central-European breeds (Piemontese, Simmental, Montbéliard and related breeds) and north-western European breeds (Friesian, Red Holstein, Jutland and related breeds).

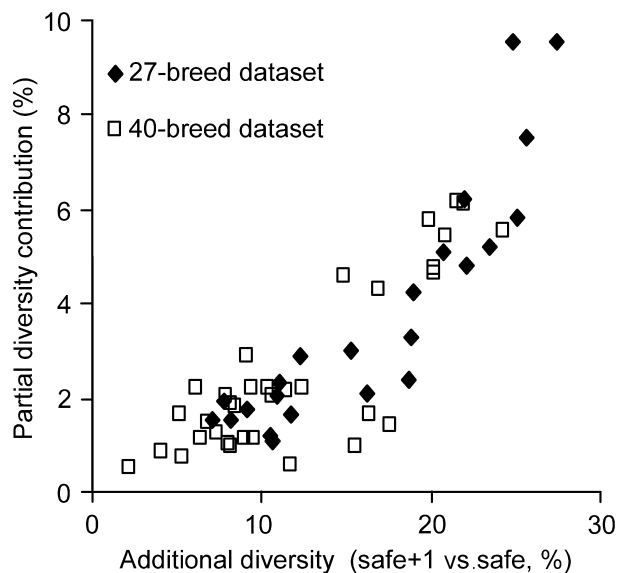


Figure 1 Weitzman partial diversity contributions, calculated for separate data sets of 27 north-western breeds and 40 central and Mediterranean breeds respectively and plotted again the Weitzman additional diversity contributions derived from the gain in diversity if a breed is added to set of nine non-endangered breeds.

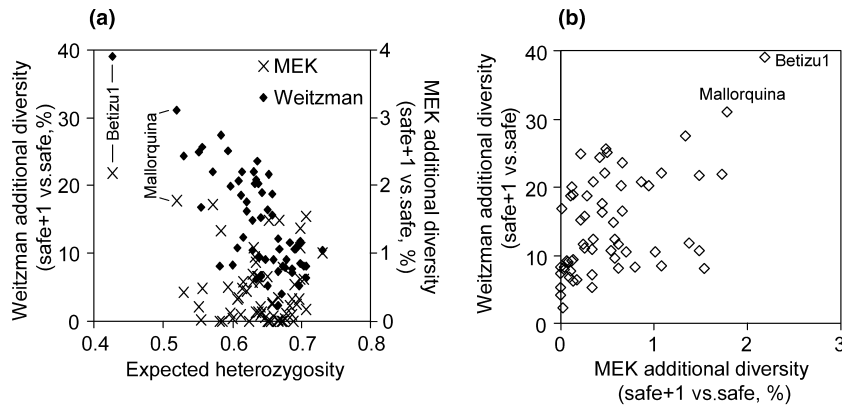


Figure 2 (a) Effect of expected heterozygosity on the gain in diversity by adding breeds to the safe set according to the Weitzman (scale on left axis) and marker-estimated kinship (MEK) approaches (scale on right axis). (b) Lack of correlation of the gain in diversity according to the Weitzman and MEK approaches respectively. The points of Betizu A and Mallorquina, the two most inbred breeds, are indicated.

With optimized breed contributions, the set of nine safe breeds has a diversity (defined as $1 - \text{average kinship}$) of 0.754, which was increased to 0.791 by including all other breeds (Table S1). Diversity gained by adding each breed separately to the safe set, giving the safe + 1 sets, varied from 0% to 1.97%. As shown in Fig. 2a, the two breeds with the highest additional diversities, Betizu1 and Mallorquina, also had the lowest expected heterozygosity, but there was no correlation of expected heterozygosities and additional diversities for the other 58 breeds ($r = 0.05$).

Discussion

Optimal allocation of funding for conservation (Simianer 2002; Simianer *et al.* 2003) has so far not yet been based on molecular analyses. The use of genetic distances as indicators of genetic uniqueness has been criticized (Ruane 1999) because of a poor correlation with phenotypic variation: breed-specific phenotypes may be controlled by only few loci, while genetic distances are most sensitive to genetic drift in small populations. For several livestock breeds this is a recent or still ongoing process.

In this paper, we have evaluated two methods for calculation of conservation priorities on the basis of molecular data. We used a comprehensive data set of European breeds, including all cosmopolitan cattle breeds and several local breeds with varying degrees of inbreeding. For both the Weitzman and the MEK approach, we compared the additional diversity of a safe set of nine non-endangered breeds with a safe + 1 set to which one breed was added. This approach accepts the existence of several industrial breeds (or wildlife populations) that are not likely to be threatened. In contrast, the less realistic Noah's ark problem (Weitzman 1998) implies a replacement of the present cattle population and a *de novo* optimization of diversity. Evidently, the additional diversity of the safe + 1 sets will decrease if a related breed has already been chosen for conservation, so the safe set has to be adapted to the situation. In this paper, we selected cattle breeds with at least 500 000 animals, but national safe-sets with breeds of at least 100 000 animals

yielded similar rankings of conservation priorities (data not shown).

For the Weitzman calculations, the safe + 1 vs. safe approach has the additional benefit of reducing the demand on computation time, which is prohibitive for any data set with a realistic number of breeds. However, there is a poor correlation between the gain in diversity calculated by the Weitzman approach and by the MEKs (Fig. 2b; $r = 0.51$, without the Betizu1 and Mallorquina 0.33). The Weitzman additional diversities are biased towards the most inbred breeds, so prioritization based on the most homozygous breeds differs only slightly from prioritization based on Weitzman diversity. The same trend was present in diversity values published for European pig breeds (Laval *et al.* 2000; $r = -0.89$ for F_{ST} -derived diversities), Spanish breeds (Cañón *et al.* 2001; $r = -0.58$), African taurine and zebu breeds (Reist-Marti *et al.* 2003; $r = -0.58$ and -0.28 respectively) and north Eurasian breeds (Tapio *et al.* in press; $r = -0.72$ for diversity based on chord distance). However, no influence of heterozygosity has been observed for Spanish and French breeds with an implementation of the Weitzman approach that explicitly combines inter- and intra-population information (Garcia *et al.* 2005).

The percentage gain in diversity by adding breeds to the safe set on the basis of the Weitzman approach is clearly higher than according to kinships (Table 1). Most breeds, including those contribute substantially to the Weitzman diversity of the safe + 1 set have been kept as genetically isolated populations for only the last 100–200 years. The most extreme example is the 39% additional diversity calculated for an isolated Betizu population, while a less inbred Betizu contributes only 10.3% (Table S1). So conservation priorities on the basis of genetic distances may reflect genetic isolation rather than realistic contributions to diversity, which violates the assumption that genetic distance is commensurate with 'utility' or 'value' (Weitzman 1998).

The MEK approach (Eding & Meuwissen 2001, 2003; Eding *et al.* 2002) estimates intra- and interbreed diversity

in the same way. Furthermore, a low kinship between individuals implies a higher degree of genomic divergence and hence a higher sequence diversity. In quantitative-genetic terms, lower kinship corresponds to a higher additive genetic variance and therefore to a higher selective gain. By weighing the markers according to the heterozygosity in the base population, kinship is expected to be a better indicator of additive genetic variance than heterozygosity (Falconer 1989).

Inbreeding is not expected to change the kinships across breeds because any individual remains a sample of the original gene pool at the time of the divergence with other breeds (Eding & Meuwissen 2001). However, for the inbred Betizu1 population with several fixed alleles, a higher gain in diversity was calculated than for the less-inbred Betizu2 populations. In addition, the relatively inbred Mallorquina and German Shorthorn have relative high additional diversities. A further refinement of the MEK estimation is required to avoid this apparent effect of inbreeding, which is clearly less than for the Weitzman approach. Other breeds with relatively high contributions to the MEK-defined diversity, like the Podolica, Chianina and Retinta, are from southern Europe. These breeds have genetic histories that are different from those in the safe by their arrival in Europe via the Mediterranean rather than via the Danubian route (Cymbron *et al.* 2005).

Our results suggest that molecular data may indicate conservation priorities, but current methods need to be improved. The incorporation of intrabreed diversity into the Weitzman approach (Garcia *et al.* 2005; Ollivier & Foulley 2005) or into other diversity measures (Tapio *et al.* 2005) may be optimized and tested with a realistic number of breeds as shown in this paper. Interestingly, Simianer (2005) combined the Weitzman approach with expected allele number as a diversity measure, but this approach has not yet been applied to large data sets. Estimation of kinships are sensitive to sampling and may be improved by bootstrapping (Bennewitz & Meuwissen 2005), while the effect of genetic drift in extremely inbred populations on the MEK-based diversity contributions should be accounted for. In addition, for decisions on conservation priorities, the diversity of all local breeds related to the endangered population should be taken into account in order to assess their unique contribution to diversity.

However, it is plausible that selective breeding has led to phenotypic changes encoded by gene variants that are not necessarily linked to any of the 30 microsatellites. Possession of valuable traits may be an explicit and independent criterion for conservation, which would become easier if the causal mutations are identified. Furthermore, the value of breeds in the local tradition and history should not be ignored (Gandini & Villa 2003). Finally, several breeds are of mixed origin (Felius 1995; Hall

2004), which should not be considered as undesirable genetic contamination, but as an integral part of the history of a breed.

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Supplementary Material

The following supplementary material is available for this article online from <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2052.2006.01511.x>

Table S1 European breeds, within-breed diversity parameters and diversity contributions.

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Appendix

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