Conserv Genet (2010) 11:635–641
DOI 10.1007/s10592-009-0007-x

RESEARCH ARTICLE

Perspectives of genomics for genetic conservation of livestock

Jack J. Windig · Krista A. Engelsma

Received: 13 July 2009 / Accepted: 12 October 2009 / Published online: 5 November 2009

Abstract Genomics provides new opportunities for conservation genetics. Conservation genetics in livestock is based on estimating diversity by pedigree relatedness and managing diversity by choosing those animals that maximize genetic diversity. Animals can be chosen as parents for the next generation, as donors of material to a gene bank, or as breeds for targeting conservation efforts. Genomics provides opportunities to estimate diversity for specific parts of the genome, such as neutral and adaptive diversity and genetic diversity underlying specific traits. This enables us to choose candidates for conservation based on specific genetic diversity (e.g. diversity of traits or adaptive diversity) or to monitor the loss of diversity without conservation. In wild animals direct genetic management, by choosing candidates for conservation as in livestock, is generally not practiced. With dense marker maps opportunities exist for monitoring relatedness and genetic diversity in wild populations, thus enabling a more active management of diversity.

Keywords Conservation genetics · Genomics · Livestock · Genetic management · Optimal contributions · Dense marker maps

J. J. Windig (✉) · K. A. Engelsma
Animal Breeding and Genomics Centre, Wageningen UR Livestock Research, The Netherlands, Wageningen UR, P.O. Box 65, 8200 AB Lelystad, The Netherlands
e-mail: Jack.Windig@wur.nl

J. J. Windig · K. A. Engelsma
Centre for Genetic Resources, The Netherlands, Wageningen UR, P.O. Box 65, 8200 AB Lelystad, The Netherlands

Introduction

Conservation genetics aims to preserve genetic diversity within and across populations. It is applied to both wild animals and plants as well as to domesticated species, although workers in the field of wild and agricultural biodiversity largely operate separately. With the arrival of genomics new opportunities open up for a detailed understanding of genetic diversity across the genome and the processes involved in generating or losing this diversity. In many livestock species whole genome sequencing generated large numbers of markers across the genome. These dense marker maps start now being used in animal breeding (Green 2009). In conservation of livestock breeds new methods for the utilization of dense marker maps (genome scans) for prioritization in conservation are being developed which may also have a relevance for wild organisms.

The availability and type of markers available for DNA typing has changed dramatically. SNP-markers are now becoming the standard and for example in cattle DNA-chips with more than 50,000 SNPs are now available and a 600,000 SNP chip is planned (Gibbs et al. 2009). In chicken close to 2,800,000 SNPs are available (Wong et al. 2004). Traditionally in animal breeding markers have been used for parentage testing to validate pedigrees, and are increasingly used for deciding which animals to use in breeding. Until recently, in animal breeding the focus was on QTL detection, but now breeding value estimation with markers, so called genomic selection, has been developed (Goddard and Hayes 2007).

For conservation genetics dense marker maps provide the opportunity to follow in detail the effect of selection, genetic drift and other processes influencing genetic diversity. In contrast to micro-satellites this means that variation in diversity within the genome, and even within

chromosomes or parts of chromosomes, can be investigated. Consequently, the effect of processes on the pattern of genetic diversity across the genome can be investigated, and the reverse from the pattern of genetic diversity across the genome processes in the past such as selective sweeps and bottlenecks can be inferred. However, in conservation genetics dense marker maps have not been widely used yet.

This paper explores the possibilities dense marker maps offer for conservation of livestock breeds. We first outline conservation genetics in animal breeding and then outline possibilities offered by genomics. There are many more applications of 'omics' technologies that can be useful in conservation genetics (e.g. Kammenga et al. 2007; Kristensen et al. 2010). We focus, however, on dense marker maps since these may enable the application in wild species of tools developed for genetic management of livestock species. We end the paper with some thoughts on how this can be achieved.

Conservation of livestock diversity

Livestock provides food for the world in the form of eggs, milk and meat, and billions of people depend for their livelihood on livestock. Globally, there is a growing demand for livestock products and production systems are changing and intensifying to meet this demand. As a consequence a few high input–high output breeds dominate globally, while local low input breeds are at risk. Yet, local breeds may provide the genetic diversity needed to cope with climate change, may provide ecosystem services, are important in the light of the millennium development goals to reach global food security and harbor genetic diversity to anticipate changes in food quantity and quality demand. Therefore actions are taken worldwide to preserve genetic diversity in livestock breeds and to safeguard the genetic basis of livestock production, which objectives are reflected in the FAO Global Plan of Action for Animal Genetic Resources (FAO 2007a) and the Convention on Biological Diversity (CBD 1992).

Worldwide efforts are undertaken to conserve diversity of Livestock. Monitoring the number of breeds, their population sizes and degree of endangerments is coordinated by the FAO on a global level. The FAO State of the World's Animal Genetic Resources report shows that roughly one-third of all breeds is considered to be at risk (FAO 2007b). Moreover, even within breeds that dominate the world intensive selection and use of a few sires has lead to low effective population sizes and a loss of genetic diversity (Taberlet et al. 2008).

Molecular characterization of diversity is undertaken for many breeds, for example with large scale projects in cattle (Lenstra 2006), and pigs (Megens et al. 2008). Genetic management and conservation of endangered breeds take place in situ (e.g. breeding/conservation by farmers/breed societies) and ex situ (e.g. cryopreservation in gene banks). Tools for genetic management and conservation have been developed such as computer programs that select parents for breeding to minimize inbreeding levels and conserve genetic diversity, and procedures for estimating relatedness and diversity from molecular markers.

Conservation genetics: the animal breeders view

Animal Breeders and other quantitative geneticists focus on additive genetic variance and heritability of traits when analyzing genetic diversity. Diversity is generally measured as $1 - f$ [f = average kinship or coancestry in a (sub)population] or $1 - F$ [F = average inbreeding in a (sub)population] (Toro 2006). $1 - F$ is directly related to both additive variance and heterozygosity. Theoretically the relative loss in heterozygosity is $H_t/H_0 = 1 - F$ where H_t is heterozygosity in generation t and H_0 in the founder generation (Falconer and Mackay 1996). For additive variance (V_A) a similar relationship exists: $V_{A,t}/V_{A,0} = 1 - F$ (Gilligan et al. 2005). Consequently, in order to manage genetic diversity it is best to minimize the average kinship in a population (or its equivalent average relatedness $r = 2f$).

The choice of parents determines the level of inbreeding and genetic diversity in the next generation. Consequently, maximization of genetic diversity is achieved by minimizing the average relatedness of the parents. The average relatedness of parents can be estimated by $r = \mathbf{c'Ac}$, where $\mathbf{A}$ is the relationship matrix of all potential parents and $\mathbf{c}$ is a contribution vector. In this vector each element gives for each potential parent the fraction of genes it contributes to the next generation. Meuwissen (1997) derived equations for the optimal contributions, i.e. selecting parents with the minimum average relatedness and the additional constraint that for biological reasons 50% of the contributions have to be of male origin and the other 50% of female origin. Optimal contributions have been applied in conservation of, for example, a sheep breed (Windig et al. 2007), a goat breed (Mucha and Windig 2009), and a pig breed (Fabuel et al. 2004).

The principle of minimizing relatedness not only applies to the choice of parents for producing the next generation in breeding programs, but also to the choice of candidates for a gene bank (ex situ) in order to maximize the genetic diversity conserved in the gene bank. It can also be applied to prioritization of breeds for conservation when (financial) resources are limited. Eding and Meuwissen (2001) worked out the principles to estimate average relatedness between different breeds based on microsatellite markers and to determine the optimal contributions of different breeds to a

gene bank, so that the maximum amount of diversity is conserved. Based on this method, an interesting approach is to determine a *safe set* of breeds (Eding et al. 2002) which, for example, consists of the large commercial breeds that are not endangered or breeds that are already in the gene bank. The next step is to determine what genetic diversity each additional (non-safe) breed would add to the *safe set*. Those breeds that add most to the *safe set* then have the highest priority for conservation.

European-wide research projects for sheep (Peter et al. 2007) and cattle (Lenstra 2006) indicate that at the genetic level clusters correlate with geography rather than function. This suggests that for prioritization one could decide to choose one breed from each region, rather than one breed from each functional type (e.g. dairy, meat, dual purpose and in case of sheep wool breeds). Indeed optimal contributions for cattle indicate as the top three for prioritization a breed from South Europe (Chiannina, from Italy) a breed from NW Europe (German Shorthorn from Germany with British ancestors) and a breed from Central Europe (Normand from France). This may suggest that selection for production (e.g. milk production or muscle growth) has been either on different sets of genes influencing production in different breeds or that genes influencing production only form a small part of the total genetic diversity. A limited set of micro-satellites cannot distinguish between the two options, but genomics may provide answers.

Conservation genomics

The development of molecular techniques is advancing rapidly in many areas. Here we focus on the use of high throughput genetics to type large numbers of animals for large numbers of SNPs (e.g. >10,000). With this number of markers not only the average relatedness between individuals or breeds can be estimated, but also relatedness of parts of the genome. Up to now conservation is based on pedigree relatedness, as a measure of diversity, which indicates the probability that two alleles drawn at random from the genome in two individuals (or breeds) will be the same. However, diversity varies over the genome due to, for example, selection on specific genes. Consequently, maximizing the amount of genetic diversity with optimal contributions based on the average relatedness may not maximize diversity for all parts of the genome. Simulations showed that when a population has been selected with the help of QTL information (Gene Assisted Selection) inbreeding rate in the region surrounding the QTL was much higher than the overall pedigree estimated inbreeding rate (Pedersen et al. 2009). Consequently, there is a risk that when selection of candidates for a gene bank is based on average relatedness genetic diversity in and around QTLs for selected traits is lost.

Dense marker maps enable a more precise location of QTLs on the genome, while sequencing enables the detection of causative mutations (e.g. Meuwissen et al. 2002; Karlsson et al. 2007). In animal breeding, however, the use of QTLs and causative mutations proved not to be easy. Generally only a few QTLs underlying a trait are detected and the bulk, those with a small effect, remain undetected. When concentrating selection on a QTL there is a risk that the polygenic background is depleted and in the longer run selection gains are less (Chakraborty et al. 2002). Moreover, it is generally not needed to know the function and location on the genome of genes underlying traits for efficient breeding. Consequently, the focus in animal breeding shifted to genomic selection. In genomic selection markers are associated with breeding values without identifying the underlying QTLs. Using this information breeding values can be estimated based on marker genotypes for individuals without phenotypes or (enough) relatives for breeding value estimation. Similar techniques can be used in conservation to determine genetic variation across the genome for specific (groups) of traits.

Variation over the genome is caused by mutation, selection and random processes. The latter was demonstrated in a simple computer simulation (Engelsma submitted). A base population was set up with 2000 SNP markers on a single chromosome of 1 Morgan, each allele drawn with a 50% probability. Each generation consisted of 50 males and 50 females that mated at random. After 100 generations relatedness was estimated for each marker interval. Fixation occurred for 192 markers. The variation at the remaining loci is illustrated in Fig. 1. Clearly, although the variation was only generated by drift, mating and recombination, it was large and average relatedness was a poor predictor of relatedness at single loci. Consequently if conservation is based on average relatedness, as is common practice, variation at specific sites across the genome will be missed.

Dense marker maps provide the opportunity to monitor genetic variation at small stretches of the genome. In other words, instead of working with the fraction of DNA that is similar between two individuals (or breeds) one can look at which fraction is similar. For choosing candidates to maximize diversity, whether as parents for the next generation, candidates for a gene bank or breeds for conservation efforts, this means that we can monitor the genetic diversity that is actually preserved and target our efforts towards specific parts of the genome. In this respect one can make use of tools that have been developed to identify regions where diversity has been decreased or increased under the influence of selection, admixture, bottlenecks or population subdivision.

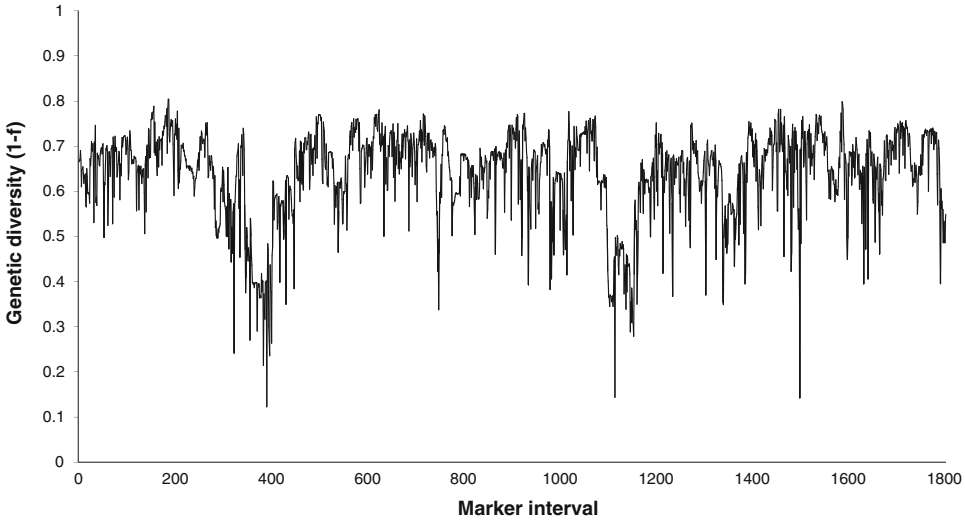

Fig. 1 Genetic diversity, estimated as 1—average population relatedness, across a chromosome simulated in a computer. Variation was generated by neutral processes (drift, mating and recombination) in 100 generations for a 1 M chromosome with 2,000 markers in a random mating population with an effective population size of 100. 1,792 markers still segregated at generation 100

Gene banks are used to conserve diversity ex situ and ex vivo. The advantage is that all diversity in the gene bank is conserved for an indefinite time. The disadvantage is that adaptation to changing environments cannot occur. Conservation herds are sometimes formed to conserve breeds in vivo, but ex situ, in which some adaptation may occur. In the long run this may be less sustainable as these herds generally depend on subsidies. The general argument is that the most sustainable way to conserve breeds is on farms on a commercial basis, although this may lead to a loss of genetic diversity when intensive selection is applied. The loss in genetic diversity and adaptation under these different schemes have never been quantified. Genomics provides interesting opportunities, not only to quantify the loss in diversity, but also to link it to genetic variation underlying traits or, for example, inbreeding.

A long standing question is whether special attention is needed for specific traits when storing material in gene banks. When storing is based on pedigree relatedness and optimal contributions the assumption is that for polygenic traits, such as fitness and production traits, all variation is adequately captured. One assumption is that the coding DNA for trait variation is randomly distributed over the genome. With dense marker maps this can be actually investigated. Perspectives, however, go further. One may also investigate what variation is lost. For example, variation lost or conserved can be compared with variation in known QTL or regions with known QTL (Salih and Adelson 2009). Such comparisons can be made for different methods of selection of candidates e.g. random selection, selection based on pedigree relatedness and optimal contributions or on variation of a single trait (either phenotypically or in breeding values). Results can help to decide whether attention to genetic variation of single traits is needed when conserving diversity.

An example where the usefulness of directing conservation efforts on single traits is an issue is selection for scrapie resistance. Scrapie is a disease for which the ARR allele of the causative prion protein gene confers full resistance. To eradicate the disease a European wide program was initiated to fixate the ARR allele, or at least eliminate the most susceptible allele VRQ in all breeds in Europe. In some European countries this was combined with an effort to preserve material from animals with alleles to be eliminated in gene banks. Calculations on the genetic diversity conserved in both the prion gene and the rest of the genome showed that a different set of animals is selected when both criteria are used (Fernandez et al. 2006).

The future of livestock diversity continues to be under pressure. Domination of food production by a few high input/high output breeds is likely to increase, and so is the loss of diversity within breeds. In most species the latest animals produced by breeding companies are superior in performance compared to previously produced animals. It is likely that these high genetic merit animals will replace the low genetic merit animals in the near future. Genomics may help to predict the associated loss of genetic variation and detail what variation where on the genome will be lost. Unwanted side effects of selection for high production, such as the decreased fertility seen in breeds with a high milk production (Rauw et al. 1998) may be better predicted and conservation efforts be tailored to this predicted loss.

Conservation may at first sight seem less important for animal breeders of common high input/high output breeds. However, maintaining genetic diversity within those breeds in order to secure future genetic responses to selection is relevant. Conserving diversity in the form of low input/low output breeds is also relevant for high input breeds, since genes conserved in these breeds may be needed in the high

input breeds in the future. In cattle, for example, there is currently much interest to introgress the naturally hornless gene into high production breeds (Prayaga 2007). Dense marker maps can be very useful in introgression programs (Hospital 2001).

Conservation of low input breeds may benefit from efforts in high input breeds. Sequencing efforts and SNP discovery programs will produce large numbers of markers useful for all breeds of the same species. A cautionary note is needed here: a SNP panel generated in another breed will be incomplete. Polygenic markers in one breed can be fixed in another breed, and consequently, variation may be underestimated. Also, linkage disequilibrium between markers will be different, and marker associations with traits will vary over breeds. De Roos et al. (2008) estimated that therefore a panel of at least 300,000 markers is needed to effectively use marker associations derived for one breed in another breed for genomic selection.

Dense marker maps developed for one species (e.g. domesticated) can also be of use for other species (e.g. wild). SNPs may be polymorphic in both species. Pertoldi et al. found that 2.9% of the bovine markers were polymorphic in the Bison as well. MacEachern et al. (2009) found 10.7% of bovine markers to be polymorphic in either the Yak or the Bantang or both. This implies that not all, but still a large numbers of polymorphic markers are available for relatives of sequenced species. However, one must bear in mind that these are only markers that have remained polymorphic since the last common ancestor (typically more than 1 million years ago). Most polymorphic markers will be missed in the non-sequenced species, and the used panel is not a random sample. The selection history will be different for markers that remained polymorphic for 1 million years or more compared to more recently derived markers. Maceachern et al. (2009) used this difference by comparing allele frequencies for derived alleles with ancestral polymorphisms (e.g. polymorphic markers in cattle and Yak, Bison or Banteng). They showed that the frequency spectrum of derived alleles indicated non-neutrality. They also could estimate a historic effective population size of around 90,000 animals for cattle with a sharp decrease after domestication.

Relevance of genomics for conserving genetic variation in wild populations

Up to now we have spoken about conservation genetics in livestock. Although there are clear differences with wild species there are also similarities. Conservation genetics in livestock focuses on breeds, while in wild organisms the focus is on populations. From a population genetic viewpoint breeds and (sub)populations behave the same. Interactions such as matings generally take place within populations (breeds) but occasional exchange between populations (breeds) is possible and indeed happens now and then. Populations (breeds) are dynamic and may split into sub-populations (lines) which may become populations (breeds) themselves.

The main difference between livestock breeds and wild populations is in the degree of management that is applied. In livestock it is generally the farmer who decides which animals mate, how many of the offspring are maintained, which animals are culled and which animals are brought in from outside. Consequently, genetic conservation often consists of direct actions such as selecting parents based on optimal contributions (Fabuel et al. 2004) or exchanging individuals between herds (Windig and Kaal 2008). Genetic conservation in wild populations is generally indirect such as, for example, maintaining corridors between populations to facilitate exchange of individuals. Active management, such as selecting parents for the next generation, is generally only possible in captive populations in, for example, zoos or those used for supportive breeding.

Genomics may facilitate genetics in wild populations (e.g. Slate et al. 2009). Tools developed for genetic conservation of livestock species generally require knowledge of genetic relations (e.g. optimal contributions). With the use of markers, relatedness can also be estimated without pedigrees in the field (Oliehoek et al. 2006). This opens up the possibility to base management decisions on relatedness and inbreeding coefficients of individuals. Such management decisions can be to introduce or remove individuals within populations or exchange individuals between populations to reduce inbreeding rates and increase genetic diversity. Such active involvement is generally not practiced, although culling does occur frequently. This culling may be targeted towards specific phenotypes e.g. on for example antler size in deer (Allendorf and Hard 2009). If instead targeted culling is based on relatedness genetic diversity may be better conserved.

Targeted culling to maintain genetic diversity was practiced in semi-wild cattle population in the Netherlands (Windig unpublished), from which each year a certain number of animals had to be removed. Animals had been typed and based on marker estimated relatedness and optimal contributions animals not selected as parents were removed. As a consequence inbreeding increased less than expected based on effective population size. An unexpected consequence was that the formerly rare blond genotype became more abundant, to the dislike of the nature conservancy owning the population. Thus, targeted culling based on relatedness can reduce inbreeding rates but conserving all diversity (e.g. for coat colour) is not always desired. Genomics may help distinguish between

desired and unwanted genetic diversity, but deciding what is wanted and what is not is a big challenge.

Since pedigrees generally lack in wild populations it is difficult to determine breeding values in the field. However, the techniques developed for genomic selection in livestock enable the estimation of breeding values without pedigree information (Meuwissen et al. 2001; Goddard and Hayes 2007). This may be useful in, for example, detailing the effects on genetic diversity when population sizes decrease. Questions that may be answered with the help of genomics are whether the proportion of genetic diversity lost is equal for all traits, whether there is a difference between neutral genetic variation and adaptive genetic variation, or differences between chromosomal regions with low and high diversity. Similarly differences between populations can be detailed.

Acknowledgements Sipke Joost Hiemstra provided comments on an earlier version. This study was financially supported by the Dutch Ministry of Agriculture, Nature and Food (Programme KB-04-002-021).

References

Allendorf FW, Hard JJ (2009) Human-induced evolution caused by unnatural selection through harvest of wild animals. Proc Natl Acad Sci USA 106:9987–9994

CBD (1992) Convention on Biological Diversity

Chakraborty R, Moreau L, Dekkers JCM (2002) A method to optimize selection on multiple identified quantitative trait loci. Genet Sel Evol 34:145–170

De Roos APW, Hayes BJ, Spelman RJ, Goddard ME (2008) Linkage disequilibrium and persistence of phase in Holstein-Friesian, Jersey and Angus cattle. Genetics 179:1503–1512

Eding H, Meuwissen THE (2001) Marker-based estimates of between and within population kinships for the conservation of genetic diversity. J Anim Breed Genet 118:141–159

Eding H, Crooijmans R, Groenen MAM, Meuwissen THE (2002) Assessing the contribution of breeds to genetic diversity in conservation schemes. Genet Sel Evol 34:613–633

Fabuel E, Barragan C, Silio L, Rodriguez MC, Toro MA (2004) Analysis of genetic diversity and conservation priorities in Iberian pigs based on microsatellite markers. Heredity 93:104–113

Falconer DS, Mackay TFC (1996) Introduction to Quantitative Genetics. Longman Group, Essex, UK

FAO (2007a) Global plan of action for animal genetic resources and the Interlaken declaration. FAO, Rome, Italy

FAO (2007b) The state of the world's animal genetic resources for food and agriculture. FAO, Rome, Italy

Fernandez J, Roughsedge T, Woolliams JA, Villanueva B (2006) Optimization of the sampling strategy for establishing a gene bank: storing PrP alleles following a scrapie eradication plan as a case study. Anim Sci 82:813–821

Gibbs RA, Taylor JF, Van Tassell CP et al (2009) Genome-Wide Survey of SNP Variation Uncovers the Genetic Structure of Cattle Breeds. Science 324:528–532

Gilligan DM, Briscoe DA, Frankham R (2005) Comparative losses of quantitative and molecular genetic variation in finite populations of Drosophila melanogaster. Genet Res 85:47–55

Goddard ME, Hayes BJ (2007) Genomic selection. J Anim Breed Genet 124:323–330

Green RD (2009) ASAS Centennial Paper: future needs in animal breeding and genetics. J Anim Sci 87:793–800

Hospital F (2001) Size of donor chromosome segments surrounding introgressions and the reduction of linkage drag in marker-assisted backcross programs. Genetics 158:1363–1379

Kammenga JE, Herman MA, Ouborg NJ, Johnson L, Breitling R (2007) Microarray challenges in ecology. Trends Ecol Evol 22:273–279

Karlsson EK, Baranowska I, Wade CM et al (2007) Efficient mapping of Mendelian traits in dogs through genome-wide association. Nat Genet 39:1321–1328

Kristensen TN, Pedersen KS, Vermeulen CJ, Loeschcke V (2010) Research on inbreeding in the 'omic' era. Trends Ecol Evol (in press)

Lenstra JA (2006) Marker-assisted conservation of European cattle breeds: an evaluation. Anim Genet 37:475–481

MacEachern S, Hayes B, McEwan J, Goddard M (2009) An examination of positive selection and changing effective population size in Angus and Holstein cattle populations (Bos taurus) using a high density SNP genotyping platform and the contribution of ancient polymorphism to genomic diversity in Domestic cattle. BMC Genomics 10:181

Megens HJ, Crooijmans R, Cristobal MS, Hui X, Li N, Groenen MAM (2008) Biodiversity of pig breeds from China and Europe estimated from pooled DNA samples: differences in microsatellite variation between two areas of domestication. Genet Sel Evol 40:103–128

Meuwissen THE (1997) Maximizing the response of selection with a predefined rate of inbreeding. J Anim Sci 75:934–940

Meuwissen THE, Hayes BJ, Goddard ME (2001) Prediction of total genetic value using genome-wide dense marker maps. Genetics 157:1819–1829

Meuwissen THE, Karlsen A, Lien S, Olsaker I, Goddard ME (2002) Fine mapping of a quantitative trait locus for twinning rate using combined linkage and linkage disequilibrium mapping. Genetics 161:373–379

Mucha S, Windig JJ (2009) Effects of incomplete pedigree on genetic management of the Dutch Landrace goat. J Anim Breed Genet 126:250–256

Oliehoek PA, Windig J, Arendonk JAM, Bijma P (2006) Estimating relatedness between individuals in general populations with a focus on their use in conservation programs. Genetics 173:483–496

Pedersen LD, Sørencen AC, Berg P (2009) The number of genes underlying a trait under selection affects the rates of expected and true inbreeding more than their distribution over the genome recovery. In: Book of abstracts of the 60th annual meeting of the European association for animal production. Wageningen Academic, Wageningen, p 319

Peter C, Bruford M, Perez T, Dalamitra S, Hewitt G, Erhardt G (2007) Genetic diversity and subdivision of 57 European and Middle-Eastern sheep breeds. Anim Genet 38:37–44

Prayaga KC (2007) Genetic options to replace dehorning in beef cattle—a review. Aust J Agric Res 58:1–8

Rauw WM, Kanis E, Noordhuizen-Stassen EN, Grommers FJ (1998) Undesirable side effects of selection for high production efficiency in farm animals: a review. Livest Prod Sci 56:15–33

Salih H, Adelson DL (2009) QTL global meta-analysis: are trait determining genes clustered? BMC Genomics 10:184

Slate J, Gratten J, Beraldi D, Stapley J, Hale M, Pemberton JM (2009) Gene mapping in the wild with SNPs: guidelines and future directions. Genetica 136:97–107

Taberlet P, Valentini A, Rezaei HR, Naderi S, Pompanon F, Negrini R, Ajmone-Marsan P (2008) Are cattle, sheep, and goats endangered species? Mol Ecol 17:275–284

Toro MA (2006) Assessing genetic diversity between breeds for conservation. J Anim Breed Genet 123:289

Windig JJ, Kaal L (2008) An effective rotational mating scheme for inbreeding reduction in captive populations illustrated by the rare sheep breed Kempisch Heideschaap. Animal 2:1733–1741

Windig JJ, Meuleman H, Kaal L (2007) Selection for scrapie resistance and simultaneous restriction of inbreeding in the rare sheep breed "Mergellander". Prev Vet Med 78:161–171

Wong GKS, Liu B, Wang J et al (2004) A genetic variation map for chicken with 2.8 million single-nucleotide polymorphisms. Nature 432:717–722