# Objectives, criteria and methods for using molecular genetic data in priority setting for conservation of animal genetic resources

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**Summary**

The genetic diversity of the world's livestock populations is decreasing, both within and across breeds. A wide variety of factors have contributed the loss, replacement or genetic dilution of many local breeds. Genetic variability within the more common commercial breeds has been greatly decreased by selectively intense breeding programs. Conservation of livestock genetic variability is thus important, especially when considering possible future changes in production environments. The world has more than 7500 livestock breeds and conservation of all of them is not feasible. Therefore, prioritization is needed. The objective of this paper is to review the state of the art in approaches for prioritization of breeds for conservation, particularly those approaches that consider molecular genetic information, and identify any shortcomings that restrict their application.

The Weitzman method was among the first and most well-known approaches to use molecular genetic information in conservation prioritization. This approach balances diversity and extinction probability to yield an objective measure of conservation potential. However, this approach was designed for decision making across species and measures diversity as distinctiveness. For livestock, prioritization will most-commonly be done among breeds within species, so alternatives that measure diversity as co-ancestry (i.e. also within-breed variability) have been proposed. Although these methods are technically sound, their application has generally been limited to research studies; most existing conservation programs have effectively based decisions primarily on extinction risk. The development of user-friendly software incorporating these approaches may increase their rate of utilization.

**Key Words:** livestock, genetic diversity, conservation, prioritization

## Introduction

***Justification for conservation of animal genetic resources***

Wide agreement exists on the need to conserve the genetic diversity of animal genetic resources (AnGR). Genetic diversity is necessary for genetic change within a biological population. Genetic diversity of AnGR allows for the sustained ability of a breed or population to respond to selection to increase productivity and for adaptation to changing environmental conditions, including not only those conditions associated with climate, but also to changes in markets, management and husbandry practices and disease challenges. In turn, conservation of diversity of AnGR helps ensure long-term food security. In addition, conservation of specific AnGR may be necessary to preserve particular cultural and historical values, to sustain the bequest value of livestock, and to fulfill the rights of an existing genetic resource to continue to exist (Hanotte *et al.*, 2005). Conservation is one of the four Strategic Priority Areas of the recently adopted Global Plan of Action for Animal Genetic Resources (FAO, 2007a), underlining the need for governments to address the topic in national plans for management of AnGR.

Conservation of AnGR involves a cost. For some breeds of livestock, i.e., those that are independently economically sustainable under the existing market conditions, costs may be imperceptible. Conservation of genetic diversity may simply involve application of selection and mating strategies to optimize genetic response in the long term, potentially diminishing somewhat the gains in the short term. In other situations, conservation of AnGR will require a specific financial investment. Breeds that are not economically sustainable under the current market conditions will require subsidies or incentives to remain viable *in situ*. Otherwise, expenditures will be needed to establish *ex situ* conservation programs. In addition, *ex situ* conservation of economically feasible breeds may be undertaken as insurance against a possible future catastrophe, which would also require real investment of funds.

### *The need to prioritize animal genetic resources for conservation*

More than 7500 different breeds of livestock are recognized globally (FAO, 2007b). Conservation of all livestock breeds is considered to be financially infeasible (Bennewitz *et al.*, 2007). A large proportion of global AnGR are in developing countries, and increasing productivity in the short term is often the main goal of breeding activities in such countries. Only a limited amount of funding would be available for conservation in such conditions. In industrialized countries, for-profit companies often have some control over genetic resources and investment in long-term conservation may not be considered as important financially as in maximizing genetic response, especially when planning horizons are short and competition exists among multiple countries. Alternatively, if conservation programs are supported by the government, including all breeds may not be the most responsible way to spend the money of taxpayers.

Conservation of all breeds may also not be necessary or scientifically justifiable, depending on the goal of the conservation program. Some breeds may be judged to have no particularly unique or valuable characteristics worth conserving, either for the immediate or long-term, and have little historical or cultural significance. In other cases, a group of breeds may be genetically similar, meaning that a sufficiently large proportion of the genetic diversity of the group can be captured by conserving only a subset of breeds. Assuming that all AnGR can not be conserved, a process of prioritizing breeds is necessary.

### *Factors influencing priority of breeds for conservation*

A wide number of factors could potentially contribute to the decision regarding the priority of breeds for conservation. In most instances, a primary objective of a conservation program will be to preserve as much genetic diversity as possible. For AnGR, this objective usually refers to

conservation of as much intra-species diversity as possible. In this regard, conserving diversity both within and among breeds is important. Pedigree information or knowledge of a breed's history can be used to assess the genetic diversity of a breed and can be expressed quantitatively through estimates of population genetic parameters such as effective population size. In many instances, however, pedigree information will not be available or will be variable across breeds, especially in developing countries.

Alternatively, molecular genetic information can be used and selectively-neutral, anonymous genetic markers, primarily microsatellites, have typically been to date the genomic tool of choice for the capture of information relative to the genetic diversity of AnGR. Such markers give an insight on breed history and provide information regarding both the distinctiveness (across-breeds) and the (within-breed) diversity of a breed. They can also be used to help quantify the potential for future evolution.

Phenotypic performance for traits associated with productivity and adaptation may also influence priority for conservation. Data for such traits can be used to formally estimate quantitative genetic merit and genetic variability. Molecular information about known genes with putative effects on traits of current and future interest may also be considered in the priority of a breed for conservation, as breeds with large frequencies of favourable alleles would generally be preferred.

In addition to genetics related variables, breed demographics will also impact decisions regarding conservation. Reist-Marti *et al.*, (2006) proposed a number of factors that contributed to priority for conservation among a group of African cattle breeds. Among these factors were the total population size of the breed and trends in population size in the previous 10 years, distribution of the breed within the country, degree or risk of indiscriminate crossbreeding, level of organization of farmers, existence of ongoing conservation schemes, political stability of the country, sociocultural importance of the breed and the reliability of the information. In general, these

factors all contribute to the risk of extinction of the population. Breeds with small population sizes and large risk for extinction should generally receive greater priority in conservation programs. However, when population size of a breed is too small or risk for extinction is too great, its conservation may not be justified. The probability of extinction may remain high, despite conservation efforts or the effective population size may be very small, meaning that diversity within the breed is too little and attempts at conservation may not be cost-efficient (Ruane, 2000).

Finally, other factors such as the existing level of technical capacity of a given country and practical considerations may influence decisions on conservation and may affect choices of species as well as breeds. For example, cryopreservation of bovine germplasm, both semen and embryos, is more simple from a technical perspective than for most other livestock species. A given country may also have existing semen collection activities for certain breeds, which would make conservation less expensive for those breeds than for other breeds for which conservation would require new expenditures for acquisition and training of semen donors.

***The need for decision support in prioritization of breeds for conservation***

Because most countries have a large number of livestock breeds and the relative importance of breeds for conservation relies on many different factors, each with different levels of importance and with possible interactions among them, prioritization can be a complicated process. Various researchers have tried to address this problem, by proposing mathematical approaches to summarize the multiple variables associated with conservation and AnGR by priority or propose a set of AnGR for conservation given a certain amount of resources for conservation (e.g. Weitzman, 1992; Eding *et al.* 2002; Caballero & Toro, 2002; Simianer *et al.*, 2003). The proposed methods each have their advantages and disadvantages and their respective

appropriateness depends upon the situation to which they are applied. The objective of this paper is to critically review the currently available methods, to provide advice on their use and propose improvements for the future. Emphasis is placed on approaches that utilize molecular genetic information in the evaluation of genetic diversity.

## Methods to analyse information and combine criteria affecting conservation priority

### *Applicable methods in the absence of molecular genetic information*

When a number of sources of information are available on breeds, general multivariate statistical methods may often be applied to the process of choosing breeds to emphasise in conservation programs. The main uses of multivariate methods are to arrange objects or variables in relation to each other (e.g., ordination and scaling), to classify objects into groups (classification, clustering, prediction) or to test hypotheses about differences among objects or relationships between response and predictor variables. Breed information could consist of population means for traits of interest, population sizes or estimates of extinction risk, and subjective rankings for cultural significance, for example.

Principal components analysis (PCA) may be used to summarize information from a large number of variables and reduce their dimension to smaller number of variables that nonetheless explain a large proportion of the original variability. PCA may be applied to any type of qualitative data and to any number of data points, at least within computational limits. This approach could be used to rank the breeds to be considered for conservation for sets of quantitative variables. The breeds that rank highest (and/or lowest) for the various summarized variables (the principal components) could then be targeted for conservation.

Cluster analysis (Tryon 1939) may be used to assign breeds to groups according to a set of

characteristics that could include both genetic and non-genetic factors. Cluster analysis is the name given to a general set of algorithms for exploratory data analysis approaches that sort different "objects" (breeds, in this instance) into groups. In theory, the degree of association between any two objects is maximised if they are members of the same group and minimised across groups. Thus, to achieve high diversity while decreasing the number of breeds conserved, a single breed or subset of breeds from each cluster could be chosen for emphasis in conservation programs.

Another multivariate approach was used by Zander and Drucker (2008), who applied a choice model for evaluation of local cattle breeds in East Africa. They established a set of six different attributes, for which different combinations of values yielded profiles that described different breeds or breed subtypes. Local farmers were then given questionnaires to rank breeds based on their respective profiles. Marginal values of unit changes in each of the attributes were calculated and used to estimate total economic values of each breed or subtype. The economic values were proposed to be used for prioritizing breeds for conservation. The authors pointed out that the economic value ranking could be combined with measures of genetic diversity (such as with genetic markers) to obtain an overall ranking.

Geographic information could also contribute to breed prioritization and specific multivariate methods have been developed to consider geographical variables in procedures related to management of animal genetic diversity. Such approaches may be particularly useful in identifying animals or groups of animals to conserve when no distinct breeds are defined and the genetic make-up of the population of animals is expected to vary according to the geography of a given landscape. Among landscape features, space is most likely to influence the genetic structuring of a set of individuals or populations (Jombart *et al.* 2008). In spatial principal component analysis, the main goal is to describe the genetic variability according to geography.

Novembre *et al.* (2008) used this approach and found a close correspondence between genetic and geographic distances among human populations in Europe. An analogous approach could be applied to livestock breeds for which not genetic data (such as molecular genotypes) were available.

***Prioritization of breeds with molecular genetic information***

Molecular genetic information is primarily used to evaluate the genetic diversity of the breeds under consideration for conservation. Different methods have been developed both for estimation of genetic diversity according to molecular information and combining such estimates of genetic diversity with data for other variables affecting conservation priority.

*The Weitzman method.* Weitzman (1992, 1993) suggested a general theory of diversity that provides a rational framework for prioritizing populations for conservation activities. The basic concept is as follows: suppose a genetic entity (say, a farm animal species) consists of a set of N populations (say, breeds) for which the phylogenetic structure is available in the form of a distance matrix that comprises all $N \times (N - 1)$ pairwise distances. From this distance matrix, the actual diversity can be computed, which is a positive quantity reflecting the amount of diversity in the species. For each breed *i*, an extinction probability $0 \leq z_i \leq 1$ is defined, which reflects the probability that the breed is lost within a defined time horizon (say, 50 years) without any specific intervention to conserve this breed. Using these extinction probabilities, the expected diversity at the end of the defined time horizon can be calculated, which is smaller than the actual diversity because some breeds will go extinct. The marginal diversity $m_i$ is the first derivative of the expected diversity with respect to $z_i$, the extinction probability of breed i. The marginal diversity reflects how much the expected diversity of the entire set changes if the extinction

probability of breed i. is increased by one unit. Inasmuch as an increase in extinction probability will always result in a greater risk of loss of a breed, $m_i$ is always negative. Taking these factors into consideration, Weitzman (1993) suggests the conservation potential

$$CP_i = -m_i z_i, \qquad (1)$$

as the '... single most useful species alert indicator'. The conservation potential reflects how much expected diversity could be maintained if breed *i* were made completely safe (i.e. $z_i$ was decreased to 0) by some conservation activity. Breeds with the greatest conservation potential should be given priority in conservation programs. The strengths of this concept are that information on the risk status and the genetic contribution of breeds are taken into account in a natural and justifiable way. It was shown that greatest priority is not necessarily given to the most endangered populations, especially so if an endangered breed was closely related to a relatively safe breed. Then it would be a better investment to rescue a less endangered, but genetically more unique breed.

Nevertheless, some the approach of Weitzman has some shortcomings, particularly due to the definition of diversity used. Weitzman starts with the intuitive idea that the diversity can be computed easily if one establishes how the addition of the element *i* (*i* = 1 to N) increases the diversity of a given set *S*. Then he proposes to define recursively *V(S)* as

$$V(S) = \max_{i \in S}[V(S \mid i) + d(i, S \mid i)] \qquad (2)$$

where *V(S)* is the diversity of the set *S*, *V(S | i)* is the diversity of the set *S* without element *i*, *d(i, S | i)* is the distance of element *i* to set *S | i* that it is measured as the minimum genetic distance between *i* and any of the elements of *S*. The contribution of breed *i* to the diversity of set S will be

$$m_i = V(S) - V(S \mid i). \qquad (3)$$

The Weitzman definition of diversity was originally proposed for comparison of species, and several authors have criticized the application of the approach in the context of within-species diversity (Caballero & Toro, 2002; Eding *et al.,* 2002; Toro & Caballero, 2005; Chevalet *et al.*, 2006; Toro *et al.*, 2008). The European Cattle Genetic Diversity Consortium (2006) concluded that prioritization based on Weitzman diversity differs only slightly from prioritization based on the most homozygous breeds. In effect, if one defines total genetic diversity ($GD_T$) within a conserved population as

$$GD_T = wGD_W + GD_B, \qquad (4)$$

where $GD_W$ and $GD_B$ are genetic diversity within and between breeds, respectively, and w is a weighting factor, Weitzman's definition assumes that w = 0 (Meuwissen 2009), hence completely neglecting within breed diversity.

Realizing that ignoring within-breed diversity is unacceptable for livestock conservation, several scientists have developed methods to incorporate within breed diversity into the Weitzman approach (Ollivier & Foulley , 2005; García *et al.* 2005, Simianer 2005b) whereas others developed alternative approaches for defining genetic diversity.

*Alternatives to the Weitzman's definition of diversity.* The marker-estimated kinship method is one approach to consider diversity both within and across breeds in prioritization. This method is based on the assumption that the genetic similarity between individuals is largely determined by the kinship coefficient (*f*) between them (Eding & Meuwissen, 2001; Caballero & Toro, 2002; Toro & Caballero, 2005). The mean kinship in a population or set of populations or individuals gives an indication of the fraction of (additive) genetic variance originally in the founder population surviving in the present. A limited number of sufficiently polymorphic markers would be enough to estimate mean kinships and hence quantitative genetic variation.

Relating coefficients of kinship to genetic diversity is straightforward. Over t generations, the

loss in heterozygosity is directly related to the inbreeding coefficient:

$Het_t / Het_0 = 1 - F,$ (5)

where $Het_t$ is heterozygosity in generation t and $Het_0$ in the founder generation, and F is the inbreeding coefficient relative to the founder generation. Kinship, also called coancestry (f ), is used to calculate the inbreeding coefficient and

$F_X = f_{PQ},$ (6)

where $f_{PQ}$ is the coancestry of the parents P and Q of individual X. Twice the kinship, the coefficient of additive relationship is used to calculate the additive genetic variance $\sigma^2_A$. Because $\sigma^2_A$ is proportional to heterozygosity, over t generations we have (Falconer & Mackay, 1996; Gilligan *et al.* 2005):

$\sigma^2_{A,t}/\sigma^2_{A,0} = 1 - F.$ (7)

There are many different estimators for relatedness. Coancestry based estimators of kinship are most appropriate for most livestock populations.

Various scientists used measures of coancestry or kinship to establish core set of breeds for prioritization and conservation of diversity (Eding *et al.,* 2002; Bennewitz & Meuwissen, 2005a; Oliehoek *et al.*, 2006). The concept of a core set is the smallest set of lines or strains of a plant species that still encompasses the genetic diversity in the species (Frankel & Brown, 1984). The aim is the elimination of genetic overlap between breeds in the core set. The genetic overlap or genetic similarity between individuals and populations is described by the coefficient of kinship. Hence, eliminating genetic overlap is equal to minimising kinship in a set of breeds by adjusting the contribution of each population or individual to the core set. One can maximise genetic diversity and find the relative importance of populations or individuals in conserving the genetic diversity. The kinship approach effectively balances (i.e., w = 1) the contribution of within- and between-breed diversity as defined in Equation (4) (Meuwissen, 2009).

The kinship method of Eding *et al.*, (2002) implicitly maximizes genetic diversity and the opportunity for genetic response in a single hypothetical population consisting of all conserved breeds, which is not likely to mimic reality in livestock conservation. As an alternative, Piyasatian & Kinghorn (2003) developed an approach for breed prioritization with measures of $GD_T$ and $GD_W$ based on allelic variation and obtained $GD_B$ as their difference. They weighted these fractions with a somewhat arbitrary w = 0.2, explaining that such a weight allowed for the distinction of similar breeds and reflected the relative speed of selection within and across breeds.

A second core set approach of Bennewitz and Meuwissen (2005a) based prioritization on maximization of total genetic variance for a hypothesized quantitative trait. This approach, similar to the method of Eding *et al.*, (2002), incorporated genetic markers in the construction of a kinship matrix for prioritization. However, it implicitly uses w = 0.5, rather than w = 1.

*Approaches for estimation of extinction probability*. An estimate of the extinction probability of each breed is needed for computation of conservation priority with the Weitzman method or with modified methods based on another estimate of diversity, but knowing the general degree of endangerment of a breed can be useful for many reasons. The monitoring of the degree of endangerment of livestock breeds provides information on the erosion process of breed diversity and on the urgency with which conservation strategies need to be implemented.

The analysis of approaches to estimate breed endangerment needs to consider the methods in use by organizations such as FAO (2007b), the European Association for Animal Production (EAAP - Simon & Buchenauer, 1993) and the Rare Breed Survival Trust (RBST - Alderson, 2008).

Three general approaches can be identified. The first approach detects factors assumed to affect breed extinction and uses them as parameters to define endangerment categories to which breeds are assigned. The second estimates the persistence of populations through models of population dynamics. The third focuses on expected loss of genetic variation through time.

In the first approach, major factors that have been proposed to affect breed extinction risk include population size and its distribution, cultural and social farming context. Population size is usually measured as number of breeding females, adjusted for recent demographic trends, percentage of females mated with males of the same breed and number of males. Breed distribution has been considered in two ways, in terms of number of herds (EAAP; FAO), and as size of the geographical range (Reist-Marti *et al.*, 2003; Alderson, 2008). Social and cultural aspects, such as farmers' affection to their breeds, as well as presence of conservation programs, have been suggested in comparing African cattle breeds for degree of endangerment (Reist-Marti *et al.* 2003; Gizaw *et al.*, 2008). Species fecundity has been included in procedures to evaluate extinction risk, because of its association with potential for demographic recovery (Alderson 2008). Reist-Marti *et al.* (2003), Gizaw *et al.* (2008) assigned values to some of these parameters and computed for African breeds relative extinction probabilities, as a sum of these values. A limit of this first approach is the poor knowledge we have, for most of the above mentioned factors, of how, in general and under different farming conditions, they can affect endangerment. In addition, category thresholds are somewhat arbitrary and, therefore, breed endangerment values should be always considered as relative. Nevertheless, this approach can be used with minimal detailed information about each breed.

The second approach aims to estimate extinction probabilities by projecting population size with demographic models to different time horizons. Gandini *et al.* (2004) proposed a simplified approach by computing expected number of years needed to reach a critical population size or extinction. The method implies to the estimation, from time series census data, of the growth (or loss) rate of the population, and then to project it to a given time horizon population size assuming no change in growth rate. The authors underlined that the assumption of a constant population growth rate may not be realistic because growth rate usually varies and this variability

and its pattern can be critical elements influencing extinction time and probability (e.g. Goodman, 1987). However, because data insufficiency, it is not possible to estimate variance of growth rate for most of European breeds, and the situation is worse outside Europe. More generally, this approach bears a precise operation value, as it measures the time available for intervention to counteract breed extinction. However, a transformation to extinction probability would also be needed for inclusion in Weitzman's method.

One approach for this transformation would be to assume that time to extinction follows a certain known distribution, such as the Weibull distribution, and evaluate the cumulative distribution function to obtain probability of extinction at a specific time point. The Weibull distribution is frequently used in survival analysis to evaluate failure time of a given process, and failure could be defined as extinction of a breed. The cumulative distribution can be expressed as a function of the expected time to extinction and a parameter *k*. A value of $k = 1$ assumes that the instantaneous probability of failure (extinction) is constant throughout time, whereas $k < 1$ and $k > 1$ indicate that extinction probability decreases and increases with time, respectively. For livestock populations that decrease in size over time, $k = 3$ is a reasonable value. Under this assumption, probability of extinction at time t can be obtained with the following formula:

$$pe_t = 1 - e^{-\left(\frac{0.893t}{te}\right)^3}, \qquad (8)$$

where $pe_t$ is the probability of extinction at time t, and *te* is the expected time to extinction. Bennewitz & Meuwissen (2005b) used a diffusion approximation model to estimate growth rate and extinction probabilities in five German cattle breeds with census data for large numbers of milk recorded cows available over several decades. The results obtained are appealing, allowing one to estimate extinction probabilities at different time horizons, which could be incorporated directly into Equation (1). In addition, they suggest a transformation that could be used to convert

other estimators of future population size (e.g. that of Gandini, *et al.* 2004) to extinction probability. However authors suggest to restrict the analysis to a short term time horizon because estimation of future growth rate in livestock populations remains difficult.

The third approach, introduced by EAAP (Simon & Buchenauer, 1993), focuses on expected loss of genetic variation, expressed as cumulated inbreeding within a given time horizon and measured in terms of effective population size and species generation interval. Mean generation interval varies among species and, therefore, large differences in degree of endangerment can be observed in comparing methods that refer to generation interval or to year interval (Gandini et al, 2004). The focus on inbreeding takes into consideration not only breeds with small population size but also large stable populations with small effective size, for example, because of intensive selection. However, in this regard, it should be underlined that methods to control inbreeding in selected populations are available (e.g. Sonesson *et al.*, 2000) and selection programs should be used to decrease, rather than increase, breed endangerment. More recently Simianer (2005b) proposed to use the expected number of alleles segregating in the population after a given time period as measure of extinction probability.

All these methods obviously imply that storage of gametes and embryos does not affect degree of endangerment.

Measuring the degree of endangerment of livestock breeds requires understanding of the dynamics of populations, under the various farming systems and geographical areas of the world that remains poorly known. Livestock breed extinction has to be framed in both demographic and genetic terms that interact in several ways and partially overlap. The major challenge for all above approaches is to understand the role of factors affecting population dynamics and extinction and to detect elements for early monitoring. This challenge is particularly difficult, however, due to limitations on data available. A constant and accurate data collection worldwide,

together with investigations on sets of breeds with good information, might help to develop more efficient and homogeneous methodologies to estimate breed endangerment and extinction probabilities.

*Extensions to the Weitzman method.* Although the Weitzman measure of diversity is not appropriate for livestock populations, the general framework of balancing diversity and extinction probability is solid. However, prioritizing breeds to become part of a conservation program is a complex and multifaceted decision making process that may need to consider factors other than the genetic diversity and extinction probability of each breed (Simianer 2005a). Other factors to consider may be special features of the population (like unique traits, or a specific role in a social or cultural context), that a population may have (Ruane, 2000, Gandini & Villa, 2003) or productivity level and genetic variability for economically important traits (Piyasatian & Kinghorn, 2003).

A number of researchers have proposed modifications to the Weitzman-related methods to account for these additional factors. As previously mentioned, Reist-Marti *et al.* (2003) incorporated a large number of factors in the estimation of extinction risk. Simianer *et al.* (2003) developed a framework for the optimal allocation of limited conservation resources to a defined set of breeds and showed, that optimum allocation can double the cost efficiency (conserved units of diversity per conservation dollar spent) compared to naïve approaches like an equal distribution of the available funds to all breeds, or very targeted conservation measures only in the most endangered breeds. However, the optimal allocation strategies require definition of typically unknown parameters, but were found to prioritise the breeds with the highest conservation potential, so that conservation decisions can be made based on the conservation potential alone. Using results of an empirical economic analysis of conservation programs in the field, Reist-Marti *et al.* (2005, 2006) included a detailed cost and benefit model of different

conservation strategies. The suggested method identifies not only the optimum allocation of limited conservation funds to different breeds, but also identifies the most cost-effective conservation program (among, say, various in-situ or cryoconservation strategies). Another extension was developed by Simianer (2002), who suggested to combine expected diversity and conservation of special traits (like a mode of genetic resistance to a specific disease that may be present in several breeds) in one objective function termed expected utility. In this approach, diversity of future breed constellations is penalized if the special trait is entirely lost, resulting in greater conservation priorities for breeds carrying the special trait. In part due to criticism by van der Heide *et al.* (2005) regarding the consideration of ecological relationships by Weitzman's method, Simianer (2008) demonstrated that it is straightforward to assume interdependencies between extinction probabilities allowing a flexible modelling of both concurrence and synergistic relations between different sub-populations within a species.

Weitzman (1998) also extended his own approach, to account for costs of the conservation program and utility of the species to be conserved. Considering these factors, and using notation similar to equation (1), this updated approach can be represented as

$$R_i = (-m_i + U_i)\, \Delta z_i / C_i \,, \qquad (9)$$

where $R_i$ is the priority value for conservation of species i, $-m_i$ is the genetic distinctiveness (marginal diversity) of species i, $U_i$ is the utility obtained through conservation of species i, and $C_i$ is the cost of the conservation program that decreases the probability of extinction of species i by $\Delta z_i$. In applying this approach, a definition of diversity other than that of Weitzman (1992, 1993), such as one based on kinship, could also be used. In addition, factors such as phenotypic performance, the presence of special traits, or a measure of cultural importance could be included as a measure of utility, $U_i$, which has been proposed by Simianer *et al.* (2003) and applied by Gizaw *et al.* (2008).

Joseph et al. (2009) recently added another modification to Equation (9), accounting also for the probability of success of the proposed conservation activities. This method was applied to rank wildlife conservation projects, rather than livestock breeds, but could also be applicable in the latter context.

## Discussion

### *Application of methods of prioritization for conservation*

As outlined in the preceding sections, the general theoretical framework exists for combining marker-based measures of genetic diversity, information on productive and cultural factors that can contribute to breed utility, and an estimate of extinction probability to prioritize breeds for conservation. In fact, several groups of scientists have used such formal approaches, such as Weitzman's method (either with Weitzman's measure of diversity or another approach), to prioritize local breeds for conservation programs. For example, variations of Weitzman's original approach have been applied for breed prioritisation for conservation in cattle (Cañón *et al.* 2001, Simianer *et al.* 2003, Tapio *et al.* 2006, European Cattle Genetic Diversity Consortium, 2006; Zerabruk *et al.*, 2007), goats (Glowatzki-Mullis *et al.*, 2008), pigs (Laval *et al.* 2000; Fabuel *et al.*, 2004), horses (Solis *et al.*, 2005; Plante *et al.* 2007), donkeys (Aranguren-Mendez *et al.*, 2008) and poultry (Pinent *et al.* 2005, Berthouly *et al.* 2008). In addition Eding *et al.*, (2002) and Bennewitz and Meuwissen, (2005a) used kinship-based methods to prioritize chicken and cattle breeds, respectively. Gizaw et al., (2008) combined information regarding both Weitzman's measure of diversity and the core set approach of Eding *et al.*, (2002) to prioritize Ethiopian sheep breeds. However, the application of these methods has been essentially limited entirely to research, however, and they have rarely, if ever, been used in the real world.

A number of reasons explain the lack of use of these methods. Many of these are simple and practical reasons. First and foremost, only a minority of the World's >7000 livestock breeds have

been characterized by using molecular genetic markers, thus precluding the use of Weitzman's and other related methods. Some countries have sufficient resources to conserve all breeds and do not consider prioritization a major issue. The National Animal Germplasm Program (NAGR) of the United States is one such example (Blackburn, 2008). Many countries and organizations with livestock conservation programs place the primary emphasis on risk for extinction, rather than genetic diversity. the Rare Breeds Survival Trust in the United Kingdom prioritizes breeds according to extinction risk, accounting for number of breeding females, geographic distribution, and expected future inbreeding (L. Alderson, 2008, personal communication). The Norwegian Genetic Resource Centre, a government organization (N. Saether, 2008, personal communication), and the American Livestock Breeds Conservancy (2008), a private organization in the US (Pittsboro, NC) have created priority lists based on animal numbers, but also require that the breeds are native to the country or that the local populations are among the predominant populations on a global level. Some countries will consider genetic relationships when prioritizing and choosing specific animals within a breed (e.g. Blackburn, 2008). Some countries have simply identified a few breeds that are of particular national importance for conservation and are concentrating programs on those breeds. For example, Bangladesh has approved *in vivo* programs for the native Red Chittagong cattle, the Black Bengal goat, and the Asil chicken (O. Faruque, 2008, personal communication). In some instances conservation programs are supported by individual breed associations rather than a central government body. Such organizations would usually be concerned about a single breed and thus have no reason to prioritize. In other countries, breeds are simply not well defined and other methods for prioritization, such as geographical-based sampling, must be used.

Other plausible reasons for the lack of implementation of formal breed prioritization methods can be proposed as well. First, no clear consensus has been reached on the optimal method for

prioritization, in terms of both the method for evaluation of diversity and of the factors other than diversity to consider in prioritization. Agreement generally exists that the Weitzman measure of diversity, which only considers variability across breeds is not acceptable for livestock. Meuwissen (2009), however, explains that equal weight on within- vs. across breed diversity (i.e., Eding & Meuwissen, 2001; Caballero & Toro, 2002) is not ideal for most situations, either. This approach optimizes breed selection assuming that the conserved breeds would be eventually used in a single, interbreeding population and would generally favor the conservation of large, non-endangered populations. He concludes that moderate weighting of within- vs. across breed diversity, such as that obtained by the approaches of Piyasatian & Kinghorn (2003) and Bennewitz & Meuwissen (2005a) is more reasonable. The non-diversity parameters to consider, such as cultural and socio-economic factors, are likely to vary from country to country. Thus, the use of a particular approach for prioritization has not been promoted by any international organizations dealing with animal genetic resources, such as the FAO. Second, understanding and applying the various methods may be considered somewhat complicated and simple computational tools to perform the required analyses from start to finish have not yet been developed or are at least not widely available. Table 1 lists software available that can be used to perform various steps in the prioritization process, organized according to task performed. Most of the software is available free of charge from the author. Although some of the programs listed can perform multiple tasks, no software can perform all of the steps required for breed prioritization, nor does there exist a "pipeline" software that integrates the various programs together.

Table with methods and available software here

***What is still needed to increase the use of breed prioritization methods?***

As mentioned previously, one constraint that is clearly limiting the application of conservation prioritization methods that formally account for breed diversity is the lack of molecular characterization for many breeds. Thus, the first step would be to promote this process, while simultaneously performing the characterization of breeds in terms of their phenotypes, farming systems, geographic distribution and social economic and cultural significance. Then, a scientific consensus should be obtained with regard to the most practical and scientifically sound approaches for breed prioritization, as well as related matters such the frequency with which the exercise must be repeated. The general approach of Weitzman (1998), which considers genetic diversity, breed utility and extinction risk, sets a solid foundation, although a measurement of diversity balancing within- and between-breed diversity appropriately for livestock must be used (Meuwissen, 2009). The agreed-upon approaches should then be presented to and discussed with national policy makers to increase awareness with regard to their efficiency, utility and flexibility. The resulting policies should then be promoted by international and national organizations concerned with management of animal genetic resources, including the provision of training in their implementation and interpretation and other technical support. Finally, simple, user-friendly and flexible computational tools for the organization and analysis of the data required for implementation of formal prioritization methods must be developed and made available for those directly responsible for management of livestock conservation programs.

**Acknowledgements**

Action GLOBALDIV AGRI GEN RES 067 received financial support from the European Commission, Directorate-General for Agriculture and Rural Development, under Council Regulation (EC) No 870/2004.

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**Table 1.** Information about software that can be used in the process of prioritization of breeds for conservation.

| Name | URL | Reference | Interface | Features |
|---|---|---|---|---|
| General genetic diversity analysis | | | | |
| Genepop | http://kimura.univ-montp2.fr/%7Erousset/Genepop.htm | Rousset (2008). | Command-line | Reference population genetics software. Its file format has become a standard input/output option for many other applications. Performs HW and LD tests and estimates heterozigosities, Fstats and other population differenciation parameters. Has a web-based implementation at http://genepop.curtin.edu.au/ |
| Arlequin | http://lgb.unige.ch/arlequin | Schneider *et al.* (2000) | GUI | Popular and versatile application for population genetic data analysis. Reads many different types of molecular data and performs a plethora of different analyses. |
| PHYLIP | http://evolution.genetics.washington.edu/phylip.html | Felsenstein (2005) | Set of command-line applications | General purpose philogeny inference software, frequently used for the calculation of genetic distances and NJ/UPGMA trees with bootstrap values. |
| GenAlEx | http://www.anu.edu.au/Bo | Peakall and Smouse | Excel Add- | Multipurpose package covering from basic standard parameters (allelic frequencies, He, Ho, effective number of alleles, Fstats, genetic distances |

| | | | | |
|---|---|---|---|---|
| | Zo/GenAlEx/ | (2006) | In | or pairwise relatedness matrices…) to more ellaborate procedures (geographic distances and Mantel test, AMOVA), including multivariate techniques such as PCA, Spatial Autocorrelation. |
| Genetix | http://www.genetix.univ-montp2.fr/genetix/genetix.htm | Belkhir *et al.* | GUI | General purpose population genetics software. Calculates distances, Fstats, etc. Performs correspondence analysis and displays 2 and 3 axes plots. |
| Fstat | http://www2.unil.ch/popgen/softwares/fstat.htm | Goudet (2001) | GUI | Calculates Fstats, allelic richness, allelic frequencies and tests for population differenciation |
| Microsatellite toolkit | http://www.animalgenomics.ucd.ie/sdepark/ms-toolkit/ | Park (2001) | Excel Add-In | Useful macro to format data for other common genetics software. Also calculates allelic frequencies, heterozigosities, PIC and expected number of alleles |
| Hp-rare | http://www.montana.edu/kalinowski/Software/HPRare.htm | Kalinowski, (2005) | GUI | Allelic richness calculation with rarefaction methods. |
| Pedigree analysis, inbreeding and effective size estimation | | | | |
| MLNE | http://www.zoo.cam.ac.uk/ioz/software.htm | Wang & Whitlock (2003) | Command-line | Maximum-likelihood estimation of effective size. |

| | | | | |
|---|---|---|---|---|
| TM | http://www.rubic.rdg.ac.uk/~mab/software.html | Berthier *et al.* (2002) | Command-line | Population effective size estimation by the temporal method. |
| CFC | http://www.agr.niigata-u.ac.jp/~iwsk/cfc.html | Sargolzaei *et al.* (2006) | GUI | Inbreeding, coancestries and pedigree tools. |
| Pypedal | http://pypedal.sourceforge.net/ | Cole (2007) | | Pedigree analysis. Not very user-friendly (runs from a Python command line, or using a script that is run using the Python interpreter), but it has some useful visualization tools. |
| Pedig2007 | http://www-sgqa.jouy.inra.fr/article.php3?id_article=110 | Boichard (2002) | Set of command-line applications | Inbreeding calculation and pedigree analysis. |
| Endog | http://www.ucm.es/info/prodanim/html/JP_Web.htm | Gutiérrez and Goyache (2005) | GUI | Inbreeding and relatedness calculation from pedigree information, effective size estimation following different approaches and other pedigree tools. |
| Contributions to genetic diversity | | | | |
| Weitzpro | http://www-sgqa.jouy.inra.fr/article.php3?id_article=3 | Derban *et al.* (2002) | Set of command-line | Calculate the Weitzman diversity and marginal loss for individual units and predefined groups. |

| | | | | |
|---|---|---|---|---|
| | | | applications | |
| Metapop | http://webs.uvigo.es/anpefi/metapop/ | Pérez-Figueroa *et al.* (2008) | GUI | Java-based application that calculates traditional measures (He, Fstats, etc.) plus contributions to within- and between-breed diversity and to a core set of maximum diversity following Caballero & Toro (2002). Also allows for metapopulation management analysis, calculating number of migrants to keep a given inbreeding rate, following Fernández *et al.* (2008). |
| MEKSAFE | Available upon request from authors Dr. Herwin Eding at eding@tzv.fal.de or Dr. Steffen Weigend at steffen.weigend@fli.bund.de. | | Command-line application | Marker Estimated Kinship (MEK) estimation following Oliehoek *et al.* (2006), calculation of contributions to the core set as in Eding *et al.* (2002). |
| Contrib | http://www.pierroton.inra.fr/genetics/labo/Software/Contrib/ | Petit et al (1998) | GUI | Calculates contributions of populations to total diversity measured as He or allelic richness, calculated with rarefaction procedures. |
| Molkin | http://www.ucm.es/info/prodanim/html/JP_Web.htm | Gutiérrez *et al.* (2005) | GUI | Calculation of molecular coancestry and kinship distance matrix in addition to other classical parameters (PIC, Fstats, other distance measures, allelic richness with rarefaction method…). Also computes contributions to diversity after Caballero & Toro (2002) or Petit *et al.* (1998). |

| | | | | |
|---|---|---|---|---|
| Multivariate analyses | | | | |
| GenAlEx | http://www.anu.edu.au/BoZo/GenAlEx/ | Peakall and Smouse (2006) | Excel Add-In | Multipurpose package covering from basic standard parameters (allelic frequencies, He, Ho, effective number of alleles, Fstats, genetic distances or pairwise relatedness matrices…) to more ellaborate procedures (geographic distances and Mantel test, AMOVA), including multivariate techniques such as PCA, Spatial Autocorrelation. |
| Genetix | http://www.genetix.univ-montp2.fr/genetix/genetix.htm | Belkhir *et al.* | GUI | General purpose population genetics software. Calculates distances, Fstats, etc. Performs correspondence analysis and displays 2 and 3 axes plots. |
| GIS | | | | |
| Worldmap | http://www.nhm.ac.uk/research-curation/research/projects/worldmap/ | | GUI | Easy-to-use software for exploring geographical patterns in diversity, rarity and conservation priorities from large biological datasets. rather than concentrating on database and graphics flexibility, WORLDMAP is designed to perform specialist biological analyses for unlimited numbers of species at maximum speed. Many of the biological tools are not yet available from commercial GIS. |
| DivAGis | http://research.cip.cgiar.or | | GUI | Open source GIS application to make maps of species distribution data and |

| | | | | |
|---|---|---|---|---|
| | g/confluence/display/divagis/Home | | | analyze them (richness, diversity indexes, distances, autocorrelation,…). Specifically developed for use with genebank data such as available through national or international genebank documentation systems. Imports molecular information and output files from the Structure software. |
| CommonGIS | http://www.commongis.com | | GUI | Java based multipurpose GIS application to interactively explore and analyse geo-referenced data. |
| GeoVISTA Studio | http://www.geovistastudio.psu.edu/jsp/index.jsp | Takatsuka and Gahegan (2002) | GUI | Programming studio to develop custom GIS applets to fit potentially complex models and scenarios. A much more flexible platform to work with, but also more complex to handle. |
| GRASS | http://grass.osgeo.org/ | | GUI | Popular open source multipurpose GIS software. Runs in Linux or Windows through Cygwin. |
| Idrisi | http://www.clarklabs.org/products/index.cfm | | GUI | Easy access, useful for geographical analysis. It is efficient for spatial analysis, statistical analysis, decision making (search of optimal site) and offers numerous functions. **Commercial software**. |
| Manifold | http://www.manifold.net | | GUI | Easy to use multipurpose GIS software with multiple up-to-date features. **Commercial software**. |

| Population Viability Analysis and extinction risk estimation | | | | |
|---|---|---|---|---|
| Metapop | http://www.ramas.com/ramas.htm#metapop | Akçakaya and Root (2002) | GUI | Within- and metapopulation dynamics software. Calculates risk of extinction among other parameters useful in viability studies. **Commercial software**. |
| Vortex | http://www.vortex9.org/vortex.html | Lacy (1993). | GUI | Most popular freeware PVA software. Provides graphs and reports on projections of population sizes under given scenarios. Calculates and plots probability of extinction and near extinction. Allows for genetic information to enter the analysis with pedigree and molecular (allele frequencies) data and inbreeding minimization mating conditions. Very comprehensive and instructional manual. |
| Alex | http://www.rsbs.anu.edu.au/ResearchGroups/EDG/Products/Alex/ | Possingham and Davies (1995) | GUI | Another option to calculate extinction probabilities. Faster simulations, but doesn't allow for genetic information. |