



ANALYSIS

An approach to the optimal allocation of conservation funds to minimize loss of genetic diversity between livestock breeds

H. Simianer^{a,*}, S.B. Marti^b, J. Gibson^c, O. Hanotte^c, J.E.O. Rege^d

^a *Institute of Animal Breeding and Genetics, Georg-August-University Goettingen, Albrecht Thae-Weg 3, 37075 Goettingen, Germany*

^b *Institute for Agricultural Economics, Swiss Federal Institute of Technology, Sonneggstr. 33, ETH-Zentrum, 8092 Zurich, Switzerland*

^c *International Livestock Research Institute, P.O. Box 30709, Nairobi, Kenya*

^d *International Livestock Research Institute, P.O. Box 5689, Addis Ababa, Ethiopia*

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Abstract

About 30% of all farm animal breeds worldwide are at risk of extinction. To prevent this irreversible erosion of genetic diversity, the limited funds available for conservation need to be allocated in the most efficient way. Applying the diversity concept of Weitzman [Quart. J. Econ. CVII (1992) 363; Quart. J. Econ. CVIII (1993) 157] this paper presents a framework for the allocation of a given budget among a set of breeds such that the expected amount of between-breed diversity conserved is maximized. As a novel methodological contribution, a functional relationship between conservation funds spent in one population and the conservation effect in terms of reduced extinction probability is suggested. Based on arguments from population genetics, three different functions are derived, which may reflect the range of possible functions in typical conservation situations. The methodology is illustrated with an example of 23 African zebu and zenga cattle breeds. The results indicate that conservation funds should be spent on only three to nine of the 23 breeds, depending on the model used. Highest priority is given to breeds, for which the ‘conservation potential’, that is, the product of extinction probability and marginal diversity is maximum, and these are not necessarily the most endangered breeds. The methodology can be extended to the maximization of total utility, which incorporates diversity, as well as other direct use, and special value, characteristics. However, a number of essential input parameters such as extinction probabilities and economic values are lacking and realistic models for developing cost-efficient conservation strategies have to be derived. Given these lacking bits of information become available, the methodology suggested provides a breakthrough towards applicability of diversity-based approaches for decision taking in conservation programs.

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1. Introduction

Farm animal genetic diversity is threatened with extinction of breeds. Of the estimated 6400 breeds of farm animal species worldwide, about 30% are

* Corresponding author. Tel.: +49-551-39-5604; fax: +49-551-39-5587.

E-mail address: hsimian@gwdg.de (H. Simianer).

endangered and 1% becomes extinct every year (Scherf, 2000).

The value of farm animal genetic diversity is multiform, comprising present production values as well as ecological and socio-cultural values. Option values are of specific interest, representing potential values of breeds under future, presently unknown conditions (Rege, 1999).

In many cases, the public has become aware that the loss of breeds and diversity within farm animal species is critical and that measures need to be taken to prevent, or at least slow down, this irreversible genetic erosion.

Financial and other resources to be invested into conservation are always limited. Therefore, these resources have to be spent in the most efficient and cost effective way. The need to develop a framework to allow rational decision-making in conservation programmes with regard to the question: ‘what to conserve’ has been a subject of research (Vane-Wright et al., 1991; Crozier, 1992). Weitzman (1993) has suggested the use of conserved diversity per unit of expenditure as measure of the efficiency of a conservation scheme.

An efficient use of conservation funds encompasses two levels of activity:

- To spend money within a breed such that the risk of extinction for this breed is immunized and the within-breed diversity is maintained.
- To distribute the total available amount of conservation funds among a subset of all endangered breeds such that the conserved diversity between breeds is maximized.

This study focuses on the second level of activity, i.e. the optimum allocation of resources among a defined set of breeds.

Although the study is largely based on the pioneering work of Weitzman (1992, 1993), the suggested approach is quite general and can be used with any measure of aggregate population distinctiveness that has the basic characteristics of a diversity.

Diversity can be derived from different types of raw data, which can be a genetic distance matrix (Weitzman, 1992, 1993; Solow et al., 1993; Thaon d’Arnoldi et al., 1998; Marti et al., 2003) or a set of

weighted or unweighted characteristics, features or attributes (Faith, 1996; Weitzman, 1998; Nehring and Puppe, 2000) which may or may not reflect purely genetic properties of the considered unit. If, for example, the degree of adaptation of a species/breed to a certain environment is used as a feature to assess diversity, this feature is certainly not completely genetically determined. Although the present application is largely based on Weitzman’s (1992, 1993) diversity concept, the core of the methodology should work with any reasonable diversity measure. The arguments will only make use of the ‘non-negativity’ and of the ‘monotonicity’ property in the methodological considerations.

The structure of the paper is as follows. Section 2 starts with the definition of the basic quantities. Computational aspects will be mentioned briefly. Based on arguments from population genetics, three models will be suggested, that link conservation expenditure to reduction in extinction probability. Examples for the applicability of the three models will be given and they will be compared in a small, illustrative example. Based on this achievement, it will be shown how the allocation of a fixed amount of conservation funds to a single breed out of a set of breeds affects expected diversity of the set. Finally, an algorithm is suggested, how a given budget can be allocated to a set of breeds, such that expected diversity is maximized.

The suggested methodology will be illustrated with a reasonably comprehensive set of African zebu and zenga type cattle breeds, which will be presented in Section 3.

The results will show, that optimum allocation of resources follows certain patterns, but is difficult to assess without a detailed model and reliable values of the required parameters.

In Section 5, strengths and shortcomings of the presented approach will be discussed and differences to alternative approaches, that have been suggested, will be highlighted. Also, a more general approach aiming at the maximization of the total ‘utility’ of the conserved set will be suggested. Finally, the main achievements of the paper will be pointed out and research needs to put this approach into practice will be indicated.

2. Methods

2.1. Definitions

Diversity is a property of a set S of ≥ 2 elements, reflecting the distinctiveness of the elements in the set. For any diversity measure, the following properties should hold:

- 1) the diversity $D(S)$ is a non-negative number;
- 2) if an element is added to a given set S , the resulting diversity of the augmented set S^+ , $D(S^+)$ is not smaller than the diversity $D(S)$ of the original set. This property is called ‘monotonicity in species’ (Weitzman, 1992);
- 3) if to a given set S one element is added which is an identical copy of an element that is already in the set, the diversity remains unchanged.

There is an infinite number of possible ‘diversity measures’ that fulfil these rather broad conditions. Therefore, as an additional requirement, it is desirable that the diversity measure should reflect the distinctiveness of the elements of the set in a ‘tight’ way, i.e. a metric should take the smallest possible value while still fulfilling the above mentioned properties. Weitzman (1992) argues that ‘tightness’ is the fourth desirable, but not always fully achievable property of operationally useful diversity measures. If a diversity measure is derived from a tree structure, like in Weitzman (1992) and Faith (1994), tightness is achieved by constructing the ‘minimum spanning tree’ (Faith, 1994).

In his pioneering work on diversity, Weitzman (1992) suggested a diversity measure computed from a distance matrix which has the desired ‘tightness’ property only if the underlying distances are ultrametric, i.e. if, in each triplet of elements, the two largest pairwise distances are identical. If this is not the case—which is the usual real life situation—the ‘tightness’ property can not be proven mathematically but the resulting diversity measure is still suggested based on pragmatic arguments.

For a set S of N breeds with the pair-wise distance between breeds $i, j \in S$ denoted as d_{ij} , a

diversity metric $D(S)$ can be computed from an $N \times N$ distance matrix with a recursive algorithm suggested by Weitzman (1992). The methodology also yields a tree with maximum likelihood properties.

Let Z be a vector of size N containing extinction probabilities of the N breeds, with z_i being the extinction probability of breed i in a given time period t ($t = 50$ years, say). Thus, a breed existing today will still be around in 50 years with probability $1 - z_i$ and will be extinct with probability z_i .

Let K be a vector of size N containing the indicator variables $k_i, i = 1, \dots, N$, where $k_i = 1$ if breed i is still existing and $k_i = 0$ if it is extinct at a given point in time. Hence, K reflects a situation where a subset of the total breeds is still existing and the complementary subset is extinct.

The probability that a specific situation, characterized through a specific vector K , arises can be computed as:

$$P(K) = \prod_i (k_i + (-1)^{k_i} z_i) \tag{1}$$

From the above, 2^N different combinations of present and extinct breeds are possible, for which the respective probabilities can be computed as described.

Let D_K be the diversity of the set of breeds not extinct, i.e. with $k_i = 1$, in vector K . Then, the expected diversity at the end of the assumed time period can be computed as

$$E(D) = \sum_{\forall K} P(K) D_K. \tag{2}$$

Using the same approach, the variance of expected diversity can be computed as

$$Var(D) = \sum_{\forall K} P(K) D_K^2 - \left(\sum_{\forall K} P(K) D_K \right)^2,$$

and the expected distribution of diversity at the end of the time period can be assessed.

The marginal diversity for a breed describes the magnitude of change in expected diversity if the extinction probability of the respective breed is increased by one unit. That is, the marginal diversity of breed i is

$$D'_i = \frac{\partial E(D)}{\partial z_i}$$

Note that this definition differs from that of Weitzman (1993), who uses the negative value of the given expression as marginal diversity.

Weitzman (1993) has suggested the use of ‘conservation potential’, the most useful species-alert indicator. In the present parameterization, the conservation potential CP_i of breed i is $CP_i = z_i \times D'_i$, which reflects the possible increase in expected diversity, if an endangered breed i was made completely safe.

2.2. Computational aspects

The first derivative of the expected diversity with respect to the extinction probability of a given breed in the set is a scalar. If we consider breed $i \in S$, we can define the two conditional expectations $E(D|k_i = 1)$ and $E(D|k_i = 0)$, i.e. the expectation of diversity in the case of breed i being conserved or extinct, respectively. Then, the overall expectation is

$$E(D) = (1 - z_i)E(D|k_i = 1) + z_iE(D|k_i = 0).$$

The first derivative of $E(D)$ with respect to z_i , i.e. the marginal diversity of breed i is:

$$\frac{\partial E(D)}{\partial z_i} = E(D|k_i = 0) - E(D|k_i = 1) \tag{3}$$

which is independent of z_i , hence the expected diversity is a linear function of the extinction probability of any breed, if extinction probabilities of all other breeds in the set are kept constant.

Eq. (3) provides a basis for an efficient algorithm to compute the marginal diversities for all breeds, since

$$E(D|k_i = 0) = \frac{\sum_{\forall K:k_i=0} P(K)D_K}{z_i} \quad \text{and}$$

$$E(D|k_i = 1) = \frac{\sum_{\forall K:k_i=1} P(K)D_K}{1 - z_i}.$$

The numerators of these two expressions can be accumulated for all breeds i simultaneously while

going through all 2^N constellations of breeds just once.

2.3. Linking conservation expenditure to reduction in extinction probability

In population genetics, the increase of the average inbreeding coefficient in a population, ΔF , is considered to be a useful criterion for the risk that the population might become extinct. The change of the average inbreeding is directly linked to the effective population size, N_e , since $\Delta F =$

$\frac{1}{2N_e}$. The effective population size is defined as the size of a hypothetical ideal population that leads to the same ΔF as the actual population (Falconer and Mackay, 1996).

The basic assumption used here is that the actual extinction probability z_i of breed i is directly proportional to the ΔF in this population, i.e. $z_i = \gamma \Delta F_i = \gamma \frac{1}{2N_{e_i}}$ where $0 < \gamma \leq 1/\Delta F_i$ is a constant.

The key mechanism of conservation is, that a certain budget b spent in one population will increase the effective population size with the consequence, that the extinction probability z_i of this population is reduced to $z_i^* < z_i$, where $\Delta z_i = z_i^* - z_i$. For the further considerations it is necessary to define a functional relationship between the budget spent, b , and the actual extinction probability of the breed, z_i , on one side and the reduction of the extinction probability, Δz_i , on the other side.

In the following section, the function $\Delta z_i = f(z_i, b)$ is derived under three assumptions regarding the mechanism that links conservation expenditure to the effect of conservation. For each of the three models, an example will be given to illustrate the situation it may reflect.

2.3.1. Model A: additive effect on N_e proportional to the funds spent per animal

Under this model, it is assumed that the effect of a conservation scheme is an increase in the effective population size by an additive increment

which is proportional to the amount of money spent *per (effective) animal* in this population.

A real life example for this model may be a situation, where animals of an endangered breed X are continuously replaced by the animals of a more productive breed Y. A conservation program may use a fixed amount of money per year to pay a premium to those farmers that keep their animals of breed X, balancing some of the economic inferiority of those animals. With a fixed amount of money to be spent for the whole population, the premium per animal may be small and the incentive for the farmer to keep the breed may be minor, hence only few farmers will keep the breed. Thus, in 1 year, the population size will decrease from N_e to $N_e - \Delta N_e$, where ΔN_e is an additive increment inversely proportional to the height of the premium per animal. If, however, the population size of breed X decreases, the possible premium per animal increases, which leads to a higher incentive for each farmer to keep the remaining animals.

Consider a breed i with effective population size N_{e_i} . If a sum b is spent for conservation of this breed, the expenditure per effective animal in this breed is $\frac{b}{N_{e_i}}$. We assume that the effective popula-

tion size is increased from N_{e_i} to $N_{e_i}^* = N_{e_i} + \lambda \frac{b}{N_{e_i}}$, where $\lambda > 0$ is a constant which is valid for all breeds considered in this study.

Then the extinction probability is reduced to

$$z_i^* = \frac{\gamma}{2 \left(N_{e_i} + \lambda \frac{b}{N_{e_i}} \right)}$$

Hence,

$$\Delta z_i^A = z_i^* - z_i = \frac{\gamma}{2 \left(N_{e_i} + \lambda \frac{b}{N_{e_i}} \right)} - \frac{\gamma}{2N_{e_i}}$$

Using the equation $N_{e_i} = \frac{\gamma}{2z_i}$, this expression can be reduced to

$$\Delta z_i^A = - \frac{4\lambda b z_i^2}{\gamma^2 + 4\lambda b z_i^2} z_i. \tag{4}$$

2.3.2. Model B: multiplicative effect on N_e proportional to the funds spent per animal

Under this model a multiplicative effect of a conservation scheme on effective population size is assumed which is proportional to the amount of money spent *per individual* in the population.

This situation may be given in the following example: One of the basic strategies for maintaining diversity in small populations is to keep family sizes constant. A practical approach is to raise one male offspring of each sire and one female offspring of each dam for replacement. If this is practiced, effective population size can be doubled (Hill, 1979). In extensive production systems, as given in most developing countries, this information has been brought to the animal owners through extension specialists. In this case, costs are clearly proportional to the population size, because you need more extension specialists with more animals. The return, on the other hand, is a multiplicative effect on the effective population size.

Formally, this means, that by spending an amount $\frac{b}{N_{e_i}}$ per animal in population i , N_{e_i} is changed to

$$\left(1 + v \frac{b}{N_{e_i}} \right) N_{e_i} = N_{e_i} + vb$$

where v is a constant.

Note that on the right hand side of the equation the effective population size cancels out in the additive term. Thus, model B represents also a model with an *additive* effect on effective population size which is proportional to the amount of money spent *per population*.

This situation may be reflected by the following scenario: In an ex situ conservation scheme, a fixed number of, say, ten male and 50 female animals is sampled from the population and brought to a ‘safe place’, where the germplasm can be kept and reproduced under safe conditions for a given time

period. In this case, the effective size (and thus the cost) of taking and maintaining the sample will be independent of the size of the endangered population, and the ‘reserve population’ kept ex situ will contribute a fixed effective population size increment to the total population size of the breed.

The resulting change in extinction probability

$$\Delta z_i^B = z_i^* - z_i = \frac{\gamma}{2(N_{e_i} + vb)} - \frac{\gamma}{2N_{e_i}}$$

can be reduced to

$$\Delta z_i^B = -\frac{2vbz_i}{\gamma + 2vbz_i} z_i. \tag{5}$$

2.3.3. *Model C: multiplicative effect on N_e proportional to the funds spent per population*

Under model C, the effect of a conservation scheme on effective population size is assumed to be multiplicative with a factor that is only depending on the amount of money spent in any one population, irrespective of its (effective) size.

This situation may be given, if the information, that keeping family size constant does increase effective population size can be brought to the animal owners through some established information channels with negligible extra costs. If, say, a breeding organization for the endangered breed is established and farmers get information on a regular basis, the cost to disseminate information on the optimal mating scheme is not depending on the number of farmers, but is more or less identical for smaller or larger populations. While the cost are independent of the population size, the effect on effective population size will be multiplicative.

Formally this means, that by spending a given amount of money b in population i , N_{e_i} is changed to

$$(1 + \eta b)N_{e_i}$$

where η is a constant. Thus,

$$\Delta z_i^C = z_i^* - z_i = \frac{\gamma}{2(1 + \eta b)N_{e_i}} - \frac{\gamma}{2N_{e_i}}$$

which can be reduced to

$$\Delta z_i^C = -\frac{\eta b}{1 + \eta b} z_i. \tag{6}$$

2.3.4. *Comparing the three models*

The rationale underlying the three models can be illustrated with the following simple example: assume a given amount of money is spent on a population with population size $N_e = 100$ with the effect that effective population size increases by 10 to $N_e^* = 110$. What would happen if the same amount of money was spent on a population of size $N_e = 200$?

Compared with the reference scenario, the amount of money spent *per animal* is halved, and so is the additive increment expected under model A, leading to $N_e^{*A} = 205$.

Under model B, the multiplicative factor in the reference scenario is 1.1, i.e. an increase by 10% of the actual effective population size. Since the budget *per animal* is halved, this increase is reduced to 5%, leading to a factor of 1.05. Hence, with the doubled population size $N_e^{*B} = 1.05 \times 200 = 210$. This is equivalent with an additive effect being proportional to the money spent not on a per individual, but on a per population basis, meaning that the increment of +10 effective animals is achieved independent of the actual population size.

Under model C we assume a multiplicative effect proportional to the money spent per population. Since this amount does not change, the multiplicative factor 1.1 remains constant leading to $N_e^{*C} = 220$.

2.4. *Comparing efficiency of allocation to different populations*

We assume that a fixed limited amount of conservation funds, b , is to be allocated in total to one single breed out of a limited set of N breeds. The choice of the breed should be made in such a way, that the efficiency, defined as the amount of diversity conserved through this effort, is maximum. If we have accepted one of the models linking conservation expenditure to reduction of extinction probability through a function $\Delta z_i =$

$f(z_i, b)$, we can compute, for each breed i , the expected change of extinction probability Δz_i from Eqs. (4)–(6).

Multiplying the reduction of the extinction probability with the marginal diversity of the breed, i.e.

$$E(\Delta D|z_i, b) = \Delta z_i D'_i,$$

gives the increase in the expected diversity of the whole set if the available conservation funds are spent exclusively on breed i .

This quantity can be computed for all breeds in the set, and the most efficient strategy is to spend the money on the breed for which the resulting increase in expected diversity is maximum.

2.5. An example

To demonstrate the properties of the approach, it makes sense to define the parameters of the model in such a way that spending a given amount of conservation funds yields the same effect in a defined reference situation. Considering the three models A, B, and C, the reduction of the extinction probability will be identical for a given effective population size N_{e_0} if

$$\nu = \frac{\lambda}{N_{e_0}}$$

and

$$\eta = \frac{\lambda}{N_{e_0}^2}$$

Thus, if we choose N_{e_0} to be 50 and λ to be 0.05, model B and C will yield the same reduction of extinction probability with $\nu = 0.001$ and $\eta = 0.00002$.

Consider two breeds with given extinction probabilities $z_1 = 0.50$ and $z_2 = 0.40$, respectively. With $\gamma = 45$, this corresponds to an assumed effective population size of

$$N_{e_1} = \frac{\gamma}{2z_1} = \frac{45}{2 \times 0.50} = 45$$

and $N_{e_2} = 56.25$, respectively. Note, that the lower extinction probability of breed 2 corresponds to a higher assumed effective population size.

Suppose we have to decide if a share of $b = 500$ monetary units is more effectively invested in the conservation of breed 1 or breed 2. To do this, we compute the expected reduction of the extinction probability under all three models for both breeds using Eqs. (4)–(6). The results are given in Table 1. For breed 1, the reduction of extinction probability is highest under model A with $\Delta z_1^A = -0.00610$, while for breed 2, the maximum reduction is achieved.

The reason for this difference is that the three models yield the same reduction at $N_{e_0} = 50$, which corresponds to the extinction probability $z_0 = 0.45$. For extinction probabilities below this value (e.g. for breed 2), $\Delta z_i^A > \Delta z_i^B > \Delta z_i^C$. Since all these terms are negative, the reduction in extinction probability is highest under model C. On the contrary, for values of z_i above $z_0 = 0.45$ as in breed 1, $\Delta z_i^A < \Delta z_i^B < \Delta z_i^C$, with a maximum reduction under model A. Fig. 1 depicts the three functions for the set of parameters chosen in this example.

To identify the most efficient allocation of available funds, the marginal diversities of the breeds have to be taken into account. Suppose the marginal diversity of breed 1 is $D'_1 = -0.15$, i.e. the expected diversity of the total set of breeds is reduced by 0.15 if the extinction probability of breed 1 is increased by one unit. Correspondingly, the marginal diversity of breed 2 is $D'_2 = -0.25$. The return in terms of expected conserved diversity, $E(\Delta D|z_i, b)$ is the product of the reduction in extinction probability and the marginal diversity. The results are presented in Table 1.

Table 1
Change in extinction probability (Δz_i) and expected change of diversity $E(\Delta D|z_i, b)$ for two hypothetical breeds obtained with the three models linking conservation expenditure to change in extinction probability

Model	Breed 1		Breed 2	
	Δz_1	$E(\Delta D z_1, b)$	Δz_2	$E(\Delta D z_2, b)$
A	-0.00610	9.150×10^{-4}	-0.00314	7.850×10^{-4}
B	-0.00549	8.235×10^{-4}	-0.00352	8.800×10^{-4}
C	-0.00495	7.425×10^{-4}	-0.00396	9.900×10^{-4}

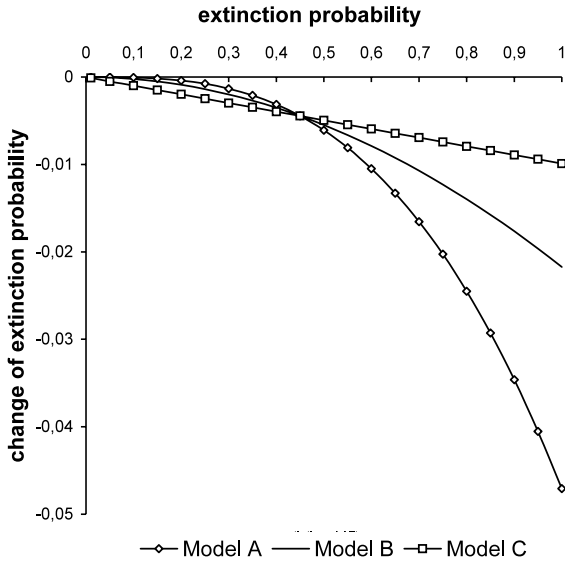


Fig. 1. Change of extinction probability (Δz_i) as function of the actual extinction probability (z_i) under the three models with the chosen model parameters.

If we assume model A to provide the true function linking conservation expenditure to reduction of extinction probability, we clearly would decide to spend the share in breed 1, since $\Delta z_1^A D_1' = 9.150 \times 10^{-4}$ is the maximum under this model. For model B and C, however, the more efficient strategy would be to spend the conservation funds on breed 2. In fact, the return in terms of conserved diversity would be 6.8 and 33.3% higher by spending the funds on breed 2 than on breed 1 under models B and C, respectively.

2.6. Optimum allocation of a limited budget to a set of breeds

Let B be the total budget for conservation activities that is to be spent on a set of breeds, and let M be a vector of size N containing elements $m_i, i = 1, \dots, N$ where element $m_i \geq 0$ reflects the amount of money spent on conservation of breed i . Note that $\sum_i m_i = B$.

There are two basic problems to solve:

- 1) Which of the breeds in the set will receive financial support, and which ones will not receive any funding.
- 2) How (in what proportions) should the available funds be distributed to those breeds that will receive funding.

The two problems can be solved simultaneously with the following strategy: the total budget, B , is divided in n_b equal (small) shares of money $b = \frac{B}{n_b}$ to be allocated. Then, the following iterative procedure is suggested:

- 1) Set $m_i = 0$ for all breeds; start with the first share b .
- 2) Compute the expected reduction of extinction probability Δz_i for each of the breeds under the assumption that b is spent on only this breed.
- 3) Compute the increase in expected diversity $E(\Delta D | z_i, b)$ for each breed.
- 4) Allocate this share on breed j , for which the increase of expected diversity is highest; update the extinction probability of this breed from the actual value z_j to $z_j + \Delta z_j$ and add b to m_j .
- 5) Recalculate marginal diversities for all breeds.
- 6) Allocate the next share, beginning with step 2, until all shares are allocated.

After going through the described iterative algorithm, the vector M contains the optimal allocation of the available funding to the set of breeds in the sense that no other pattern of allocation would lead to a higher quantity of conserved diversity under the assumptions made.

3. Material

The suggested framework will be illustrated with the data of 23 African zebu and zenga type cattle breeds. The data used in the present study are a subset of the data used in a companion paper (Marti et al., 2003) to illustrate the usefulness of the Weitzman approach for the quantification and dissection of the genetic diversity of a set of breeds.

More details on the data and the breeds can be found in that paper.

Table 2 gives the names of the breeds and the respective values of the extinction probability and the marginal diversity taken from Marti et al. (2003). Extinction probabilities were estimated from a variety of breed-specific characteristics, including population size and its change over the last 10 years, geographical distribution, presence of a breeding infrastructure or a conservation scheme and socio-cultural importance of the breed. This parameter reflects the probability that the corresponding breed becomes extinct within a period of 50 years and ranges from 0.70 for Highland Zebu to 0.34 for Kenya Boran. Note that the breeds with highest extinction probabilities are either not classified in the FAO World Watch List (Scherf, 2000), as the Kenyan Highland Zebu and the Tanzanian Kilimanjaro Zebu,

or are listed as already extinct like the Iringa Red from Tanzania.

Based on allele frequencies for 15 microsatellite markers, estimated from samples of 35 animals (33 for Highland Zebu, 31 for Orma Boran) per breed, Reynolds (1983) distance was computed and a distance matrix was set up.

With this distance matrix, the actual and the expected diversity were computed using the approach suggested by Weitzman (1992). The actual diversity for the whole group was 1.214, and the expected diversity after 50 years would be 0.622 ± 0.137 . The loss of about half of the diversity over this time period corresponds well with the average extinction probability of 0.49.

The maximum likelihood tree resulting from the application of the Weitzman approach is depicted in Fig. 2, showing a clear separation of the set in two major groups with some additions:

Table 2

Breed types, abbreviations of breed names, countries the breed is found, extinction probabilities and marginal diversities for the zebu and zenga breeds considered in this study

Breed	Type	Abbreviation	Countries ^a	Extinction probability	Marginal diversity
Angoni	Zebu	ANGONI	Malawi, Zambia	0.40	-0.0595
Arashie (Beja)	Zebu	ARASHIE	Sudan, Eritrea	0.53	-0.0805
Arsi	Zebu	ARSI	Ethiopia	0.53	-0.0410
Bale	Zebu	BALE	Ethiopia	0.57	-0.0360
Butana (Foya)	Zebu	BUTANA	Sudan	0.43	-0.0560
Ethiopian Boran	Zebu	ETHBORAN	Ethiopia, Kenya, Somalia	0.48	-0.0350
Gobra	Zebu	GOBRA	Senegal	0.37	-0.0655
Highland Zebu	Zebu	HIGHZEBU	Kenya ^c	0.70	-0.0385
Iringa Red	Zebu	IRINGARED	Tanzania	0.60	-0.0685
Kavirondo	Zebu	KAVIRONDO	Kenya	0.47	-0.0480
Kenyan Boran	Zebu	KENYBORAN	Kenya, Tanzania ^b , Zambia ^b	0.34	-0.0480
Kilimanjaro Zebu	Zebu	KILIMANJA	Tanzania ^c	0.63	-0.0465
Madagascar Zebu	Zebu	MADAZEBU	Madagascar	0.50	-0.1215
Malawi Zebu	Zebu	MALAZEBU	Malawi	0.50	-0.0655
Maure	Zebu	MAURE	Mali, Mauritania	0.40	-0.0485
Mbororo	Zebu	MBORORO	Nigeria	0.37	-0.0630
Nuba Mountain	Zebu	NUBA	Sudan	0.57	-0.0565
Ogaden	Zebu	OGADEN	Ethiopia	0.60	-0.0460
Orma Boran	Zebu	ORMABORAN	Kenya ^b , Ethiopia ^b	0.40	-0.0610
Sokoto Gudali	Zebu	SOKOTO	Nigeria ^b	0.53	-0.0560
Arado	Zenga	ARADO	Eritrea	0.50	-0.0385
Fogera	Zenga	FOGERA	Ethiopia	0.43	-0.0385
Horro	Zenga	HORRO	Ethiopia	0.43	-0.0350

^a DAD-IS 2.0 (FAO, 2000).

^b DAGRIS (ILRI, 2001).

^c Hanotte et al. (2000).

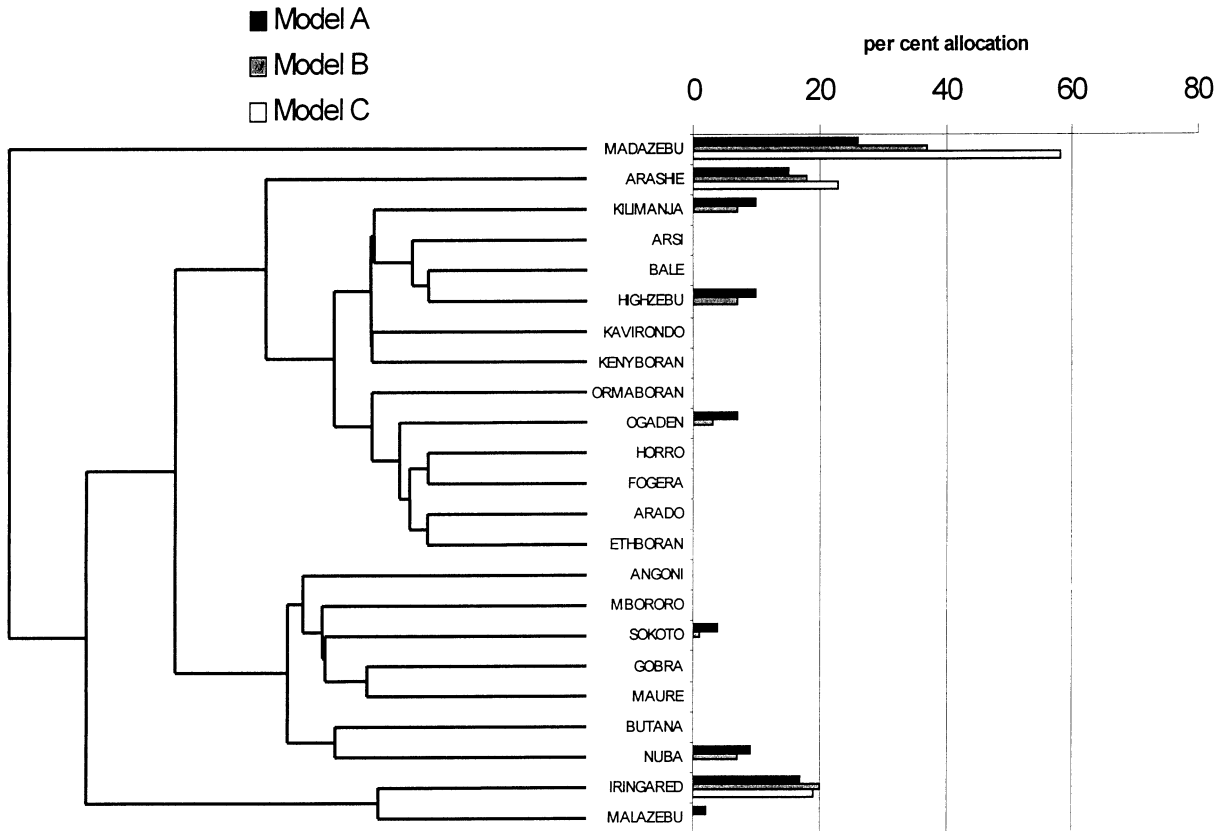


Fig. 2. Maximum likelihood tree from the application of the Weitzman (1992) algorithm and optimum allocation of resources resulting from the three models considered.

- An East-African sub tree (Arashie to Ethiopian Boran) with the Sudanese Arashie breed being somewhat an outlier in this group. This branch also contains the three zenga breeds Arado, Fogera and Horro from the Ethiopia/Eritrea area.
- A West African subtree (Mbororo to Maure) with the Sudanese breeds Butana and Nuba and the Angoni breed from the Malawi region attached.
- A small separate branch consisting of Iringa Red and Malawi Zebu both from the Malawi/Tanzania region.

Madagascar Zebu is most distinct from all other breeds, which may reflect the geographical separation on the island of Madagascar inhibiting

unintended exchange of genes with other breeds, but this breed may also have quite a different breed history compared with the zebu breeds on the African continent (Felius, 1995; Payne and Hodges, 1997).

This outstanding position in the tree is also reflected by the high (absolute) value of 0.122 for the marginal diversity of Madagascar Zebu as shown in Table 2. This means that a hypothetical change of the risk status of this breed from completely endangered (extinction probability one) to completely secure (extinction probability zero) would increase the expected diversity of the whole set of 23 breeds by 19.6% ($0.122/0.622 \times 100$). The Horro breed had the smallest marginal diversity (-0.035), the average over all breeds being -0.054 .

4. Results

It was assumed that a total of $B = 50\,000$ units of conservation funds were available to be allocated to the set of breeds. Allocation was done in $n_b = 100$ shares of $b = 500$ units of currency. The same parameters as in the example given were used, i.e.

$$\gamma = 45; \quad \lambda = 0.05; \quad \nu = 0.001; \quad \eta = 0.00002.$$

The resulting optimal allocation of resources under the three assumed models is given in Fig. 2.

Under all three models, the largest share of the available funds is allocated to conserve the Madagascar Zebu. Model C suggests spending 58% of the total funds in this breed, while using models B and A we would allocate 38 and 26% to this Madagascar Zebu, respectively. This is due to the fact that the extinction probability of Madagascar Zebu $z_i = 0.50$ is above the threshold value $z_0 = 0.45$, so that investments are more effective in terms of reducing extinction probability under the assumptions of model A and B than under model C. In other words, under Model C you have to invest more shares to achieve the same reduction of extinction probability of that breed compared with the other models.

Apart from the Madagascar Zebu, model C allocates funds only to two more breeds, i.e. to Arashie (23%) and to Iringa Red (19%). As allocation to Madagascar Zebu and Arashie is reduced under models B and A, respectively, funds are allocated to five other breeds under these models, i.e. to Highland Zebu, Kilimanjaro Zebu, Nuba, Sokoto and Ogaden. Only under model A is a small share (2%) of the total funds allocated to Malawi Zebu.

It should be noted that in this application, funds are only allocated to breeds which have an extinction probability of 0.50 or higher. There are, however, other breeds, like the Arado, Arsi, or Bale, that also have an extinction probability ≥ 0.50 but do not receive any funds under any of the three models. Thus, high extinction probability seems to be a necessary, but not a sufficient prerequisite to qualify a population for conservation expenditure. However, there is a clear association between the ‘conservation potential’ $CP_i =$

$-z_i \times D'_i$ of a breed and its ranking in the priority list for funding.

In Fig. 3, the conservation potential is shown for all breeds and it is shown that only breeds exceeding a given threshold T_A or T_C are candidates for conservation funding under models A and C, respectively.

Madagascar Zebu clearly has the highest conservation potential with $CP_i = -0.50 \times -0.1215 = 0.0607$ followed by Arashie ($CP_i = 0.0427$) and Iringa Red ($CP_i = 0.0411$). However, breeds with very similar values for CP_i might obtain very different funding. Under model A and B, Malawi Zebu ($CP_i = 0.0327$) receives only 3% of the funds, while Highland Zebu ($CP_i = 0.0269$) receives 10 or 7%, respectively. Hence, the conservation potential may serve as an indicator for conservation priorities, but does not allow an assessment of the proportions for the optimum allocation of shares.

The change of expected diversity as a consequence of allocating conservation funds under the assumptions of the three models is shown in Fig. 4. The highest increase in expected diversity is obtained with model A, leading to an expected diversity of 0.670, which is a 7.7% gain compared

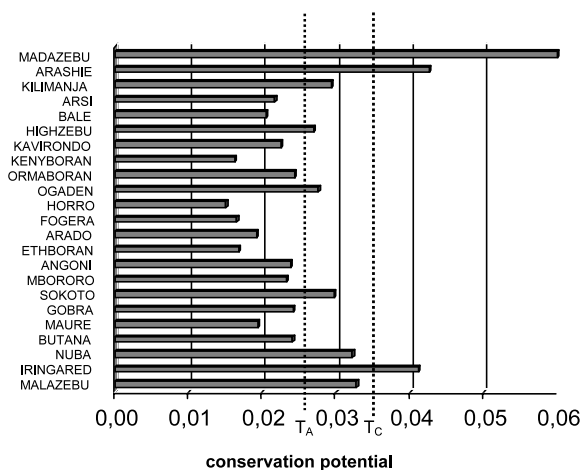


Fig. 3. Conservation potential CP_i for the 23 breeds. All breeds with a value of CP_i above the threshold T_A (T_C) receive conservation funds under model A (C).

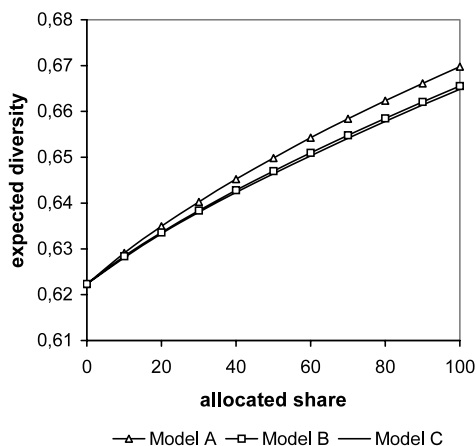


Fig. 4. Development of the expected diversity as a function of the proportion of allocated shares under the three models considered.

with the expected diversity without spending any funds for conservation.

Under model B and C, we observe a very similar increase in expected diversity with 0.666 (+7.0%) for model B and 0.665 (+6.9%) for model C.

In all three models, returns (in terms of conserved diversity) to investment are diminishing. Under model A, the first 10% (10×500 monetary units) spent lead to an increase in expected diversity of 1.07%, while the last 10% (after having already spent 90% of the budget) lead only to an increase of 0.54%.

5. Discussion and conclusions

The discussion will mainly focus on three issues. First, methodological aspects will be discussed, especially with respect to seemingly contradicting findings presented by Weitzman (1998). In the second part, an extension of the suggested approach to maximizing expected utility will be presented. Finally, the observed optimum allocation for the given example will be compared with other allocation criteria suggested in the literature and general conclusions will be drawn.

5.1. Methodological aspects

Other than in wildlife conservation, farm animal genetic valuation has to look primarily at direct use values of breeds, which are much more relevant (or, at least, much easier to quantify) for farm animal breeds than for wildlife species. In the first place it is the difference in productivity (e.g. milk yield, growth) of a local versus an exotic breed, that motivates farmers to replace animals of one breed through the other. In many cases, this narrow economic view has been found to be misleading, since high yielding animals turned out to be incapable of dealing with the environment, nutritional, and disease challenges. Therefore, total economic performance has to be taken into account.

Hence net conservation costs have to be considered, since in many cases conservation activities will have 'secondary' effects that improve the productivity of an endangered breed and thus have the potential to pay back within a reasonable time span. In many instances, well chosen conservation measures may lead to an economically sustainable use of locally adapted farm animal breeds under the given environmental and market conditions.

In the presented illustration of the methodology, available resources are allocated to three to nine different breeds with the effect of reducing extinction probabilities of these breeds to some extent, but making none of them completely safe from extinction. This result seems to be in contradiction with the central theorem of Weitzman (1998). This 'extreme policy' theorem says that the optimum policy will always make a subset of the considered populations completely safe and leave another subset completely endangered, and only one population will be 'partially' safe, basically because the available resources are exhausted before it could also be made completely safe.

The reason for the apparent discrepancy of the two results is that Weitzman (1998) implicitly assumes constant cost for a fixed change of extinction (or in his 'Noah's Ark'-analogue 'boarding') probability, irrespective of whether a breed is already close to being safe or it is highly endangered. In the approach presented here con-

ervation expenditure is assumed to yield diminishing returns, so that it is cheaper to reduce the extinction probability of a highly endangered breed by one unit, than to make a relatively safe breed even safer by the same increment. Since one of the basic assumptions is that the extinction probability is proportional to ΔF and therefore

$$z_i \propto \frac{1}{2N_{ei}},$$

z_i only becomes 0 (i.e. breed i is completely safe) if N_{ei} becomes infinitely large, which, under any model, requires infinite funds. For this reason, the approach suggested here allocates money to different breeds to reduce their risk of extinction without making any of them completely safe.

The three models A, B, and C linking conservation expenditure to the effect of reducing extinction probability are largely theoretical, but reflect a range of typical conservation strategies in real life. Detailed analysis of different conservation strategies in practice will certainly reveal a need for more complex and more variable modeling options. The framework provided here can encompass different models of conservation applying to different breeds. This might be the case when emergency programs, using *ex situ in vivo*, or *in vitro* cryopreservation techniques are considered for the most endangered breeds, while for less endangered breeds cheaper options, including focused extension activities may be sufficient (Meuwissen, 1999). Another factor that needs to be taken into account in real life applications is that there are fixed costs to set up a conservation scheme. This means, that some basic expenditure (e.g. the first ‘shares’) allocated to a breed will have little or no effect on its extinction probability because the money is primarily required to set up the operation of the conservation scheme.

5.2. Extension to utility

The presented methodology to optimize the allocation of resources in order to maximize the conserved diversity is a generic one and is independent of the diversity measure used. More importantly, the approach can be extended to

maximize the total utility of the set of breeds conserved within one species. Components of utility can be defined on three levels:

- The first component of total utility is the diversity within the species. The rationale of this is that species will more likely be able to adapt to future needs if there is a large diversity within the species. Since the possible changes in the future, such as different market needs, new diseases, climatic changes, etc. are unknown, it is essential to conserve diversity in the whole genome, and not only known functional genes, even if they were identified with sufficient accuracy. Total genetic diversity within farm animal species is estimated to be about 50% within and 50% between breeds (Hammond, 1994). Therefore, activities to conserve between-breed variation have to be accompanied by activities to conserve within-breed variation. Considering the framework suggested in the present paper, these two objectives overlap to some extent, since reducing extinction probability by increasing the effective population size is also a measure to prevent a loss of the within-breed genetic variability (Falconer and Mackay, 1996).
- There are certain features or characteristics of breeds which should be maintained, since they have an actual or potential future value. Such features may include adaptation to certain environments and resistance to specific diseases. From a conservationist point of view, it is desirable to maintain such features by maintaining at least one breed which has the respective characteristic. As a consequence, the marginal utility of a breed in this context is heavily dependant on the composition of the set of breeds. If, say, a certain feature is common in a number of breeds, of which one is perfectly safe, the marginal utility of the other breeds is low or zero. If, however, only one breed is left with the defined feature, its marginal utility will be very high, because if it goes extinct, the feature will be lost for the whole species.
- Beyond the features shared by a group of breeds, each breed has a specific value of its

own. This may be its adaptation to a very special environment, the special social, religious or cultural role it is used for, etc., i.e. all specific functions of a breed that can not be also fulfilled by animals of a different breed.

Weitzman (1998) suggested an approach to combine the first two components of utility in a concept to allocate conservation resources in an optimum way. The conceptual approach is straightforward, but the crucial problem is to value the different components of diversity appropriately. Only few attempts have been made to assess the economic value of certain features of breeds, for example disease tolerance (Kristjansson et al., 1999). Hedonic pricing, contingent valuation and assessment of buyer preferences provide some assessment of relative values of breeds even in developing countries (Jabbar, 1998; Jabbar et al., 1998). A systematic economic valuation of animal genetic resources and special characteristics of breed groups has only recently been identified as a high priority area of research (Rege, 1999).

Suppose we are able to quantify the relative economic value of the three components of utility:

- w_D is the value of a ‘unit’ of diversity;
- w_{F_j} is the value of feature j ;
- w_{B_i} is the specific value of breed i .

Then the total utility U_K of a set of breeds K can be written as

$$U_K = w_D D_K + \sum_{j \in K} w_{F_j} + \sum_i k_i w_{B_i}$$

where $j \in K$ stands for feature j being present in at least one of the ‘non-extinct’ breeds in set K .

This ‘total utility’ can be used analogously to the diversity in Eq. (2) of the present paper to derive the expected utility of the conserved set of breeds, allowing use of the suggested stepwise allocation algorithm to find the optimum allocation with respect to expected utility.

5.3. Suggested allocation

The application presented illustrates nicely the key features of a simple, optimal strategy to

allocate conservation resources. Although the degree of endangerment is relevant, it is not the only nor even the most important factor that conservation priorities should be based upon. Among the four most endangered breeds in the example considered (Highland Zebu, Kilimanjaro Zebu, Ogaden and Iringa Red), only Iringa Red would receive 19% of the allocated conservation funds under model C, while in model A and B all of them would be funded to some extent. The two breeds that are awarded the highest conservation funds, i.e. Madagascar Zebu and Arashie, have intermediate extinction probabilities.

Conservation decisions also have to take into account the contribution of breeds to the within species diversity, the cost effectiveness of conservation activities in different breeds, and the economic values of different characteristics of the breed. Combining all these factors appropriately may sometimes lead to ‘counterintuitive’ suggestions. A good example is the ‘crowned crane paradox’ presented by Weitzman (1993), where the optimum solution is to ‘sacrifice’ one highly endangered species to make a closely related, but less endangered species even more safe.

Ruane (2000) collected information on a set of criteria for different breeds which are considered as ‘candidates’ for a conservation scheme, but the lack of a sufficient conceptual framework led him to suggest defining conservation priorities primarily based on the degree of endangerment. This seems to be a sub-optimal decision rule, since most of the available information is not taken into account. Maximizing the expected overall utility would be the best optimization criterion in this context, integrating information on the phylogenetic structure, the degree of endangerment, values of breeds and traits, and other factors appropriately.

The suggested approach is useful to allocate a limited budget available for conservation of a given subset of breeds in an optimal way. What it does not provide is to say how much money should be poured into this effort in the first place, should we use €10m or €100m to preserve African cattle diversity, as compared e.g. to preserve diversity of African goats, chicken, or even crops (see the similar arguments given by Mainwaring,

2001)? Eventhough it is difficult or virtually impossible to quantify, money is spent for this purpose presently. The suggested methodology could be used to find the optimum allocation of this actual budget to achieve as much conserved diversity as possible.

This situation was considered by Simianer (2002) who found that allocating all (hypothetically) available funds to the three most endangered breeds in a set of 26 African taurine cattle breeds was 9% less efficient than distributing the funding in equal shares to all the breeds. Using the optimum allocation strategy described in the present paper led to a 57% increase of expected diversity compared with the uniform allocation strategy.

Given the limitations of available funding compared with the size of the challenge, the need for a general framework to derive rational strategies for decision-making, taking all relevant factors into account, is evident. This study has provided an appropriate methodological framework. Other than in most species in general biology (Mainwaring, 2001), the phylogenetic structure (based on genetic distances estimated from molecular marker data) is well known for many breeds or breed groups within farm animal species. Additional key parameters such as extinction probabilities based on more than population size are rarely available.

Even more scarce are economic data on the value of breed diversity, of certain traits of breed groups and of single breeds. On the cost side, the cost-efficiency of different conservation strategies under different circumstances need to be assessed. While it should be possible to quantify the full cost of conservation schemes (see e.g. Brem et al., 1984; Smith, 1984a,b; Cunningham, 1996), it is not trivial to assess the effect on extinction probability. This task will require a close co-operation of economists and conservation geneticists.

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