Weitzman's Approach and Conservation of Breed Diversity: an Application to African Cattle Breeds

S. B. REIST-MARTI,* H. SIMIANER,† J. GIBSON,‡ O. HANOTTE,‡ AND J. E. O. REGE§

*Institute for Agricultural Economics, ETH Zurich, Sonneggstrasse 33, 8092 Zurich, Switzerland,
email sabine.marti@iaw.agrl.ethz.ch
†Applied Genetics Network, Sternstrasse 5, 37083 Göttingen, Germany, and Department of Animal Breeding and Genetics, University of Göttingen, Albrecht Thaer Weg 3, 37075 Göttingen, Germany
‡International Livestock Research Institute, P.O. Box 30709, Nairobi, Kenya
§International Livestock Research Institute, P.O. Box 5689, Addis Ababa, Ethiopia

Abstract: *To evaluate the Weitzman approach for assessing alternative conservation strategies for breed (population) diversity, we used genetic distance measures between 49 African cattle breeds divided into two groups of 26 taurine (*Bos taurus*) and sanga (*Bos taurus × Bos indicus*) breeds and 23 zebu (*Bos indicus*) and zenga (sanga ×* Bos indicus*) breeds. The derived maximum-likelihood trees clearly displayed the geographic distribution and the zebu-taurine admixture of the breeds. We developed a novel scheme to estimate the extinction probability for each breed which considered total population size, change of population size over the last 10 years, distribution of the breed, risk of indiscriminate crossing, organization among farmers, establishment of conservation schemes, political situation of the countries, special traits, sociocultural importance, and reliability of information. This scheme yielded reasonable estimates of extinction probabilities for the analyzed breeds, which were significantly influenced by the population size and its recent change, distribution of the breed, organization among farmers, establishment of conservation schemes, and reliability of information. The average extinction probability over all breeds and for each breed group was around 48%. Diversity in the zebu-zenga group was only half the diversity in the taurine-sanga group, mainly because of the lower number of breeds and their genetic origin. For both groups, the expected diversity after 20–50 years was about half the current diversity, and the coefficient of variation was about 20%. Our results suggest that the optimum conservation strategy is to give priority to those breeds with the highest marginal diversity, rather than to the most endangered breeds; thus, Madagascar Zebu and Muturu should be given conservation priority in their respective groups. Our study demonstrates that efficient conservation of genetic diversity with limited funds has to take genetic and nongenetic factors into account. Nongenetic factors are accounted for within our scheme to derive extinction probabilities. Within-breed and within-population diversity are not accounted for. Extending Weitzman's basic approach accordingly could yield an effective methodology for determining conservation strategies under highly varying circumstances and for many species, including wild organisms.*

Key Words: Africa, cattle breeds, diversity, extinction probability, Weitzman approach

El Método de Weitzman y la Conservación de la Diversidad de Razas: una Aplicación a Razas de Ganado Africano

Resumen: *Para evaluar el método de Weitzman de valoraración de estrategias alternativas para la conservación de la diversidad de razas (poblaciones), utilizamos medidas de distancia genética entre 49 razas de ganado africano divididas en dos grupos de 26 razas de taurinos (*Bos taurus*) y sanga (*Bos taurus × Bos indicus*) y 23 razas de cebú (*Bos indicus*) y zenga (sanga ×* Bos indicus*). Los árboles de similitud máxima derivados mostraron claramente la distribución geográfica y la mezcla taurino/cebú de las razas. Desarrollamos un novedoso esquema para estimar la probabilidad de extinción de cada raza considerando el tamaño de la población, cambios en el tamaño de la población en los últimos 10 años, distribución de la raza, riesgo*

Paper submitted December 3, 2001; revised manuscript accepted January 15, 2003.

de cruzas indiscriminadas, organización de campesinos, establecimiento de planes de conservación, situación política de los países, características especiales, importancia sociocultural y confiabilidad de la información. Este esquema produjo estimaciones razonables de las probabilidades de extinción de las razas analizadas, que fueron influidas significativamente por el tamaño de la población y sus cambios recientes, la distribución de la raza, la organización de campesinos, el establecimiento de planes de conservación y la confiabilidad de la información. La probabilidad de extinción promedio para todas las razas y para cada grupo de razas fue alrededor de 48%. La diversidad del grupo cebu/zenga fue solo la mitad de la diversidad del grupo taurino/sanga, debido principalmente al menor número de razas y su origen genético. La diversidad esperada después de 20 a 50 años para ambos grupos fue casi la mitad de la diversidad actual, y el coeficiente de variación fue de 20% aproximadamente. Nuestros resultados sugieren que la estrategia de conservación óptima es darle prioridad a las razas con la diversidad marginal más alta, no a las razas en mayor peligro: por lo tanto, se le debe dar prioridad de conservación a Cebú Madagascar y Muturu en sus respectivos grupos. Nuestro estudio destaca que la conservación eficiente de diversidad genética con financiamiento limitado debe considerar factores genéticos y no genéticos. Los factores no genéticos son incluidos en nuestro esquema para derivar probabilidades de extinción. La diversidad intra-raza y poblacional no son consideradas. En consecuencia, la extensión del método básico de Weitzman produciría una metodología efectiva para determinar estrategias de conservación bajo circunstancias muy variables y para muchas especies, incluyendo organismos silvestres.

Palabras Clave: Africa, diversidad, método de Weitzman, probabilidad de extinción, razas de ganado

Introduction

Of an estimated range of 2 to 100 million species of living organisms, some 40 species are domesticated and used for food production and agriculture. Over the past 12,000 years, those 40 species have evolved into about 6000 to 7000 animal breeds, which have become well adapted to a wide range of local environments and production systems and are therefore genetically unique (Scherf 2000). When people moved, they took their domestic breeds, especially livestock, with them and relied on them as a source of food (Epstein & Mason 1984; Reed 1984). Human mobility and communication became much easier in the twentieth century, and, coupled with technologies such as artificial insemination and embryo transfer, these forces promoted a rapid global spread of certain well-marketed breeds (Hammond & Leitch 1996). Purebred or crossed, these breeds met the demand of changing farming systems and breeding objectives. They have sometimes been distributed in developing countries as part of development aid. This introduction of exotic breeds and other social and economic pressures have exposed at least 1000 breeds to the risk of extinction, representing a large loss of potentially valuable genetic diversity (Cunningham 1996). Immediate conservation of 1000 breeds would be difficult and tremendously costly. Moreover, such conservation is not only of national but also of global interest. Therefore, tools for priority setting and coordination of conservation activities on an international level are needed.

Farm-animal diversity can be assessed as genetic or phenotypic diversity, but its value is multifaceted. In economic terms, diversity can provide insurance against changes in production circumstances, a new disease, or changes in market demands (Oldenbroek 1999). Diversity also has an ecological value: environmentally adapted breeds (e.g., trypanotolerant cattle) allow sustainable food production in lower-input farming systems (d'Ieteren & Kimani 2001), which have lower impact on the environment and supply ecological animal draught power, fuel from dung, and clothing. Diversity is a precondition for breeding and research on the genetic improvement of, for example, quality traits, disease resistance, or livestock productivity. Sociocultural values, although harder to measure than monetary values, are also important.

There are different ways to represent the diversity that exists among breeds. A common approach is the construction of phylogenetic trees based on genetic-distance information (Crozier 1992). Another approach is construction of phylogenetic trees that are based on "features" (Faith 1992) and disregard genetic distances. Both approaches are illustrative but fail to incorporate important aspects of diversity, such as the economic and noneconomic values of breeds and the risk of loss of diversity, both of which are critical to the overall management of the genetic diversity in populations.

Weitzman (1992, 1993) has suggested a method that uses genetic and nongenetic information to calculate a maximum-likelihood tree and the current diversity of a group of species and to assess the expected change in diversity over a certain time horizon. This method allows evaluation of the change in the group's diversity when the degree of endangerment of one or several species is reduced (marginal diversity). Compared with other approaches (Crozier 1992; Faith 1992), mostly descriptive and illustrative, the Weitzman method provides a well-defined diversity metric, allowing quantitative assessment of the consequences of alternative conservation activities as an aid to decision-making in conservation. An application to livestock breeds was presented by Thaon d'Arnoldi et al. (1998), and the approach was used in studies on European cattle breeds (Bremond 2001; Cañon et al. 2001) and European pig breeds (Laval et al. 2000).

We sought to evaluate the potentials and limits of Weitzman's approach for decision-making in the conservation of farm-animal biodiversity in Africa. For illustration, we examined data from a long-term study of African livestock.

Methods

Breeds

The derivation of the maximum-likelihood tree with the Weitzman approach is computationally intensive. Therefore, we divided the 49 African cattle breeds we studied into two groups: the TS group included 10 taurine (*Bos taurus*) and 16 sanga (*Bos taurus* × *Bos indicus*) breeds, and the ZZ group included 20 zebu (*Bos indicus*) and 3 zenga (sanga × *Bos indicus*) breeds. The division into two groups was based on the *Bos indicus* admixture, which was presumed to be <50% for group TS breeds and >50% for group ZZ breeds. Appendix 1 gives the breed names, breed type, estimated population size, status of risk according to the Food and Agriculture Organization of the United Nations (FAO), origin and size of the sample used for estimating genetic diversity, and proportion of indicine (*Bos indicus*) Y alleles in the breed sample, which gives evidence of crossbreeding with *Bos indicus*. Information was taken from the DAD-IS 2.0 (FAO 2000) and DAGRIS (International Livestock Research Institute 2001) databases and completed by one of the authors (J.E.O.R.), based on his knowledge of the breeds where possible. The breed classification we used was based on Rege (1999); type classification and the proportions of taurine versus zebu Y-specific alleles were obtained from Hanotte et al. (2000).

For most breeds, distribution over one country was reported (FAO 2000; International Livestock Research Institute 2001). Of the 49 breeds, the FAO has declared 2 endangered and 1 (Iringa Red) extinct. Iringa Red, a zebu breed, may be declared extinct because of crossbreeding with European (*Bos taurus*) breeds. Recent molecular analysis indicates, however, that the proportion of European–Near East taurine alleles in the analyzed population of southern Tanzania is similar to the one observed in other East African zebu populations (O.H., unpublished data). We therefore considered the breed at risk, not extinct. For five breeds, no status of risk was given.

The proportion of indicine Y alleles varies substantially between breeds (Appendix 1). In the ZZ group it ranges from 100% (Arashie, Bale, Ethiopian Boran, Gobra, Highland Zebu, Iringa Red, Kavirondo, Kenyan Boran, M'bororo, Maure, Nuba Mountain, Ogaden, Orma Boran, Sokoto Gudali, Arado, Fogera, Horro) to 65% (Kilimanjaro Zebu). In the TS group it ranges from 0% indicine alleles (Kuri, N'Dama, Afrikaner, Ankole, Kavango, Mashona, Nguni, Pedi, Tuli, Watusi) to 100% indicine alleles (Afar, Danakil, Raya-Azebo). For three breeds, no information was available. Further description of the data bases is given by Eding (2002) and Hanotte et al. (2000, 2002) or O. Hanotte (email o.hanotte@cgiar.org).

Genotype Data

We used allele frequencies of 15 autosomal microsatellite loci (ILSTS50, MGTG4B, AGLA293, ILSTS006, TGLA48, ILSTS005, ILSTS036, ILSTS028, ILSTS033, ILSTS008, ILSTS023, TGLA227, TGLA126, ILSTS103, TGLA122) derived from 1694 individuals of the 49 African cattle breeds. All breeds were represented by 35 individuals, except for the Baladi (40), Highland Zebu (33), Orma Boran (31), Blonde d'Oulmès (31), and Muturu (21) (Appendix 1). The genotyping was done at the International Livestock Research Institute as part of an on-going study of the genetic diversity in African livestock populations.

Genetic Distance

To overcome the differences in sample sizes between breeds, genetic-distance matrices were derived from allele frequencies of bootstrap samples. All bootstrap samples were of equal size ($n = 35$), and 100 replicates were drawn. Reynolds' (Reynolds et al. 1983) genetic distance d_{xy} was used for all trees because it is considered to suit especially the short divergence times that occur in breed diversification (Eding & Laval 1999):

$$d_{xy} = 1/2\frac{\sum_a (x_a - y_a)^2}{1 - \sum_a x_a y_a}, \tag{1}$$

where x_a and y_a are frequencies of the ath allele drawn in populations x and y. Genetic distances were computed with the PHYLIP 3.57c software (Felsenstein 1993).

Extinction Probability

To model future trends in the diversity of breeds by the Weitzman approach, the extinction probability over a chosen time period must be defined for each breed. For most breeds, some indication of the status of risk of extinction, based mainly on population size, could be found in the literature (Rege 1999; FAO 2000). Because many other factors influence the survival of a breed (Barker 1999; Ruane 1999), we developed a new scheme to derive extinction probabilities. This scheme included 10 variables (Table 1) that were assigned values between 0, for no impact on risk, and 0.1, for high impact on risk, except for population size, for which the upper limit was 0.3. Although nine variables had equal weight, population size was weighted three times stronger because the number of animals is a direct and thus crucial measure of the extinction probability of a breed.

Four variables describe the population: total population size (POS) and its change over time (CHA), distribution of the breed (DIS), and risk of indiscriminate crossing (CRO). Organization among farmers (ORG), establishment of a conservation scheme (CON), and the political situation in the countries concerned (POL) reflect—in a broad sense—the environment. The present "value" of a breed is brought in by the variables of special traits (SPE) and sociocultural importance (CUL). The last variable, reliability (REL), acts as a correction factor for unreliable information. These 10 variables are considered the most important factors in the extinction probability of African cattle breeds.

Information on the variables for each breed was mainly retrieved from the databases DAD-IS 2.0 (FAO 2000) and DAGRIS (International Livestock Research Institute 2001). Missing information was completed by one of the authors (J.E.O.R.), based on his knowledge of the breeds. The estimates of the political situations in the countries were based on the security information for travelers from the Swiss Federal Department of Foreign Affairs (Eidgenössisches Departement für auswärtige Angelegenheiten 2001). The values for reliability were all taken from DAD-IS 2.0 (FAO 2000). Missing information was filled with default values. In general, indigenous cattle in Africa are connected to some extent with the culture of their owners. Thus, the default value for sociocultural importance was 0.05. Unknown total population size was assumed to lie between 10,000 to 100,000 animals, which means that the breed is neither very small and localized nor popular and therefore widespread. As for most African cattle breeds, the effective population size and the number of breeding males and females is unknown, so for all breeds we used the total number of

Table 1. Variables and criteria for the estimation of the extinction probability of African cattle breeds.

Variable (abbreviation)	*Criterion and value*
Total population size (POS)	0.3 < 1,000 0.2 = 1,001 to 10,000 0.1 = 10,001 to 100,000 0.0 > 100,000 missing values = 0.1
Change of total population size over the last 10 years (CHA)	0.1 = decreasing (>20%) 0.0 = increasing or stable
Distribution of the breed (DIS)	0.1 = localized (in 1 or more countries) 0.05 = spread within 1 country 0.0 = widespread over several countries missing values = 0.0
Degree or risk of indiscriminate crossing (CRO)	0.1 = high 0.0 = marginal missing values = 0.1
Organization of farmers (ORG)	0.1 = no 0.0 = yes (e.g., herdbook) missing values = 0.1
Established conservation scheme (CON)	0.1 = none 0.05 = partial 0.0 = yes
Political situation of the country (-ies) (average over all countries) (POL)	0.1 = general advice against travel 0.05 = some objections 0.0 = no objections missing values = 0.0
Special traits (SPE)	0.1 = none 0.0 = yes (e.g., trypanotolerance, adaptation to the environment) missing values = 0.1
Sociocultural importance (CUL)	0.1 = none or can easily be replaced by other breeds 0.05 = some sociocultural value 0.0 = yes (e.g., religion, traditional custom) missing values = 0.05
Reliability of the information (REL)	0.1 = not reliable 0.0 = reliable missing values = 0.1

animals. Breeds with unidentified distribution were considered widespread. Countries with no security information for travelers were considered not to have security problems (such as civil strife) that would place breeds at increased risk.

The extinction probability of breed *i*, z_i, was computed as the sum of the values of the 10 variables described above and, when the sum is rescaled to a value between 0.1 and 0.9,

$$z_i = \frac{0.8}{1.2} * \sum_{a=1}^{10} z_{ia} + 0.1. \tag{2}$$

The rescaling was done to rule out the possibilities that a breed may be considered completely safe from ($z_i = 0$) or entirely doomed to ($z_i = 1$) extinction. Such absolute predictions are not legitimate because all factors of influence can never be taken into account for the estimation and the future cannot be foreseen.

Maximum-Likelihood Tree and Current and Expected Future Diversity

We used Weitzman's (1992) recursive algorithm to generate a maximum-likelihood tree of the set that, in the case of breeds, represents only a one-dimensional projection of the distances between the breeds and does not reconstruct the actual genealogy. Illustration of the trees was done with TreeView 1.6.1 (Page 1996).

The total Weitzman diversity (*D*) of a set S, *D*(*S*), is identical to the sum of the ordinates of all nodes of the tree if the tree is drawn horizontally. The *D*(*S*) is not identical to the sum of the length of all horizontal branches, as Weitzman (1992) and Thaon d'Arnoldi et al. (1998) suggest, but the sum of the branch lengths has to be reduced by the total height of the tree to give the diversity, as can be verified easily with the example of four primate species given by Thaon d'Arnoldi et al. (1998).

The expected diversity of the set after a given time *t* accounts for the extinction probability z_i for every breed *i* of the set. The probability that, at the end of the time horizon, situation *Q* will arise, where a particular subset of breeds exists and the complementary subset is extinct, is

$$P(Q) = \prod_i (k_i + (-1)^{k_i} z_i), \tag{3}$$

where $k_i = 1$ if breed *i* still exists and $k_i = 0$ if breed *i* is extinct in the set *Q*.

The expected diversity after time *t* is thus

$$E[D(S)] = \sum_Q P(Q)D(Q), \tag{4}$$

and the variance is

$$\text{var}[D(S)] = \sum_Q P(Q)[D(Q)]^2 - (E[D(S)])^2. \tag{5}$$

Contribution and Marginal Diversity of a Breed

The contribution, *c*, of breed *i* to the diversity of the set *S* is calculated as

$$c_i = D(S) - D(S \backslash i) \tag{6}$$

where $D(S\backslash i)$ is the diversity of the set without breed *i*. The contribution depends only on the position of the breed in the tree topology, not on the extinction probability.

The marginal diversity, *m*, of breed *i* is

$$m_i = + \frac{\partial E[D]}{\partial z_i}. \tag{7}$$

This definition is taken from Simianer et al. (2003), and the positive sign of the marginal diversity makes it different from the original definition given by Weitzman (1992). The marginal diversity reflects the change of diversity when the extinction probability of breed *i* is increased by one unit. Therefore, m_i is consistently nonpositive. Its value depends on the position of the breed in the tree and the extinction probabilities of the neighboring breeds in the tree, not on the extinction probability of breed *i* itself, as shown by Simianer et al. (2003).

Results

Extinction Probabilities

The average estimated extinction probability over all breeds was 0.48, with Sheko (0.77), Highland Zebu (0.70), and Kapsiki (0.67) having the highest and Nguni (0.20), Afrikaner (0.30), and Mashona (0.32) having the lowest (Table 2). Half the estimated extinction probabilities was between 0.40 and 0.50, and one-third was higher than 50%. The average for group ZZ was 0.49 and for group TS 0.47. Group ZZ had significantly higher averages for DIS and SPE than group TS.

Statistically significant positive correlations existed between the variables CHA and POS, ORG and REL, ORG and CON, and CON and DIS (Table 3). Significantly negatively correlated variables were CHA and SPE, CRO and POL, CUL and ORG, and CUL and CON. The variables CHA, ORG, DIS, POS, REL, and CON were significantly and positively correlated with the extinction probability.

Current and Expected Future Diversities

The current diversity in group TS (2.63) was more than twice that in group ZZ (1.21) (Fig. 1). For both groups, the probability density function of the future diversity was close to a normal distribution. The expected values for the future diversities were about half those of the current diversities, 1.48 ± 0.290 in group TS and 0.62 ± 0.137 in group ZZ, with coefficients of variation around 20% (Fig. 1).

Table 2. Estimated extinction probabilities (z) of 49 African cattle breeds.

	Variable[a]										
Breed[b]	*POS*	*CHA*	*DIS*	*CRO*	*ORG*	*CON*	*POL*	*SPE*	*CUL*	*REL*	z
Sheko TS	0.2[c]	0.1[c]	0.10[c]	0.1[c]	0.1[c]	0.10[d]	0.05[e]	0.1[d]	0.05[c]	0.1[d]	0.77
Highland Zebu ZZ	0.1[f]	0.1[c]	0.10[c]	0.1[c]	0.1[c]	0.10[c]	0.05[e]	0.1[f]	0.05[c]	0.1[f]	0.70
Kapsiki TS	0.2[d]	0.0[d]	0.10[c]	0.1[c]	0.1[d]	0.10[d]	0.00[e]	0.1[f]	0.05[c]	0.1[f]	0.67
Kilimanjaro Zebu ZZ	0.1[f]	0.1[c]	0.05[c]	0.1[c]	0.1[c]	0.10[c]	0.00[e]	0.1[f]	0.05[c]	0.1[f]	0.63
Pedi TS	0.3[d]	0.1[g]	0.00[f]	0.1[c]	0.1[c]	0.05[c]	0.00[e]	0.0[d]	0.05[c]	0.1[f]	0.63
Iringa Red ZZ	0.1[f]	0.0[d]	0.10[c]	0.1[d]	0.1[d]	0.10[d]	0.00[e]	0.1[f]	0.05[c]	0.1[d]	0.60
Ogaden ZZ	0.1[d]	0.1[c]	0.10[c]	0.0[c]	0.1[d]	0.05[c]	0.05[e]	0.1[d]	0.05[c]	0.1[d]	0.60
Watusi TS	0.2[d]	0.1[c]	0.00[c]	0.1[c]	0.1[c]	0.05[d]	0.05[e]	0.0[g]	0.00[d]	0.1[f]	0.57
Bale ZZ	0.0[g]	0.0[g]	0.10[c]	0.1[c]	0.1[c]	0.10[d]	0.05[e]	0.1[f]	0.05[c]	0.1[d]	0.57
Barotse TS	0.1[g]	0.0[g]	0.05[c]	0.1[d]	0.1[c]	0.10[d]	0.00[e]	0.1[f]	0.05[c]	0.1[d]	0.57
Nuba Mountain ZZ	0.1[d]	0.0[g]	0.10[c]	0.1[d]	0.1[d]	0.10[d]	0.05[e]	0.0[d]	0.05[c]	0.1[f]	0.57
Kaokoland TS	0.1[f]	0.0[c]	0.05[c]	0.1[c]	0.1[c]	0.05[c]	0.05[e]	0.1[f]	0.05[c]	0.1[f]	0.57
Kuri TS	0.0[d]	0.1[c]	0.10[c]	0.1[c]	0.1[c]	0.10[d]	0.04[e]	0.0[d]	0.05[c]	0.1[f]	0.56
Arsi ZZ	0.0[d]	0.0[g]	0.10[c]	0.1[c]	0.1[c]	0.05[c]	0.05[e]	0.1[f]	0.05[c]	0.1[d]	0.53
Sokoto Gudali ZZ	0.0[d]	0.0[g]	0.05[c]	0.1[c]	0.1[c]	0.10[d]	0.05[e]	0.1[f]	0.05[c]	0.1[d]	0.53
Arashie (Beja) ZZ	0.1[d]	0.1[c]	0.10[c]	0.1[f]	0.1[c]	0.10[d]	0.05[e]	0.0[d]	0.00[c]	0.0[d]	0.53
Nkone TS	0.2[d]	0.1[g]	0.10[c]	0.0[c]	0.0[d]	0.05[c]	0.05[e]	0.0[d]	0.10[c]	0.0[d]	0.50
Arado ZZ	0.0[d]	0.0[g]	0.10[c]	0.0[c]	0.1[c]	0.10[d]	0.05[e]	0.1[f]	0.05[c]	0.1[d]	0.50
Danakil TS	0.0[d]	0.0[g]	0.10[c]	0.0[c]	0.1[c]	0.10[d]	0.05[e]	0.1[d]	0.05[c]	0.1[d]	0.50
Malawi Zebu ZZ	0.0[d]	0.0[g]	0.05[c]	0.1[c]	0.1[c]	0.10[d]	0.00[e]	0.1[f]	0.05[c]	0.1[d]	0.50
Madagasbar Zebu ZZ	0.0[d]	0.0[g]	0.05[c]	0.1[c]	0.1[c]	0.10[c]	0.00[e]	0.1[g]	0.05[c]	0.1[f]	0.50
Somba TS	0.1[g]	0.1[d]	0.10[d]	0.0[c]	0.1[c]	0.00[d]	0.05[e]	0.0[d]	0.05[c]	0.1[d]	0.50
Ethiopian Boran ZZ	0.0[d]	0.0[g]	0.00[c]	0.1[c]	0.1[c]	0.05[c]	0.07[e]	0.1[f]	0.05[c]	0.1[f]	0.48
Baoulé TS	0.0[d]	0.1[d]	0.00[c]	0.1[d]	0.1[c]	0.10[d]	0.01[e]	0.0[d]	0.05[c]	0.1[f]	0.48
Tonga TS	0.0[d]	0.0[g]	0.10[c]	0.1[f]	0.1[c]	0.10[d]	0.00[f]	0.0[d]	0.05[c]	0.1[f]	0.47
Namchi TS	0.1[g]	0.1[c]	0.00[f]	0.0[c]	0.1[c]	0.10[c]	0.00[e]	0.0[d]	0.05[c]	0.1[f]	0.47
Kavango TS	0.1[f]	0.0[c]	0.00[f]	0.1[c]	0.1[c]	0.05[c]	0.05[e]	0.0[d]	0.05[c]	0.1[f]	0.47
Abigar TS	0.0[d]	0.0[g]	0.10[c]	0.0[c]	0.1[c]	0.10[d]	0.05[e]	0.1[d]	0.00[c]	0.1[d]	0.47
Kavirondo ZZ	0.0[d]	0.0[g]	0.05[c]	0.1[c]	0.1[c]	0.10[d]	0.05[e]	0.1[f]	0.05[c]	0.0[d]	0.47
Blonde d'Oulmès TS	0.1[g]	0.0[d]	0.05[d]	0.0[d]	0.1[f]	0.00[d]	0.05[e]	0.1[f]	0.05[f]	0.1[f]	0.47
Ankole TS	0.1[g]	0.0[g]	0.00[c]	0.1[c]	0.1[c]	0.00[c]	0.03[e]	0.1[f]	0.00[c]	0.1[f]	0.45
Butana (Foya) ZZ	0.0[d]	0.0[g]	0.05[c]	0.1[d]	0.1[c]	0.05[c]	0.05[e]	0.0[d]	0.05[c]	0.1[d]	0.43
Fogera ZZ	0.0[d]	0.0[g]	0.05[c]	0.0[c]	0.1[c]	0.05[c]	0.05[e]	0.1[f]	0.05[c]	0.1[f]	0.43
Horro ZZ	0.0[d]	0.0[g]	0.05[c]	0.0[c]	0.1[c]	0.05[c]	0.05[e]	0.1[f]	0.05[c]	0.1[f]	0.43
Muturu TS	0.0[d]	0.0[g]	0.05[c]	0.1[d]	0.1[c]	0.10[d]	0.05[e]	0.0[d]	0.00[d]	0.1[d]	0.43
Afar TS	0.0[d]	0.0[c]	0.00[c]	0.0[c]	0.1[c]	0.10[d]	0.05[e]	0.1[d]	0.05[c]	0.1[d]	0.43
Baladi TS	0.0[d]	0.1[d]	0.00[d]	0.1[d]	0.1[c]	0.10[d]	0.05[e]	0.0[d]	0.05[c]	0.0[d]	0.43
Angoni ZZ	0.0[d]	0.0[g]	0.00[f]	0.1[d]	0.1[c]	0.00[d]	0.00[f]	0.1[g]	0.05[c]	0.1[d]	0.40
Maure ZZ	0.0[g]	0.0[c]	0.00[f]	0.1[c]	0.1[c]	0.10[d]	0.05[e]	0.0[d]	0.00[c]	0.1[d]	0.40
Orma Boran ZZ	0.0[d]	0.0[c]	0.10[c]	0.0[c]	0.1[c]	0.05[c]	0.05[e]	0.0[c]	0.05[c]	0.1[f]	0.40
Raya-Azebo TS	0.0[d]	0.0[g]	0.00[c]	0.0[c]	0.1[c]	0.10[d]	0.05[e]	0.0[d]	0.05[c]	0.1[d]	0.37
M'bororo ZZ	0.0[d]	0.0[d]	0.05[d]	0.0[c]	0.1[c]	0.10[d]	0.05[e]	0.1[f]	0.00[c]	0.0[d]	0.37
Gobra ZZ	0.0[g]	0.0[d]	0.00[f]	0.0[d]	0.1[c]	0.10[c]	0.05[e]	0.1[f]	0.05[c]	0.0[d]	0.37
Kenyan Boran ZZ	0.0[d]	0.0[d]	0.00[f]	0.1[c]	0.0[c]	0.05[c]	0.02[e]	0.1[f]	0.10[c]	0.0[d]	0.34
N'Dama TS	0.0[d]	0.0[c]	0.00[d]	0.1[c]	0.1[c]	0.05[c]	0.05[e]	0.0[d]	0.05[c]	0.0[d]	0.33
Tuli TS	0.1[g]	0.0[d]	0.00[d]	0.1[c]	0.0[d]	0.00[d]	0.03[e]	0.0[d]	0.10[c]	0.0[d]	0.32
Mashona TS	0.0[g]	0.0[d]	0.00[d]	0.1[c]	0.0[d]	0.05[c]	0.03[e]	0.0[d]	0.05[c]	0.1[f]	0.32
Afrikaner TS	0.0[g]	0.0[d]	0.00[d]	0.1[c]	0.0[d]	0.00[d]	0.00[e]	0.1[c]	0.10[c]	0.0[d]	0.30
Nguni TS	0.0[g]	0.0[d]	0.00[f]	0.1[c]	0.0[d]	0.00[d]	0.00[e]	0.0[d]	0.05[c]	0.0[d]	0.20
Average ZZ	0.026	0.017	0.059[h]	0.070	0.096	0.078	0.038	0.078[h]	0.046	0.078	0.49
Average TS	0.073	0.035	0.038	0.069	0.081	0.063	0.032	0.038	0.048	0.077	0.47
Average all	0.051	0.027	0.048	0.069	0.088	0.070	0.035	0.057	0.047	0.078	0.48
SD	0.074	0.045	0.043	0.047	0.033	0.037	0.022	0.050	0.024	0.042	0.11

[a] *See Table 1 for definitions of variable abbreviations.*
[b] *Abbreviations: TS, taurine and sanga breeds; ZZ, zebu and zenga breeds.*
[c] *Information given by one of the authors (J.E.O.R.) based on his knowledge of the breed.*
[d] *Food and Agriculture Organization (2000).*
[e] *Eidgenössisches Departement für auswärtige Angelegenheiten (2001).*
[f] *Default value used.*
[g] *International Livestock Research Institute (2001).*
[h] *Significant difference for this variable between groups ZZ and TS at the 5% level.*

Table 3. Correlation and significance among the extinction probability (z) of African cattle breeds and the variables[a] used for its estimation.

	Variable									
Variable	*POS*	*CHA*	*DIS*	*CRO*	*ORG*	*CON*	*POL*	*SPE*	*CUL*	*REL*
CHA	0.53^b									
DIS	0.13	0.14								
CRO	0.10	−0.00	−0.19							
ORG	0.01	0.08	0.27	−0.11						
CON	−0.12	0.11	0.32^c	0.01	0.47^b					
POL	−0.16	−0.02	0.19	-0.34^c	0.23	0.04				
SPE	−0.13	-0.32^c	0.20	−0.13	0.18	0.09	−0.03			
CUL	0.03	−0.02	−0.06	0.01	-0.58^b	-0.29^c	−0.25	0.06		
REL	0.11	−0.01	0.26	−0.04	0.55^b	0.17	−0.03	0.13	−0.28	
z	0.61^b	0.48^b	0.58^b	0.16	0.52^b	0.42^d	0.01	0.27	−0.13	0.51^b

[a] *See Table 1 for definitions of variable abbreviations.*
[b] $p < 0.001$.
[c] $p < 0.05$.
[d] $p < 0.1$

Maximum-Likelihood Trees

The maximum-likelihood tree of group ZZ (Fig. 2) consisted of two major subtrees: an East African subtree with a separate Ethiopian-Eritrean branch and a West African and Sudanese subtree joined by the Angoni. Malawi Zebu and Iringa Red formed a separate regional branch. Madagascar Zebu took a special position on its own branch.

The taurine and sanga maximum-likelihood tree (Fig. 3) also consisted of two major subtrees: the taurine and the southern African sanga, which were joined by the Kuri and Watusi. The East African sanga breeds and the Sheko formed their own cluster together with the Baladi and Pedi. The Muturu were distinct and had their own branch.

Contributions and Marginal Diversities of Each Breed

In addition to the maximum-likelihood tree resulting from the Weitzman algorithm, Figs. 2 and 3 also show the contributions to the group diversity c_i and marginal diversities m_i of each breed for the two groups ZZ and TS. The contributions are given as a percentage of the sum of contributions within each group; marginal diversities are given analogously. Correlation between c_i and m_i was high in both groups, with $r = 0.957$ in group ZZ and $r = 0.978$ in group TS. Neither c_i nor m_i showed a significant correlation with the extinction probability z_i (r ranged between -0.075 and -0.142).

For the zebu and zenga (group ZZ), marginal diversity was high for Madagascar Zebu (9.7%) and Arashie (6.4%), whereas corresponding estimates for the remaining members of the group were within a small range on a medium scale. Madagascar Zebu also had the highest contribution, at 10.4%, followed by Arashie and Gobra.

Marginal diversities were rather low in general for group TS, with Blonde d'Oulmès and N'Dama having moderately high values and Muturu (14.4%) having the highest value. The contribution of Muturu was highest at 16.0%. In general, the marginal diversity and the contribution to group diversity were similar.

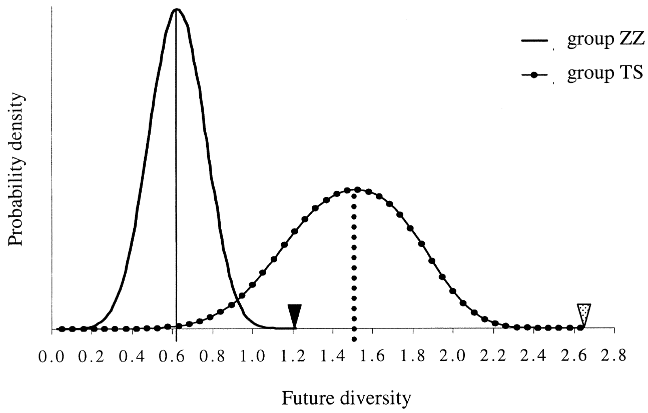

Figure 1. Current diversity (arrow) and probability density function of the future diversity for the zebu and zenga group (ZZ) and the taurine and sanga group (TS).

Discussion

Extinction Probabilities

The scheme we used to assign extinction probabilities yielded reasonable results when the values shown in Table 2 were compared with risk assessments found in the literature (Mason 1988; Felius 1995; Rege 1999; Scherf 2000). In contrast to these risk assessments, our scheme accounted for more variables considered important when it comes to priority setting for conservation. Further research and information will be necessary to allow more quantitative than qualitative measurements and the weighing of all variables. The new scheme is a first step, however, toward Ruane's (2000) suggestion that

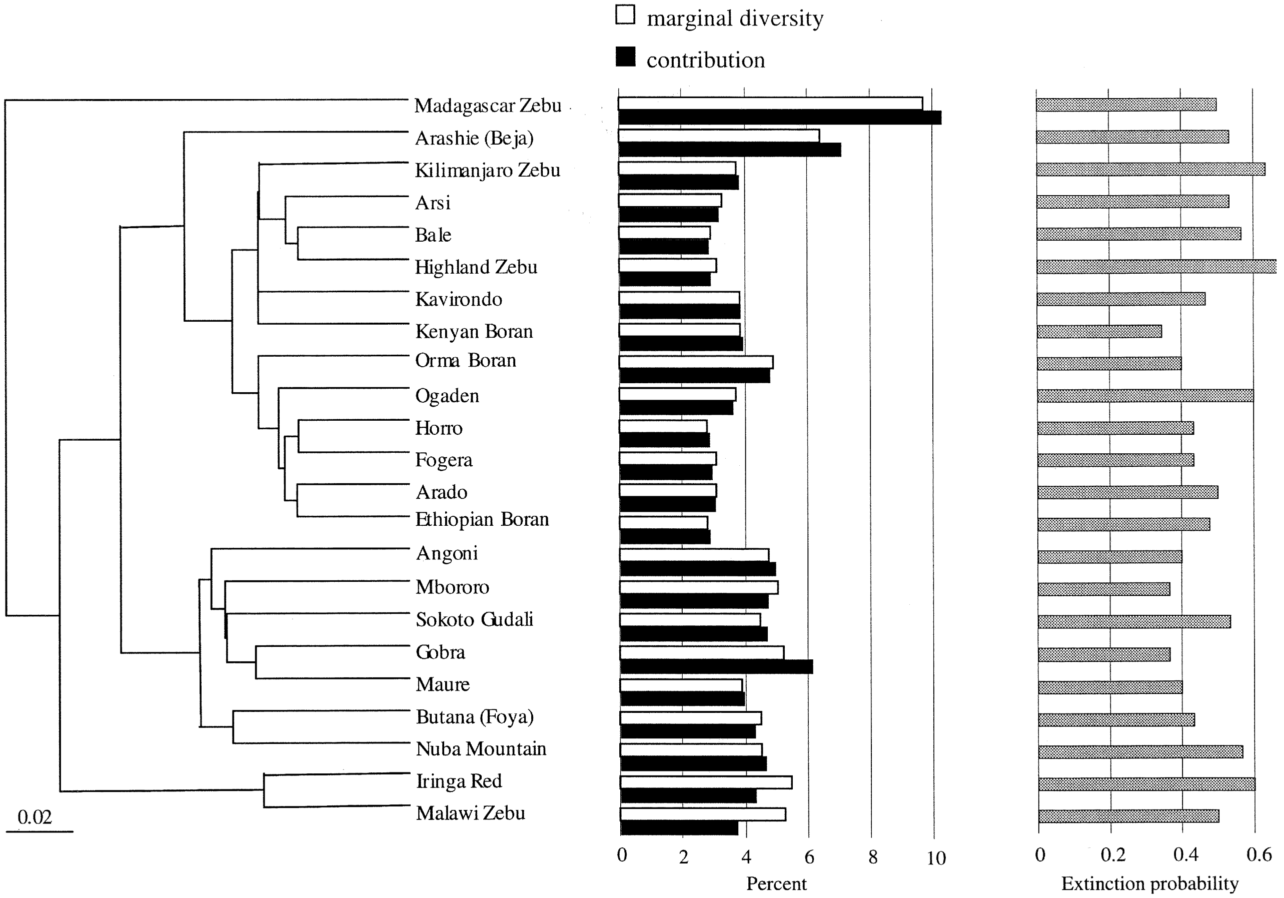

Figure 2. Maximum-likelihood tree, marginal diversities, and contribution of each breed to the actual diversity and extinction probabilities of the zebu and sanga breeds (group ZZ).

more data on prioritization criteria, other than neutral genetic marker loci, should be used for these purposes. Moreover, all schemes based on only one variable will fail if no value is available for this variable. Our scheme evaluates the threat of extinction of a breed in its environmental context, tracks the most important factors separately over time, and thus shows the specific impact of different conservation efforts on particular risk factors. Nevertheless, it cannot be validated based on actual data because the target variable, true extinction probability, cannot be obtained. Therefore, all schemes to estimate extinction probabilities are in a way arbitrary.

Although the average extinction probability seems high (48%), with one-third of the breeds having values higher than 50%, it is in line with the FAO's current estimation for the risk status of the world's cattle breeds, with about 30% considered endangered to critical (Scherf 2000). There was almost no difference between the average extinction probabilities of the ZZ and TS groups. Although small population sizes (POS) and high changes (CHA) in population size indicated the endangerment of taurine and sanga breeds and increased their extinction probabilities, they were significantly more widely distributed (DIS) and better known for special traits (SPE) than the zebus.

The positive correlation between the existence of a conservation scheme (CON) and the distribution of the breed (DIS) reflects the importance of popularity to the safety of a breed, which can be due to either a wide distribution or a conservation scheme. Most breeds with fully established conservation schemes were on the lower, favorable end of the scale of extinction probabilities, indicating the (potential) success of the measures taken. The presence of farmer organizations or societies (ORG) and the existence of CON were highly positively correlated because the concept of a breed and its conservation was developed in Western Europe (Fitzhugh 1992). Therefore, structures such as breeder unions and herdbooks were mainly introduced with Western conservation schemes. In many cases, it is farmer organizations that drive conservation or ensure the long-term maintenance of breeds.

Sociocultural importance (CUL) had no significant impact on extinction probability and was negatively correlated with ORG and CON, which offsets the part-whole correlation between CUL and extinction probability. Thus, if it is not true that high cultural value contributes

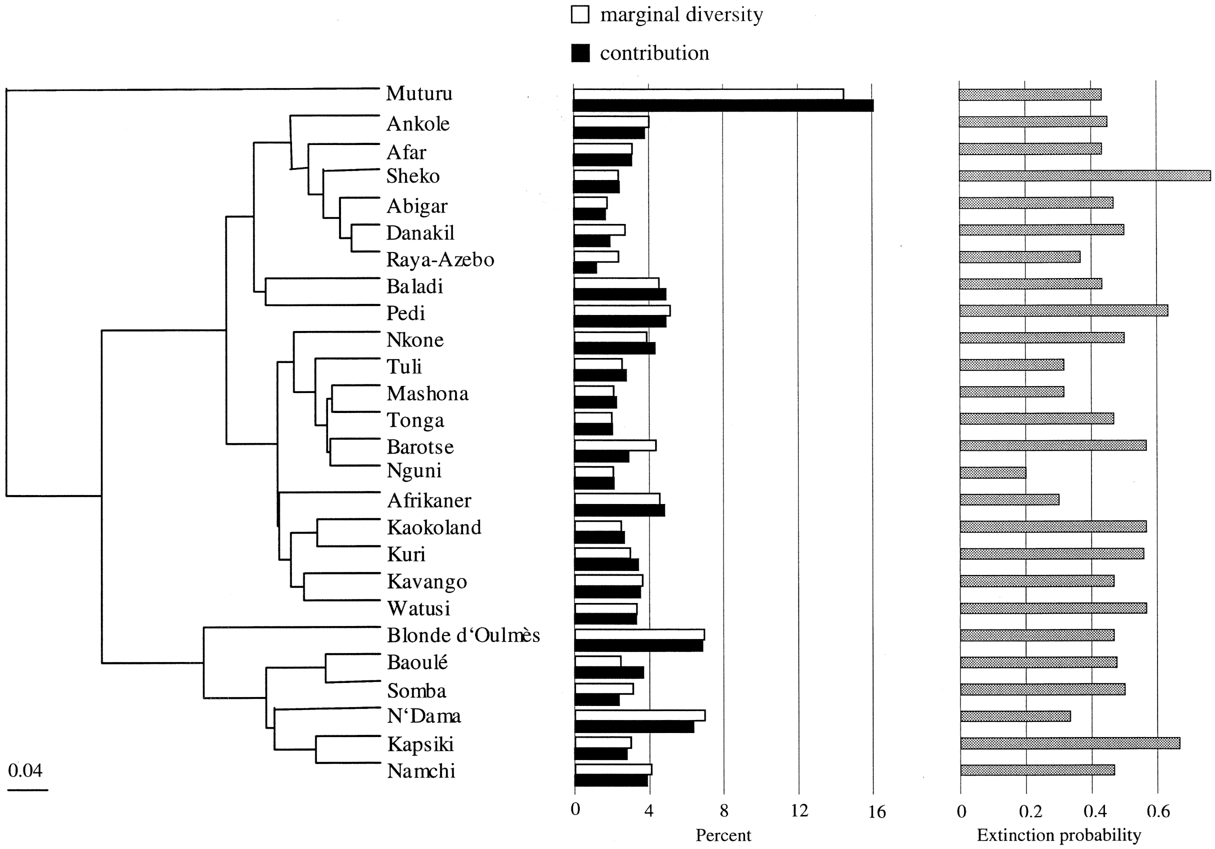

Figure 3. Maximum-likelihood tree, marginal diversities, and contribution of each breed to the actual diversity and extinction probabilities of the taurine and sanga breeds (group TS).

to lower extinction probability, such breeds may be at significantly elevated risk of extinction as a result of low organization and conservation efforts. Although CUL was not significantly correlated with extinction probability, some breeds are known to be kept mainly for sociocultural reasons (e.g., Muturu) (Felius 1995). A rapid change in the cultural value of such breeds must be of concern to conservationists.

Based on the experience of the past, it is difficult if not impossible to predict the political stability of a region or country over any appreciable period. Nevertheless, political stability can have major effects on survival. The political situation of the country (POL) was therefore kept in the model for its importance, despite the difficulty of obtaining reliable estimates. The POL and indiscriminate crossing (CRO) were negatively correlated, which may reflect the fact that crossbreeding is promoted in stable economic markets. The significance may also be partly due to the assumptions made for missing data, which were 0.0 for POL and 0.1 for CRO.

Current and Expected Future Diversities

The current diversity in group TS was about twice the diversity in group ZZ. The difference was due to the higher number of distinct breeds and to the genetic origin of the breeds. Indeed, it has recently been shown that the genetic composition of the zebu and the zenga is predominantly of Asian zebu origin, whereas the sanga breeds are crossbred Asian zebu and predominantly African taurine (Hanotte et al. 2002).

The expected future diversity of both groups was about half the current diversity, which reflects the high average extinction probability of 48%, with two-thirds of the breeds having values in the range of 40–60%. In a survey of sub-Saharan African cattle breeds, Rege (1999) found that during the twentieth century 22 breeds had gone extinct and 47 of the 145 cattle breeds identified were at risk of extinction. The total number (22 + 47) represents 48% of the total number of cattle breeds today. The study was based on an examination of historical literature on breeds. It is likely that a substantial proportion of breeds, some of them now extinct, had never been reported in the literature. Thus, these estimates of extinction rates are conservative. Our results suggest that if no conservation efforts are made and all other factors remain the same, half of the genetic diversity of African cattle breeds might be lost within the next 20–50 years.

Within-breed diversity, the effect of crossbreeding in the past, and the possibility of conserving genetic variation by creating new synthetic breeds consisting of two or more closely related breeds are not taken into account by Weitzman's (1992, 1993) method. For the same reason, factors such as inbreeding that affect genetic diversity within populations are not accounted for, although their influence might be substantial (Eding & Meuwissen 2001). Caballero and Toro (2002) therefore recommend not using Weitzman's (1992, 1993) method alone when it is important to consider or conserve within-population diversity. Future research on including within-population diversity and its effects is needed. Although genetic variation per se is valuable, the most valuable characteristics are likely to be those for which genes are fixed (or at high frequency) within the breed displaying these characteristics. Genes that appear at high frequency is an essential starting point for most genetic research and development. Blending variation into a synthetic breed would substantially reduce the probability that variation would ever be characterized or utilized. Synthetic breeds would also have no cultural or production history, and it would likely prove harder to ensure their conservation. Thus, while not perfect, the assumption of no crossbreeding in the Weitzman approach seems reasonable when conservation options and priorities are under consideration.

Maximum-Likelihood Trees

Although the maximum-likelihood tree of Weitzman (1992, 1993) does not necessarily display the real phylogeny of a set of breeds, it is a helpful tool with which to visualize genetic distances between breeds and the overall diversity of a set of breeds, as illustrated in the following examples. The scale for the TS tree is twice as big as the scale for the ZZ tree because group TS has twice the diversity of ZZ.

On the maximum-likelihood tree in group ZZ, the West African zebu breeds Mbororo, Sokoto Gudali, Gobra, and Maure were distinctly differentiated as a subgroup. These zebu breeds are geographically isolated from the taurine-dominated areas further south in the tsetse belt of West Africa and from the east African zebu breeds. Another distinct branch carried Malawi Zebu and Iringa Red, which are located in the same region in Malawi and Tanzania, quite far south from the center of zebu diversification in East Africa, with an admixture of some sanga and other breeds (Felius 1995; Hanotte et al. 2000).

In group TS, the tree structures reproduced the geographic distribution and type of the breeds. Kuri was a prominent outlier. They are a taurine enclave in a zebu-dominated area, and extensive crossbreeding with zebu is reported (Felius 1995; Tawah et al. 1997), although Hanotte et al. (2000) found no indicine Y alleles in the sample. Presumably, there is a substantial zebu admixture in the Kuri, but one that is brought in by females rather than males.

No bootstrap values were calculated for the maximum-likelihood trees because this would have demanded a very high computer capacity. But, looking at the similarities with the corresponding phylogenetic consensus trees (not shown) computed with the PHYLIP 3.57c software (Felsenstein 1993) using the average clustering or UPGMA algorithm (Takezaki & Nei 1996), we considered the structures of the maximum-likelihood trees as reliable.

Contributions and Marginal Diversities of Each Breed

A popular strategy for the conservation of animal genetic resources is to focus on breeds with the highest risk of loss. In the present study, such a strategy would place the Highland Zebu and Kilimanjaro Zebu of group ZZ and the Sheko and Kapsiki of group TS at the top of the list. With the rather low contributions and marginal diversities of these breeds, such a strategy, while appropriate to maintain a maximum of breeds, will not maintain maximum genetic diversity when resources for conservation are limited.

The strategy of conserving a high number of breeds is only as good as the definition of *breed* and the assessment of the degree of endangerment. Nevertheless, breed is the generally accepted operational taxonomic unit of conservation of farm animals, even though there is no universal agreement about its definition. Barker (1994) calls for a consistent terminology to facilitate the unambiguous communication required for conservation of global diversity. He also points out the need for a measure of the contribution of a breed to the overall genetic diversity of a species because breeds with a substantial contribution should be given higher priority. The contribution of a breed to the overall diversity of the set of breeds as calculated in this study can be used in the selection of such breeds for conservation purposes and facilitate the definition of a consistent unit. The highest contributions were made by Madagascar Zebu and Arashie in group ZZ and Muturu, Blonde d'Oulmès, and N'Dama in group TS.

Genetic contributions should not be the only basis for decisions about conservation. The marginal diversity of each breed, which takes into account the extinction probabilities of related breeds, offers a more sophisticated tool. As noted by Simianer et al. (2003), marginal diversity is not dependent on the breeds' own extinction probability.

Comparing the marginal diversities in a set allows the identification of breeds for which action to reduce risk of extinction would yield the greatest amount of conserved genetic diversity when their extinction probability is reduced. In group ZZ, investing in Madagascar Zebu would yield the highest future genetic diversity, despite the fact that the breed has a rather low degree of endangerment. Similarly, in group TS, Muturu should be chosen as the most distinct and isolated breed, with Blonde d'Oulmès and N'Dama as second and third, respectively.

Genetic contribution and marginal diversity were highly correlated in both groups. Thus, the marginal diversity of a breed was not strongly influenced by the extinction probabilities of neighboring breeds in the tree. Hence, the (nongenetic) variables that contribute to extinction probabilities would play a minor role in decision-making based on the marginal diversities only.

In addition to the endangerment of a breed, non-(functional) genetic criteria for conservation, such as traits of current or future value (e.g., trypanotolerance) or a special landscape value as suggested by Ruane (2000), should be integrated into the approach. Weitzman (1998) suggested a method to combine the actual utility of a breed and its "distinctiveness," which is closely related to the concept of marginal diversity we have used here.

Our study has provided a framework within which the Weitzman approach could assist in decision-making for the conservation of a large number of highly diverse breeds. An obvious expansion of this framework would be to include a cost function, which would allow determination of the maximum amount of diversity that can be conserved for a given input (Simianer et al. 2003).

Acknowledgments

We gratefully acknowledge helpful comments on the manuscript of three anonymous referees and the financial support of the Walter Hochstrasser Foundation, Zurich.

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Appendix 1. Information on sample and breed characteristics and endangerment of 49 African cattle breeds.

Breed	*Type*[a]	*Origin of sample*	*Indicine Y alleles in samples (%)*[a]	*Sample size*	*Population size*[b]	*Risk status*[b]
Abigar	sanga	Ethiopia	93	35	548,650	not at risk
Afar	sanga	Eritrea	100	35	680,590	not at risk
Afrikaner	sanga	South Africa	0	35	302,000[c]	not at risk
Angoni	zebu	Zambia	73	35	300,000[c]	not at risk
Ankole	sanga	Uganda	0	35	1,500,000[c]	not available
Arado	zenga	Eritrea	100	35	440,000	not at risk
Arashie (Beja)	zebu	Sudan/Eritrea	100	35	19,600	not at risk
Arsi	zebu	Ethiopia	94	35	2,011,800	not at risk
Baladi	taurine	Egypt	not available	40	>650,000	not at risk
Bale	zebu	Ethiopia	100	35	738,000	not at risk
Baoulé	taurine	Burkina Faso[c]	not available	35	>800,000	not at risk
Barotse	sanga	Zambia	17	35	<100,000	not at risk
Blonde d'Oulmès	taurine	Morocco	not available	31	80,000	not at risk
Butana (Foya)	zebu	Sudan	90	35	1,000,000	not at risk
Danakil	sanga	Ethiopia	100	35	1,500,000[c]	not at risk
Ethiopian Boran	zebu	Ethiopia	100	35	>1,896,235	not at risk
Fogera	zenga	Ethiopia	100	35	868,000	not at risk
Gobra	zebu	Senegal	100	35	1,300,000	not at risk
Highland Zebu	zebu	Kenya	100	35	not available	not at risk
Horro	zenga	Ethiopia	100	35	3,286,080	not at risk
Iringa Red	zebu	Tanzania	100	35	not available	extinct
Kaokoland	sanga	Namibia	13	35	not available	not available
Kapsiki	taurine	Cameroon	90	35	3,289	not at risk
Kavango	sanga	Namibia[a]	0	35	not available	not available
Kavirondo	zebu	Kenya	100	35	2,110,050	not at risk
Kenyan Boran	zebu	Kenya	100	35	500,000	not at risk
Kilimanjaro Zebu	zebu	Tanzania	65	35	not available	not available
Kuri	taurine	Chad	0	35	>120,000	not at risk
Madagascar Zebu	zebu	Madagascar	96	35	8,500,000	not at risk
Malawi Zebu	zebu	Malawi	83	35	<800,000	not at risk
Mashona	sanga	Zimbabwe	0	35	>500,000	not at risk
Maure	zebu	Mauritania	100	35	<500,000	not at risk
M'bororo	zebu	Nigeria	100	35	3,030,000	not at risk
Muturu	taurine	Cameroon	17	21	75,000–120,000[c]	not at risk
N'Dama	taurine	Senegal, Guinea, Guinea-Bissau, The Gambia	0–96	35	4,863,000[c]	not at risk
Namchi	taurine	Cameroon	50	35	<20,000	not at risk
Nguni	sanga	South Africa	10	35	>355,282	not at risk
Nkone	sanga	Zimbabwe	7	35	4,000[c]	endangered
Nuba Mountain	zebu	Sudan	100	35	44,000	not at risk
Ogaden	zebu	Ethiopia	100	35	100,000	not at risk
Orma Boran	zebu	Kenya	100	31	>1,655,880	not at risk
Pedi	sanga	South Africa	0	35	100–1,000	endangered
Raya-Azebo	sanga	Ethiopia	100	35	521,000	not at risk
Sheko	taurine	Ethiopia	90	35	<10,000[d]	not at risk
Sokoto Gudali	zebu	Nigeria	100	35	>4,400,000	not at risk
Somba	taurine	Benin	33	35	10,000[c]	not at risk
Tonga	sanga	Zambia	43	35	<4,500,000	not at risk
Tuli	sanga	Zimbabwe	0	35	12,339	not at risk
Watusi	sanga	Uganda	0	35	<5,000[c]	not at risk
All breeds ($n = 49$)				1,694		

[a] *Hanotte et al. (2000) and Rege (1999).*

[b] *Food and Agriculture Organization (2000).*

[c] *International Livestock Research Institute (2001).*

[d] *Completed by J.E.O.R. based on his knowledge of the breed.*