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CONSERVATION OF LIVESTOCK BREED DIVERSITY

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Summary

Mankind uses some 40 species of animals as domestic livestock to meet our needs for food, clothing, power, etc. Within these species, there are in total some 4,500 breeds that are referred to as the global animal genetic resources. Each breed comprises a unique set of genes. More than 30% of breeds are estimated to be at risk of extinction, and many more, particularly in developing countries, are threatened by inefficient utilization. The Food and Agriculture Organization of the United Nations has been mandated by its member nations to manage the global animal genetic resources, and major progress has been made in the last few years. However, resources are limited, and priorities will have to be set for breed conservation, for breed development programmes and for evaluation studies. Breeds that are taxonomically distinct should be favoured for conservation, the objective being to maintain maximum genetic diversity of each livestock species. Genetic distances and phylogenetic diversity provide the best available objective criterion, and microsatellites are the current markers of choice for obtaining the genetic data. Microsatellite-based genetic distances will describe breed similarities due to common ancestry, but cannot account for consequences of artificial or natural selection. Phylogenetic trees for 11 water buffalo populations in southeast Asia, constructed using 25 polymorphic protein coding loci or 21 microsatellite loci, show differences in both topology and branch lengths, but the microsatellite tree is a better representation of the similarities due to common ancestry. Thus phylogenetic diversity, based on microsatellite loci, should be used as an initial guide in making conservation decisions for livestock breeds.

Key words: Conservation priorities, Biodiversity measurement, Microsatellite, Phylogenesis.

Introduction

The total global biodiversity most likely includes tens of millions of species. Of this vast number, one species - our own, uses some 40 other animal species to meet our demands for food (meat, milk; eggs); clothing (wool and other fibres, skins), draft power and manure, to serve as a "bank" or hedge against hard times, and to satisfy various cultural, religious and recreational

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purposes. For these domestic livestock species, conservation at the species level (in the sense of preventing their loss) clearly is not an issue; what is of concern is conservation of diversity within each species.

The diversity within domestic livestock species is perceived generally in terms of differences among sub-groups that are referred to as breeds, where "breed" has been defined (Turton, 1974) as "a homogeneous, sub-specific group of domestic livestock with definable and identifiable external characters that enable it to be separated by visual appraisal from other similarly defined groups within the same species, or a homogeneous group where geographical separation from phenotypically similar groups has led to general acceptance of its separate identity". While generally appropriate, breeds often are not distinguished in the developing world. Local populations may have different names, but without change in phenotype; a change in phenotype may occur without change in name; or all populations may have just one name and be phenotypically similar. In the broad context of global animal genetic resources, the term "breed" is used to include strains and populations, the members of which are distinguished from other such groups in local, national or regional usage. That is, a breed is a cultural entity, recognized as such by the community where it is found.

Animal Breeding and Conservation - A Conflict?

The aim of animal breeding is to change the genetic makeup of domestic animals so that they better meet our needs. Such improvement in production, product quality or the efficiency of production is sought by either or both of selection within breeds or use of differences among breeds through cross-breeding, grading-up to a superior breed by repeated back-crossing, or formation of a synthetic population. Thus future improvement is dependent on genetic variation - both the variation within breeds, and the variation between breeds, and loss of variation will restrict the options available to meet unpredictable future requirements.

Loss of variation within breeds is continually countered by the introduction of new variation through mutation (Franklin, 1981; Hill and Keightley, 1988), but the variation among breeds cannot be readily regenerated. Each breed is the product of mutation and genetic drift, as well as separate adaptation and evolution, with differing selection pressures imposed by climate, endemic parasites and diseases, available nutrition and criteria imposed by man. Each breed thus comprises a unique set of genes.

Yet many breeds have become extinct, and many more are at risk. The global animal genetic resources almost certainly comprise some 4500 breeds, although the true number is not known. For seven mammalian species (ass, buffalo, cattle, goat, horse, pig and sheep), FAO (1995) lists 2944 breeds as recorded in the FAO Global Databank for Animal Genetic Resources, of which 498 are considered to be at risk (Table l). Extinctions of past breeds and this potential loss of more breeds is due to the demand for increased animal production, with economic pressures (primarily in developed countries) and political and social pressures (primarily in socialized economies and less-developed countries) causing some breeds to be considered unsuitable for today's needs or those of the immediately perceived future. Yet some of these breeds, and particularly those that have evolved in and become adapted to stressful environments, are likely to carry valuable genes and gene combinations controlling specific behavioural, physiological, and disease and parasite resistance traits. The genotypes of some of these breeds could be crucial to the development of sustainable animal production systems in the future.

Table 1 – NUMBERS OF BREEDS OF EACH OF SEVEN MAJOR SPECIES OF DOMESTIC LIVESTOCK THAT ARE RECORDED IN THE FAO GLOBAL DATABANK FOR ANIMAL GENETIC RESOURCES, AND THE NUMBERS ESTIMATED TO BE AT RISK

Species	Recorded	Numbers of breeds With population size data	At risk*	Per cent at risk
Ass	77	24	9	37.5
Buffalo	72	55	2	3.6
Cattle	787	582	135	23.2
Goat	351	267	44	16.5
Horse	384	277	120	43.3
Pig	353	265	69	26.0
Sheep	920	656	119	18.1
Total	2944	2126	498	23.4

*Estimated from breeds with available population data

Thus there is an apparent conflict, which will be countered only by active and effective manageinent of all animal genetic resources.

Conservation History

The realization of the need for conservation of animal genetic resources is not new, and in fact has been on the international agenda for some 50 years (Barker, 1994). Translation of this realization into action has been slow, although there have been notable achievements and recent developments are encouraging. In the developed world, organizations such as the Rare Breed

Survival Trust in the UK, Safeguard for Agricultural Varieties in Europe, and the American Livestock Breeds Conservancy in the USA have instituted effective programmes (see Alderson, 1990) for the conservation of rare and endangered breeds.

However, no such organizations and programmes exist, or are likely to be developed in the near future, in the developing world. In any case, the problems there are rather different. Many breeds are endangered, but others that are not numerically small and that are being used for production, are threatened - primarily by being cross-bred with imported breeds that are perceived (often wrongly) to be superior. But these native breeds are likely to be well-adapted to the traditional husbandry systems. Thus primary emphasis needs to be given to more effective use and genetic improvement of these breeds within the prevailing and generally sustainable production systems.

FAO has for some 25 years taken a major role in promoting awareness of the significance to mankind of the global animal genetic resources (e.g. FAO, 1984, 1992). There is now a clear recognition (FAO, 1993) that "in the global management of animal genetic resources, the fundamental distinction is not between those breeds that are, endangered and those that are not, but between those that are perceived to have little or no current utility and those which do have current utility or seem likely to have in the immediate future. For each of these latter categories, the necessary actions are then preservation (as live animals or frozen storage of embryos or semen) or utilization (including development of breeding programmes for genetic improvement)." Given this recognition, she apparent conflict between animal breeding and conservation is resolved; successful management of animal genetic resources must incorporate both utilization and conservation.

In November 1995, the FAO Conference of member governments made two major decisions in relation to animal genetic resources: (i) it provided an intergovernmental mechanism for animal genetic resources by broadening FAO's long-established Commission on Plant Genetic Resources to a Commission on Genetic Resources for Food and Agriculture, and (ii) it supported as a priority activity for FAO a Global Strategy for the Management of Farm Animal Genetic Resources. Most importantly, the Global Strategy is being designed to harmonize fully with the UN Convention on Biological Diversity, the international Law which is now ratified for use by more than 170 countries: FAO is funding the essential core activities of the Strategy (coordinating and facilitating regional and national programmes, maintaining the Global Databank and early warning system, developing technical guidelines for use by countries in establishing cost-effective action and reporting on all activities), although very substantial foundering from sources external to FAO will be required for full implementation of all aspects. Nevertheless, with the direct involvement of individual countries, other international agencies, including the International Agricultural Research Centres, and non-governmental organizations including farmer associations, implementation of the Strategy has been initiated. Its success will be vital to the future of livestock breed diversity.

Defining the Problem

Ideally, consideration of the conservation of animal genetic resources would start with complete information on all existing breeds - numbers; distribution and population structure, trends in numbers (increasing, stable or decreasing), productive performance and adaptive characters. That ideal is not even within reach - the best information available is that there are some 4500 breeds, of which some 30% are estimated to be at risk of loss (FAO, 1995). For most breeds, even basic data on population numbers and trends are not available. Of the 2944 breeds of seven mammalian species that are listed in the FAO Global Databank, 818 (28%) do not have any population data. This proportion of 28% is certainly an underestimate of the global situation, as breeds not yet listed are primarily from developing countries where census data is less likely to be available (FAO, 1995).

Clearly the first problem is lack of information, so the identification and characterization of all breeds of livestock has high priority in the FAO global strategy, and must also have high priority for all national Livestock development programmes (Barker, 1992). Once available, this documentation of existing resources would identify those breeds at risk of extinction. However, census data alone will not provide a basis for the rational choice of breeds for development programmes. Identification at the global level of priority breeds for immediate development was one of the major questions addressed by an FAO Expert Consultation (FAO, 1992). The criteria for choice of such breeds were specified as:

1. the breed possesses one or more highly desirable attributes in terms of productivity and/or adaptation,
2. the breed is endangered, or is not being utilized efficiently,
3. the breed should be one whose improvement could have the potential to influence large populations, either of the same breed in one or more countries, or other very similar breed types.

Table 2 - F-STATISTICS FOR SWAMP AND RIVER BUFFALO ESTIMATED USING 25 POLYMORPHIC PROTEIN CODING LOCI AND 21 MICROSATELLITE LOCI

	F_{IS}	F_{ST}	F_{IT}
Protein Coding			
Swamp	-.004(.062)	.182(.041)	.181(.083)
River	-.068(.048)	.108(.036)	.048(.059)
Microsatellites			
Swamp	.047(.027)	.168(.018)	.207(.034)
River	.031(.028)	.038(.008)	.068(.029)

Table 3 – CORRELATION COEFFICIENTS AMONG GENETIC DISTANCES ESTIMATED FROM DATA ON 21 MICROSATELLITE LOCI OR 25 PROTEIN CODING LOCI

	Microsatellites			Protein Coding		
	Nei D	D_A	Delta mu	Reynolds	Nei D	D_A
Reynolds	.921	.911	.748	.831	.773	.798
Nei D		.991	.890	.754	.774	.772
D_A			.897	.748	.771	.783
Delta mu				.738	.797	.772
Reynolds					.929	.965
Nei D						.937

All significant, $P < 0.001$

Again, there is an assumption of information being available with regard to "desirable attributes", but for many breeds, particularly in developing regions, this will be true, and pragmatic and subjective decisions will have to be made.

In relation to the total global biodiversity, animal production encompasses a small and finite universe - only some 4500 breeds across some 40 species, and the total genetic variation within each species. There is a critical need to develop breeding programmes to improve the production and productivity of a selected set of breeds that have major utility now or which seem likely to have in the immediate future. As already noted, selection of these breeds must be somewhat ad hoc, and the best choices may not be made. Thus breed evaluation studies are needed to compare performance, and the underlying genetics and biology, so that future choices will be more soundly based. Further, with increasing emphasis on sustainable production systems, on animal welfare and on pollution, future breeding objectives may differ quite dramatically from those now considered most important. Thus there is the need to prevent loss of breed diversity (i.e. conservation of endangered breeds).

But given all of these needs; the relatively small and finite universe of animal production is simply not manageable. On both country and global scales, financial and other resources are limited; it will not be possible to maintain every breed that is in danger of extinction, nor to develop breeding programmes for all breeds considered suitable for improvement, nor to set up evaluation studies of the many breeds that might contribute to future breeding, programmes.

For each of these different aspects of animal genetic resources conservation; priorities will have to be defined in choosing those breeds to be included.

Setting Priorities for Conservation

In the context of setting priorities for conservation, Miller (1977) suggested that the only rational criteria are the likelihood of extinction of a breed and the degree to which it possesses unique genes. Further, he suggested that immunogenetic and other biochemical polymorphism data should provide the basis for determining whether a breed is sufficiently unique (i.e. sufficiently different) from other breeds.

With emphasis on the need for planning of comparative evaluation studies, Barker (1980, 1985) suggested that the genetic relationships among breeds within each species of livestock should be determined, so that the breeds could be grouped into sets that are genetically similar, with one representative from each set then included in an evaluation study.

Both of these suggestions relate to different aspects of what is now broadly interpreted as conservation, and the concepts of genetic uniqueness and genetic relationships have become accepted as the basis for setting priorities for conservation (FAO, 1993; Barker, 1994). Inherent in this is the practical realization that breeds that are taxonomically distinct should be favoured for conservation, and that the objective is to minimize loss of genetic diversity.

An objective quantification of the magnitude of the genetic differences among a set of breeds can be obtained from allele frequency data for each breed, estimating genetic distances between each pair of breeds, and by constructing from these pair-wise distances a diagram that best represents all relationships among the populations, i.e. a phylogenetic tree. The topology of the tree shows the patterns of relationships, while branch lengths indicate the magnitude of the differences between breeds. The problem then is how to use this information to ensure maintenance of maximum genetic diversity, or realistically to ensure minimum loss of genetic diversity, given economic, social and other constraints. For non-domestic species, the analogous problem of optimizing reserve selection so that the maximum species diversity is preserved has been considered recently by several workers (see Witting and Loeschcke, 1995). Methods based on phylogerietic relationships, on genetic divergence or on both have been developed, and these have been compared by Krajewski (1994). He shows that the different measures of taxonomic diversity agree in identifying the species that contribute the most and the least to overall diversity; but disagree at intermediate levels. Although no consensus has emerged as to the relative merits of these measures, some of the complications in dealing with sets of species that are outlined by Krajewski (1994) are not relevant to the breed conservation issue. Here all breeds in one species is the set to be considered, and the diversity is specified in terms of genetic differences, i.e. allele frequencies translated to genetic distances. Thus a method combining topology and divergence information is likely to be preferred. In addition, as the objective is to minimize loss of genetic diversity in each species, within-breed genetic variation must be considered, perhaps by being incorporated into a diversity measure as suggested by Krajewski (1994). However, even without such incorporation, the breed with highest average heterozygosity should be preferred in choosing among breeds that otherwise have equal priority.

In setting conservation priorities for livestock breeds, genetic distances and phylogenetic diversity will provide the best objective criterion. However, distance measures cannot account for consequences of artificial selection on morphological or economic traits, nor for natural selection on fitness, and thus will give only the first (albeit essential) guide in making conservation decisions. Where decisions regarding conservation are to be made among a set of rare or endangered breeds, phylogenetic diversity will be the major criterion. In the choice of breeds for development programmes or for comparative evaluation studies, final decisions should also take into account any available data on traits of economic value, specific adaptive features, presence of unique genes or genotypes, local or regional importance of a breed in production systems, and availability of resources and infrastructure in the region where a breed is located (FAO, 1993).

However, before any priorities can be set, we first need the distance estimates. Some 100 studies of genetic distances among livestock breeds have been made (Barker, 1994), but these are not sufficient to provide a global overview that would be a basis for conservation decisions. Hence FAO, as part of its Strategy for the Management of Form Animal Genetic Resources, has

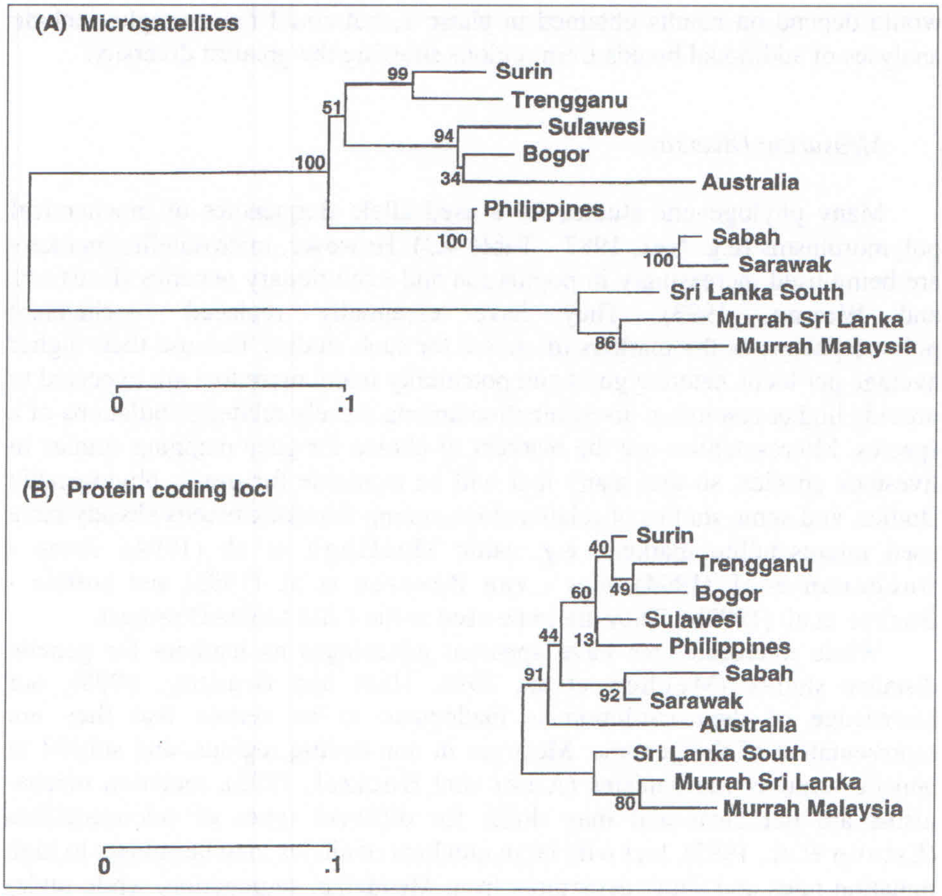

Figure 1 - NEIGHBOUR-JOINING TREES CONSTRUCTED USING THE DA DISTANCE MEASURE FOR (A) MICROSATELLITE LOCI AND (B) PROTEIN CODING LOCI

planned a global research initiative to characterize genetic diversity in each livestock species.

In 1993, an FAO Working Group concluded that a global project for estimating genetic distances among the breeds of each species of domestic livestock was feasible, and the design and procedures were outlined (FAO, 1993). Another FAO Working Group, supported by some 20 international experts, has now developed the details of this global project for fine measurement of domestic animal genetic diversity; referred to as the MoDAD project (FAO, 1996). All 4500 breeds clearly cannot be included, and a two-phase strategy is proposed, with appropriate selection of breeds in phase 1 to evaluate the range of diversity within each species. Phase 2 for each species would depend on results obtained in phase 1, but could for example, include analyses of additional breeds from regions showing the greatest diversity.

Measuring Diversity

Many phylogenetic studies have used allele frequencies of biochemical polymorphisms (e.g. Nei, 1987 - Table 9.3). However, microsatellite markers are being used increasingly in population and evolutionary genetics (Bruford and Wayne, 1993). They have essentially replaced biochemical polymorphisms as the markers of choice for such studies, because their higher average per locus heterozygosis and potentially many more loci are expected to provide higher resolution discrimination among closely related populations of a species. Microsatellites are the markers of choice for gene mapping studies in livestock species, so that many loci will be available for use in phylogenetic studies, and some studies of relationships among livestock breeds already have used microsatellite markers, e.g. cattle MacHugh et aI. (1994), sheep - Buchanan et al. (1994), pigs - van Zeveren et aI. (1995) and buffalo - Barker et al. (1997b). They are to be used in the FAO MoDAD project.

While microsatellites have apparent advantages as markers for genetic distance studies (Meghen et al., 1994; Hall and Bradley, 1995), our knowledge of their evolution is inadequate to be certain that they are representative of the genome. Most are in non-coding regions, and subject to genetic turnover mechanisms (Amos and Hoelzel, 1992), mutation mechanisms are not clear and may differ for different types of microsatellites (Estoup et al., 1995), loci with large numbers of alleles may be subject to high mutation rates and show departures from Mendelian segregation, while undetected non-amplifying (null) alleles (Pemberton et al., 1995) would cause errors in allele frequency estimates and hence in estimated genetic distances.

The question then is whether microsatellite markers will give the same phylogeny as a set of real genes. In particular, would they give the same phylogeny as one (impossible to obtain!) based on allele frequencies at the larger set of genes controlling important productive, reproductive and adaptive traits? In fact, they may not, and it should not be expected that they would because two different questions are being addressed. When genetic distances are estimated and used to construct a phylogeny of breed relationships, the aim is to describe similarities that are due to common ancestry. Thus the markers used should be selectively neutral. In contrast, the genes controlling traits of interest to animal breeders will not be selectively neutral, and breeds may be genetically similar at these loci because of convergence due to similar selection pressures, or dissimilar because of differential selection. As emphasized earlier, distance measures describing similarities due to common ancestry should be used only as an initial criterion in making breed conservation decisions.

An Example

Nevertheless, it is of interest to determine if microsatellite markers will give the' same phylogeny as a set of real genes. A possible approach to this is to compare phylogenies based on biochemical and microsatellite markers, as has been done for water buffalo populations in southeast Asia (Barker et al., 1997a,b). Seventeen populations (12 swamp type, 2 river (Murrah breed) and 3 Lankan buffalo (genetically river type)) were sampled and a total of 801 animals assayed for

53 protein coding loci, 25 of which were polymorphic. A subset of 261 animals from 11 of these populations were genotyped for 21 polymorphic microsatellite loci. Only the results for the 11 populations that were assayed for both protein coding and microsatellite loci will be discussed here, with results based only on the 25 polymorphic loci for the former.

F-statistics estimates (Table 2) show no significant departures from Hardy Weinberg expectation for either buffalo type, whether based on protein coding loci or on microsatellites. All estimates of F_{ST} (population differentiation), however, were significantly greater than zero, and for swamp buffalo (8 populations), estimates from protein coding and microsatellite loci were very similar. For river buffalo, the F_{ST} estimated from protein coding loci was about three times that from microsatellites, but not significantly different.

For both protein coding and microsatellite loci, the standard genetic distance of Nei (1978), the DA distance of Nei et al. (1983) and Reynolds' distance (Reynolds et al., 1983) were estimated, while for microsatellite loci only, the $(\delta\mu)^2$ distance of Goldstein et al. (1995) also was estimated. Correlation coefficients among these measures (Table 3) were all highly significant ($P<0.001$), although the correlations among measures using microsatellites only or protein coding loci only were higher than those between microsatellites and protein coding loci.

Neighbour joining trees (Saitou and Nei, 1987), constructed using the D_A distance measure for each of microsatellites and protein coding loci (Figure 1), show differences in both topology and branch lengths. In both trees, some of the nodes are not strongly supported and although the numbers of loci used are not small (21 microsatellite and 25 protein coding), assay of larger numbers of loci could well change the patterns of relationships. Clearly it is not possible to confirm which tree is a better representation of the true genetic relationships among these populations, but the microsatellite tree does accord better with the geography of the populations and the known history of the Australian population, which descends from a small number of animals imported from Timor some 160 years ago. The microsatellite tree is most likely a better representation of the similarities due to common ancestry, while the protein coding loci tree is distorted, reflecting additional effects due to bottlenecks in some populations and selection at some loci.

Thus these results provide empirical support for the view that phylogenetic diversity based on microsatellite loci, as in the proposed FAO MoDAD project, will provide the best objective criterion for making initial conservation decisions for livestock breeds.

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OČUVANJE PASMINSKE RAZNOLIKOSTI STOKE

Sažetak

Čovječanstvo iskorištava nekih 60 vrsta životinja kao domaću stoku za svoje potrebe, za. hranu, odjeću, snagu itd. Unutar ovih vrsta ima ukupno oko 4500 pasmina kojima se pripisuju globalni životinjski genetski resursi. Svaka pasmina. uključuje jedinstvenu skupinu gena. Računa se da je više od 30% pasmina u opasnosti od istrebljenja, i mnogo više je, osobito u zemljama u razvoju, ugroženo nesposobnim iskorištavanjem. Organizaciju za hranu i poljoprivredu Ujedinjenih Naroda (FAO) opunomoćile su zemlje članice za upravljane životinjskim genetskim resursima te je učinjen veliki napredak u zadnjih nekoliko godina. Međutim, resursi su ograničeni i trebat će odrediti prednosti za očuvanje pasmina, za programe razvoja pasmina i za radove na ocjenjivanju. Pasminama koje su taksonomski izrazite treba dati prednost za očuvanje, jer je cilj održati maksimum genetske raznolikosti svake vrste stoke. Genetske udaljenosti i filogenetska raznolikost pružaju najbolji raspoloživi kriterij, a mikrosateliti su trenutno markeri izbora za dobivanje genetskih podataka. Genetske udaljenosti na bazi mikrosatelita opisat će pasminske sličnosti zbog zajedničkih predaka. ali ne mogu biti odgovorne za posljedice umjetne ili prirodne selekcije. Filogenetska stabla populacije 11 vodenih bizona u jugoistočnoj Aziji sastavljena primjenom 25 polimorfnih mjesta za kodiranje bjelančevina ili 21 mikrosatelitsko mjesto pokazuju razlike i u topologiji i u duljinama grana, ali mikrosatelitsko stablo bolji je predstavnik sličnosti zbog zajedničkih predaka. Prema tome, mikrosatelitska raznoliost, koja se temelji na mikrosatelitskim mjestima, trebalo bi primijeniti kao početni vodič kod donošenja odluka o očuvanju pasmina stoke.

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