



## Review/Revue

## Conservation genetics of cattle, sheep, and goats

*Génétique de la conservation de la vache, du mouton, et de la chèvre*

Pierre Taberlet\*, Eric Coissac, Johan Pansu, François Pompanon

CNRS UMR 5553, laboratoire d'écologie alpine, université Joseph-Fourier, BP 53, 38041 Grenoble, France

## ARTICLE INFO

## Article history:

Available online 1 February 2011

## Keywords:

Bos  
Breeds  
Capra  
Domestication  
Genetic diversity  
Ovis  
Selection

## ABSTRACT

Cattle, sheep and goats were domesticated about 10,000 years ago, spread out of the domestication centers in Europe, Asia, and Africa during the next few thousands years, and gave many populations locally adapted. After a very long period of soft selection, the situation changed dramatically 200 years ago with the emergence of the breed concept. The selection pressure strongly increased, and the reproduction among breeds was seriously reduced, leading to the fragmentation of the initial gene pool. More recently, the selection pressure was increased again via the use of artificial insemination, leading to a few industrial breeds with very high performances, but with low effective population sizes. Beside this performance improvement of industrial breeds, genetic resources are being lost, because of the replacement of traditional breeds by high performance industrial breeds at the worldwide level, and because of the loss of genetic diversity in these industrial breeds. Many breeds are already extinct, and genetic resources in cattle, sheep, and goats are thus highly endangered, particularly in developed countries. The recent development of next generation sequencing technologies opens new avenues for properly characterizing the genetic resources, not only in the very diverse domestic breeds, but also in their wild relatives. Based on sound genetic characterization, urgent conservation measures must be taken to avoid an irremediable loss of farm animal genetic resources, integrating economical, sociological, and political parameters.

© 2011 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

## R É S U M É

## Mots clés :

Capra  
Bos  
Diversité génétique  
Domestication  
Ovis  
Races  
Sélection

La vache, le mouton et la chèvre ont été domestiqués il y a environ 10 000 ans. Ils se sont ensuite répandus en Europe, Asie, et Afrique durant les quelques milliers d'années qui ont suivi, et ont donné de nombreuses populations bien adaptées aux conditions locales. Après une très longue période de sélection non intensive, la situation a changé il y a 200 ans avec l'émergence de la notion de race. La pression de sélection a fortement augmenté et la reproduction entre races a été sérieusement réduite, conduisant à la fragmentation du pool génétique initial. Plus récemment, la pression de sélection a augmenté à nouveau par l'utilisation de l'insémination artificielle, donnant quelques races industrielles très performantes, mais avec de faibles tailles efficaces de population. Le revers de cette amélioration des performances des races industrielles est que les ressources génétiques sont en voie de disparition, en raison d'une part du remplacement au niveau mondial des races traditionnelles par des races industrielles à haute performance et, d'autre part, de la perte de diversité génétique chez ces races industrielles. De nombreuses races sont déjà éteintes et les ressources génétiques chez la vache, le mouton et la chèvre sont donc très

\* Corresponding author.

E-mail address: pierre.taberlet@ujf-grenoble.fr (P. Taberlet).

menacées, en particulier dans les pays développés. La mise au point récente de nouvelles technologies de séquençage d'ADN ouvre de nouvelles perspectives pour une meilleure caractérisation des ressources génétiques, non seulement dans les diverses races domestiques, mais aussi chez les espèces sauvages proches. Sur la base de caractérisations génétiques fiables, des mesures de conservation urgentes doivent être prises pour éviter une perte irrémédiable des ressources génétiques chez les animaux domestiques, en intégrant des paramètres économiques, sociologiques et politiques.

© 2011 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

## 1. Introduction

Conservation biology is a relatively new field of research that emerged in the seventies with the goal of preserving ecosystems, species and genes [1]. Within this field, conservation genetics deals with the application of genetic concepts and tools to conservation problems. At first glance, highlighting conservation problems in domestic ungulates may appear as a paradox [2], as the census population sizes of farm animals are extremely high (Table 1). Potential conservation issues in domestic animals were already spotted by the Food and Agriculture Organization of the United Nations (FAO) in the seventies [3] with the objective of long-term conservation of genetic resources for future use. Such a goal can be achieved by preserving the widest possible spectrum of genetic diversity because future needs are unpredictable. This FAO document [3] also emphasized the conflict between immediate improvement and conservation, indicating that “the best way of conservation would be the development of a management system which would both maintain genetic variability of existing livestock resources and at the same time permit continuous improvement in productivity and adaptability of that resource”. Unfortunately, despite this very early warning, the investments toward conservation aspects were far behind those for improving the productivity of a few industrial breeds. As a consequence, traditional indigenous breeds are still disappearing (Table 1) and the effective population size of many cattle breeds is far below a threshold that would ensure long-term sustainability. The last FAO survey [4] considered that 16, 13 and 3% of the cattle, sheep, and goat breeds already disappeared, respectively. In such a context, it is becoming more and more urgent to implement sound conservation strategies for farm animals [5].

In this paper, we first aim to review the current knowledge about the origin and the history of cattle, sheep, and goats. Such knowledge is of prime importance for properly assessing the risk concerning the loss of genetic diversity and for designing sound conservation guidelines. We also examine the current practices that lead to massive

loss of genetic resources. Then, we highlight the potential genetic resources, obviously including domestic breeds but also including wild relatives. Finally, we provide conservation guidelines for long-term sustainability based on the current situation and on the availability of new genomic tools.

## 2. The origin of cattle, sheep and goats

Data about cattle, sheep, and goat domestication first came from osteometry and morphometry evidence collected in archaeological sites [6]. More recently, these data were completed by extensive genetic studies [7] using both modern and ancient samples, thus allowing producing more precise scenarios of the domestication processes. The first archaeological evidence of the domestication of these three species traces back to around 10,500 BP (calibrated) in the Fertile Crescent (Fig. 1). It seems that goat and sheep were domesticated first [8,9], immediately followed by cattle [10].

The wild ancestor of all domesticated cattle was the auroch (*Bos primigenius*) [11] that is now extinct. Aurochs had a very wide geographic distribution, from East Asia to Europe and North Africa. The common usage accepts two taxa for the domestic cattle, namely *Bos taurus* and *B. indicus* that fully interbreed. *B. indicus* differs from *B. taurus* by the presence of a prominent hump. The presence of two mtDNA haplogroups (Fig. 2) is interpreted as an indication of two main domestication events, the one in the Fertile Crescent leading to *B. taurus* and the other in the Indian subcontinent leading to *B. indicus* [12–14]. Extensive hybridization occurred in Africa, leading to a complex intermixing of these two mitochondrial haplogroups in the field [13].

The systematics of the genus *Ovis* is controversial. The number of species that have been recognized within this genus varies from one [15] to seven [16]. Recently, an extensive mitochondrial and nuclear DNA survey including all taxa of the genus was carried out [17], confirming the presence of seven monophyletic clades corresponding to the seven species described by Nadler et al. [16]. Based on another extensive study of the mitochondrial DNA (mtDNA) of putative ancestors (*O. orientalis*, the Asiatic mouflon; *O. vignei*, the urial; *O. ammon*, the argali), it clearly appeared that the wild ancestor is *O. orientalis* [18]. Both archaeological [8] and genetic data spot the domestication center in eastern Anatolia and North-west Iran. To date, the number of mtDNA haplogroups described for the domestic sheep varies as no standard criteria are used for defining them [19,20]. However, authors agree on three main haplogroups (i.e. A, B and C in Fig. 1).

**Table 1**

Population sizes, current number of breeds, and number of extinct breeds for cattle, sheep, and goats at the worldwide level (statistics concerning 169 countries [4]).

	Cattle	Sheep	Goat
Population size ('000)	1,367,335	1,060,606	710,381
Number of breeds	1311	1409	618
Number of extinct breeds	209	180	19

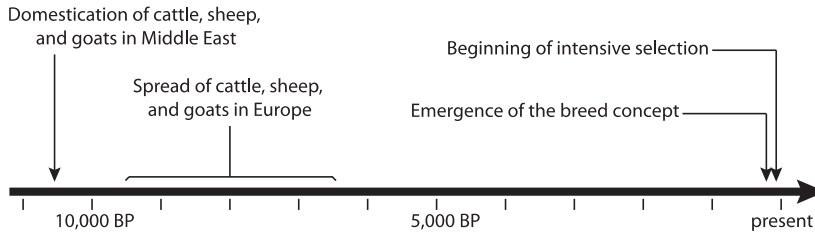


Fig. 1. The main events in cattle, sheep, and goat domestication.

Goat domestication is well documented by archaeological evidence and also by several genetic studies. The goat wild ancestor is the bezoar, *Capra aegagrus* [21–23]. A large-scale analysis of current bezoar mtDNA polymorphism over its whole geographic distribution has recently

been performed [23]. All the six current mitochondrial haplogroups found in the domestics (Fig. 2) were also found in its wild ancestor, suggesting that the domestication process occurred over a very large area encompassing eastern Anatolia and North-West Iran.

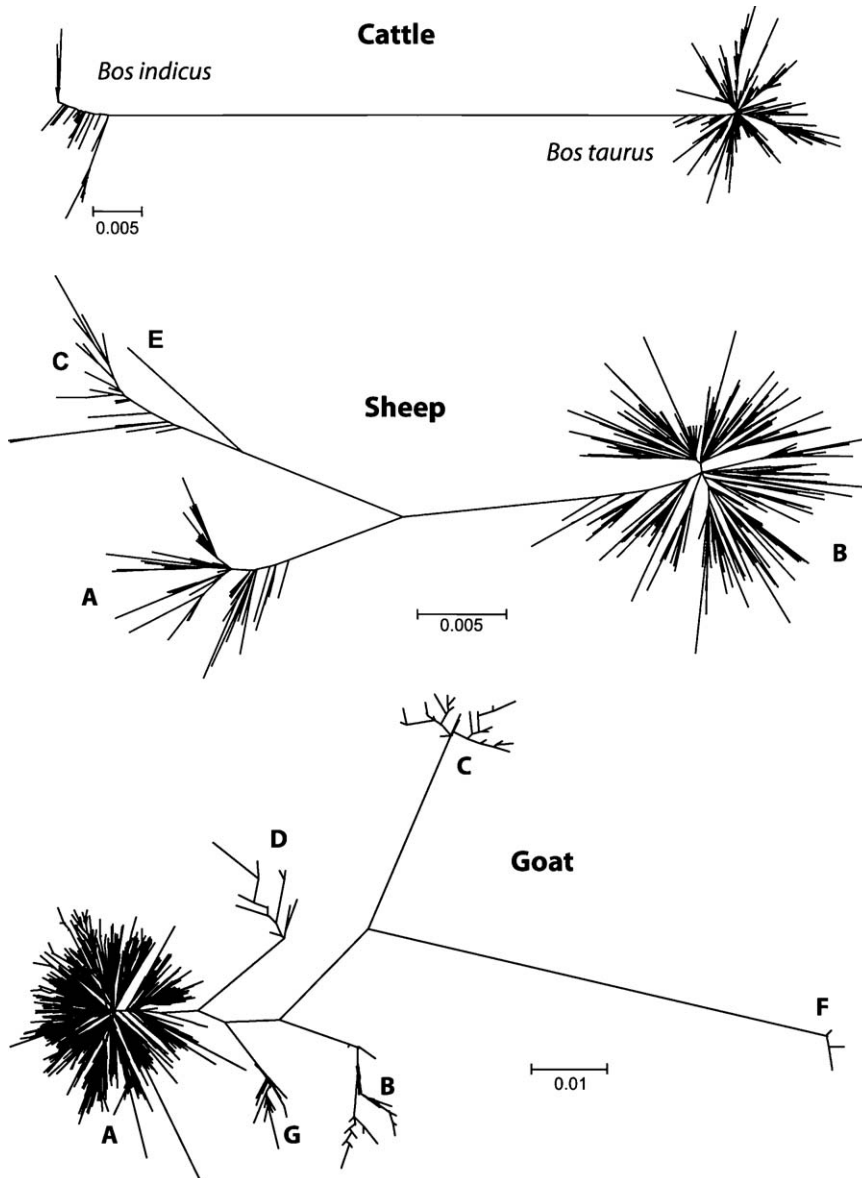


Fig. 2. Unrooted neighbor-joining trees illustrating the mtDNA polymorphism of cattle, sheep, and goats [2,51].

The cattle mtDNA polymorphism [12,13,24] seems compatible with the domestication of only two mtDNA haplotypes, leading to *B. taurus* and *B. indicus*. Such an observation is in favor of a population bottleneck at the domestication time. On the opposite, the goat mtDNA polymorphism of the A haplogroup (representing more than 90% of the haplotypes) is by far too high for originating from a single haplotype at the domestication time. A detailed analysis of this A haplogroup suggested an initial number of haplotypes higher than 1000 [23], strongly supporting the absence of bottleneck at the domestication time in goats. The sheep mtDNA polymorphism also seems to support an absence of bottleneck. How can the differences between cattle on one hand, and goat and sheep on the other hand, be explained? If we assume that a sustainable domestication must be based on a very high gene pool, we may elaborate the following scenario. As the geographic distribution of sheep and goat wild ancestors was quite restricted around the domestication centres, only a large-scale domestication event involving thousands of individuals can produce a population that will not suffer from inbreeding depression later on, during the dispersal out of the domestication centres. The cattle domestication might have followed a different trajectory, with first a bottleneck at the domestication time, followed by extensive introgressions from the aurochs later on, over large geographic areas as the wild ancestor was very widely distributed [25]. Such introgressions were able to enlarge the nuclear DNA gene pool of cattle until the extinction of the aurochs in the sixteen century. We can also imagine that these introgressions were strongly biased toward male aurochs mating with domestic females, explaining why cattle mtDNA only transmitted by female does not show significant auroch contribution. However, aurochs' mtDNA have been found at a very low percentage in Italian cattle breeds [26,27]. Recent studies [28] suggest that introgressions from aurochs into domestics may have been even more widespread than expected. This might partly explain the relatively large cattle gene pool despite a likely bottleneck at the time of domestication.

### 3. Dispersal from the domestication centres

During the 3000–4000 years following the initial domestication events in the Fertile Crescent, the Neolithic culture diffused over Europe, Africa and Asia. Archaeological evidence showed that agriculture colonized Europe by two main routes, the Mediterranean route and the Danubian route. Due to successive founder effects during the spread of agriculture, we can hypothesize a clinal decrease in genetic diversity with increasing distance to the domestication centre. Such a decrease has been demonstrated for cattle mtDNA, for which populations in Western Europe exhibit lower polymorphism than those in the Near East [14,24]. This might not be initially the case for cattle nuclear DNA if introgressions from aurochs were common. However, the pattern of variation observed may also be the result of recent selective processes; it has been recently shown that traditional cattle breeds closer to the domestication centre in Middle East show a higher nuclear

polymorphism than more heavily selected breeds in Western Europe [29]. Several secondary migrations accompanied human migrations in more recent historical times and contributed to a more complex shaping of local gene pools. For example, it has been shown that Iberian cattle breeds have been introgressed by African breeds [30–33]. Also, a close genetic relationship was discovered between Tuscan cattle breeds and Near Eastern breeds, possibly linked to the sailing and docking in Tuscany of Middle Eastern people in the late Bronze Age and to the onset of the Etruscan civilization in Central Italy [34]. Surprisingly, despite potential serial founder effect during the agriculture spread, the nuclear DNA polymorphism based on microsatellites is still relatively high in the three species [35–38], comparable to what is found in wild species. Such a result suggests a large effective population size during most of the period since the colonization.

### 4. Influence of the breed concept on genetic diversity

Fig. 1 summarizes the history of cattle, sheep, and goats. During about 10,000 years, farmers controlled the reproduction of their farm animals by favoring the reproduction of individuals with better phenotypes. As a result, farm animals slowly became adapted to local environments and fulfilled the needs of farmers in a sustainable way. At that time, gene flow among different phenotypes was possible, resulting in relatively high effective population sizes, preventing genetic drift at the regional scale. The situation dramatically changed about two hundred years ago with the emergence of the breed concept. Since that time, much stronger selection pressures have been applied to local populations followed by standardization of the morphology and the performance. All animals from the same breed began to exhibit the same phenotypic characteristics, including the same coat color. Most importantly, the gene flow among different phenotypes (i.e. among different breeds) was seriously reduced. To summarize, as illustrated on Fig. 3, the populations of farm animals that underwent relatively soft selection pressures during about 98% of their common history with humans were suddenly fragmented into many well-defined breeds, with much higher selection constraints. Population fragmentation is known to have deleterious consequences in the long term by increasing genetic drift and inbreeding, and by reducing the fitness [39]. Fragmentation is also one of the most important factors leading to extinction in wild species [39].

### 5. The current loss of genetic resources

The current loss of genetic resources concerns not only the extinction of traditional breeds, but also the loss of genetic diversity within breeds. With the development of artificial insemination during the last 50 years, only a few males were involved in reproduction schemes and consequently industrial breeds underwent another important step toward the reduction of their effective population size. For example, at the worldwide level, the Holstein cattle has an effective population size of about 50 (Table 2), leading inexorably to genetic drift and loss of alleles. All the genetic diseases observed in this breed [40], as well as the



Rosa Bonheur (1822-1899): 1849



Paulus Potter (1625-1654)



Fig. 3. Different phenotypes in the past now replaced by a homogenous breed.

strong reduction in fertility [41] may be linked to such a low effective population size. Based initially on data from livestock, conservation biologists proposed the 50/500 rule of thumb for managing wild species [42]: in the short term, the effective population size should not be less than 50 to avoid extinction risk due to genetic effects; in the long term, the effective population should not be less than 500. Surprisingly, such low effective population sizes in many cattle industrial breeds did not warn scientists in charge of the management of these breeds, maybe because a low effective population size is an advantage for short-term genetic selection and performance improvements.

Traditional breeds are threatened by the success of industrial breeds via two processes. First, the high replacement of industrial breeds tends to impose the replacement of traditional breeds by more productive ones. In many areas, farmers have a strong economic pressure to switch to industrial breeds. Such a phenomenon can be very fast, and a valuable traditional breed can

be lost within a decade. Second, autochthonous breeds are often crossbred to a more productive breed from elsewhere, most often a high production breed. Adaptive traits may be rapidly lost by poorly designed crossbreeding leading to dilution of important adaptive loci of traditional breeds. Traits such as resistance to local infectious and parasitic diseases, adaptation to poor forage, homing and gregarious behavior can be rapidly lost and difficult to rescue. They represent key traits for the survival and the management of herds in extensive farming. In developing countries, many examples illustrate this introgression threat, where indiscriminate repeated crossbreeding quickly disrupted generations of selection for adaptation to harsh environments (see examples in [2]).

## 6. The potential genetic resources

A basic approach for characterizing these resources can simply be to record phenotypic characters in all the very diverse breeds adapted to different environments and management systems. Then the genetic resources can be identified based on these phenotypic characters, assuming that phenotypes are strongly linked to genetics. An alternative approach consists to employ genetic markers. However, the characterization of genetic resources with molecular markers suffers two difficulties: the ascertainment bias of the markers used, and the problem of neutral versus adaptive markers.

Table 2  
Example of effective population sizes in the cattle Holstein breed.

Country	Period	Census population size	Effective population size ( $N_e$ )	Reference
USA	1999	8,500,000	39	[52]
France	1988–1991	2,500,000	46	[53]
Denmark	1993–2003	3,700,000	49	[54]
Germany	1999	2,200,000	52	[55]

**Table 3**

Wild species representing potential genetic resources for cattle, sheep, and goats (only the most closely related species are presented for sheep and goats).

Common name	Scientific name	Geographic distribution	Domestic form	Conservation status [56]
Gaur	<i>Bos gaurus</i>	South and southeast Asia (largest populations in India)	<i>Bos frontalis</i>	Vulnerable
Banteng	<i>Bos javanicus</i>	South Asia (Java, Borneo, Myanmar, Thailand, Cambodia, Laos, Vietnam)	Bali cattle	Endangered
Kouprey	<i>Bos sauveli</i>	Northern Cambodia, southern Laos, Western Vietnam, eastern Thailand	–	Critically endangered (possibly extinct)
Yak	<i>Bos mutus</i>	Himalayan region of south Central Asia (Tibetan Plateau, Mongolia, Russia)	<i>Bos grunniens</i>	Vulnerable
Asiatic Mouflon	<i>Ovis orientalis</i>	Caucasus, northern Iraq, northwestern Iran, Anatolia	<i>Ovis aries</i> (sheep)	Least concern
Urial	<i>Ovis vignei</i>	Asia minor	–	Vulnerable
Argali	<i>Ovis ammon</i>	Central Asia	–	Near threatened
Bezoar	<i>Capra aegagrus</i>	Central Afghanistan, southern Pakistan, Iran, western Turkmenistan, northern Iraq, Caucasus region, Turkey	<i>Capra hircus</i> (goat)	Vulnerable
Markhor	<i>Capra falconeri</i>	Northeastern Afghanistan, Gilgit-Balistan, Hunza-Nagar Valley, northern and central Pakistan, Kashmir, southern Tajikistan, southern Uzbekistan	–	Endangered

The ascertainment biases are due to the adjustment of genetic markers (microsatellites or single nucleotide polymorphisms) with the constraint of being as polymorphic as possible in the breeds under study, i.e. industrial breeds in most cases. As a consequence, the genetic diversity estimates for traditional breeds when using such markers will be biased toward low values and the estimation of heterozygosity is particularly affected [43]. Such an ascertainment bias has also been clearly shown in wild species where only the most polymorphic microsatellites are selected for further investigations [44]. Genome-wide analyses based on single nucleotide polymorphisms (SNP) are now widely used in farm animals [45], but also suffer from the same ascertainment bias [46,47]. In such a situation, only sequencing many regions of the genome would give a reliable estimate of the genetic diversity [44] and is appropriate for properly characterizing genetic resources.

The second difficulty for characterizing genetic resources is linked to an ongoing debate about the relative importance of neutral versus adaptive variations for identifying the populations to prioritize for protection purposes. The neutral variation, an indicator of global genetic diversity, can be used for assessing conservation values, based on the idea that we do not know future selection pressures and that more diverse populations at the genome-wide level will better adapt [48]. The opposite point of view claims that only adaptive variation is relevant for conservation purpose [49].

Should we include wild ancestors as potential genetic resources when they still exist? The answer to this question is not straightforward, as no extensive study has been carried out so far to properly assess the potential of wild populations as genetic resources. The value of wild ancestors will be inversely linked to the proportion of genetic diversity that has been captured during the domestication process. Within each of the *Capra* and *Ovis* genera, many species can hybridize and produce fertile offspring. As a consequence, beside the wild ancestor, several other species within these two genera can also be considered as genetic resources (e.g. *Capra falconeri* for goats, *Ovis vignei* and *O. ammon* for sheep; Table 3). For

cattle the situation is different, as the wild ancestor is extinct. Nevertheless, four or five wild species of the genus *Bos* are still alive and can produce fertile hybrids with cattle. Thus, they might also be considered as genetic resources (Table 3).

## 7. Conclusion

The effective management of farm animal genetic resources is primordial to ensure global and sustainable food security. The erosion of genetic resources has been clearly documented for farm animals [4]. Within a few decades, we might lose most of the highly valuable farm animal genetic resources that humanity has gradually selected over the past 10,500 years [2]. Urgent conservation measures must be taken to avoid such an irremediable loss [5]. These genetic resources are even not properly characterized due to the problem of ascertainment bias of the molecular markers used up to now. Fortunately, with the development of the next generation DNA sequencing technology [50], it will be possible to resequence whole genomes and to properly assess the genetic diversity and the conservation value of the different breeds, avoiding the ascertainment bias due to the use of microsatellites or single nucleotide polymorphisms. There is clearly a race between the characterization of genetic resources and their loss. In the same way, the development of genomic tools will allow to optimize the breeding strategies for ensuring the improvement of performance together with the preservation of genetic diversity.

If the integration of wild relatives in conservation planning is common in plants, it is not the case for domestic animals. Most of the wild relatives of cattle, sheep, and goats are endangered (Table 3), and no ongoing actions were implemented to preserve them based on the fact that they have the potential of representing valuable genetic resources for agriculture. Thus, it is now urgent to properly assess their potential as genetic resources.

The first step toward an efficient conservation strategy for cattle, sheep, and goat genetic resources is the proper characterization of the conservation value of the different breeds and of the wild relatives. This step relies on genetic

technologies, and we can be optimistic at that level according to the current revolution in DNA sequencing. However, the implementation of the subsequent steps is more puzzling, as conservation strategies for farm animal genetic resources must integrate economical, sociological, and political parameters.

### Conflict of interest statement

The authors have not declared any conflict of interest.

### Acknowledgements

The European Commission provided funding via the FP7 NextGen project (“Next generation methods to preserve farm animal biodiversity by optimizing present and future breeding options”; Grant agreement no. 244356).

### References

- [1] B.A. Wilcox, M.E. Soulé, Conservation biology: an evolutionary-ecological perspective, Sinauer Associates, Sunderland, Massachusetts, U.S.A., 1980
- [2] P. Taberlet, A. Valentini, H.R. Rezaei, S. Naderi, F. Pompanon, R. Negrini, P. Ajmone-Marsan, Are cattle, sheep, and goats endangered species? *Mol. Ecol.* 17 (2008) 275–284.
- [3] FAO, Animal genetic resources - Conservation and management, proceedings of the FAO/UNEP technical consultation, Food and Agriculture Organization of the United Nations, Rome, 1981.
- [4] B. Rischkowsky, D. Pilling (Eds.), The state of the world's animal genetic resources for food and agriculture, Food and Agriculture Organization of the United Nations, Rome, Italy, 2007.
- [5] P.J. Boettcher, I. Hoffmann, Conserve livestock genetic resources, *Science* 326 (2009) 365–365.
- [6] J.D. Vigne, D. Helmer, J. Peters, New archaeozoological approaches to trace the first steps of animal domestication: general presentation, reflections and proposals, in: J.D. Vigne, J. Peters, D. Helmer (Eds.), *The First Steps of Animal Domestication. New Archaeological Approaches*, Oxbow Books, Oxford, UK, 2005, pp. 1–16.
- [7] M.A. Zeder, E. Emshwiller, B.D. Smith, D.G. Bradley, Documenting domestication: the intersection of genetics and archaeology, *Trends Genet.* 22 (2006) 139–155.
- [8] J. Peters, A. von den Driesch, D. Helmer, The upper Eurphrates-Tigris basin: cradle of agro-pastoralism, in: J.D. Vigne, D. Helmer (Eds.), *The First Steps of Animal Domestication. New Archaeological Approaches*, Oxbow Books, Oxford, UK, 2005, pp. 96–124.
- [9] M.A. Zeder, B. Hesse, The initial domestication of goats (*Capra hircus*) in the Zagros Mountains 10,000 years ago, *Science* 287 (2000) 2254–2257.
- [10] D. Helmer, L. Gourichon, H. Monchot, J. Peters, M.S. Seguí, Identifying early domestic cattle from pre-pottery Neolithic sites on the Middle Eurphrates using sexual dimorphism, in: J.D. Vigne, J. Peters, D. Helmer (Eds.), *The First Steps of Animal Domestication. New Archaeological Approaches*, Oxbow Books, Oxford, UK, 2005, pp. 86–95.
- [11] F.E. Zeuner, A history of domesticated animals, Hutchison, London, 1963.
- [12] R.T. Loftus, D.E. MacHugh, D.G. Bradley, P.M. Sharp, Evidence for two independent domestication of cattle, *Proc. Natl. Acad. Sci. USA* 91 (1994) 2757–2761.
- [13] D.G. Bradley, D.E. MacHugh, P. Cunningham, R. Loftus, Mitochondrial diversity and the origins of African and European cattle, *Proc. Natl. Acad. Sci. USA* 93 (1996) 5131–5135.
- [14] D.G. Bradley, D.A. Magee, Genetics and origins of domestic cattle, in: M.A. Zeder, D.G. Bradley, E. Emshwiller, B.D. Smith (Eds.), *Documenting Domestication. New Genetics and Archaeological Paradigms*, University of California Press, Ltd, Berkeley, CA, 2006, pp. 317–328.
- [15] T. Haltenorth, Klassifikation der Säugetiere: Artiodactyla 1, Walter de Gruyter, Berlin, Germany, 1963.
- [16] C.F. Nadler, R.S. Hoffmann, A. Woolf, G-band patterns as chromosomal markers, and the interpretation of chromosomal evolution in wild sheep (*Ovis*), *Experientia* 29 (1973) 117–119.
- [17] H.R. Rezaei, S. Naderi, I.C. Chintauan-Marquier, P. Taberlet, A.T. Virk, H.R. Naghash, D. Rioux, M. Kaboli, F. Pompanon, Evolution and taxonomy of the wild species of the genus *Ovis* (Mammalia, Artiodactyla, Bovidae), *Mol. Phylog. Evol.* 54 (2010) 315–326.
- [18] H.R. Rezaei, Phylogénie moléculaire du genre *Ovis* (Mouton et Mouflons), implications pour la conservation du genre et pour l'origine de l'espèce domestique, Thesis, Université Joseph Fourier, Grenoble, 2007.
- [19] S. Pedrosa, M. Uzun, J.-J. Arranz, B. Gutiérrez-Gil, F. San Primitivo, Y. Bayón, Evidence of three maternal lineages in near eastern sheep supporting multiple domestication events, *Proc. Roy. Soc. London B Bio. Sci.* 272 (2005) 2211–2217.
- [20] J.R.S. Meadows, I. Cemal, O. Karaca, E. Gootwine, J.W. Kijas, Five ovine mitochondrial lineages identified from sheep breeds of the near east, *Genetics* 175 (2007) 1371–1379.
- [21] H. Fernández, P. Taberlet, M. Mashkour, J.D. Vigne, G. Luikart, Assessing the origin and diffusion of domestic goats using ancient DNA, in: J.D. Vigne, J. Peters, D. Helmer (Eds.), *The First Steps of Animal Domestication. New Archaeological Approaches*, Oxbow Books, Oxford, UK, 2005, pp. 50–54.
- [22] G. Luikart, H. Fernández, M. Mashkour, P.R. England, P. Taberlet, Origins and diffusion of domestic goats inferred from DNA markers: example analyses of mtDNA, Y chromosomes, and microsatellites, in: M.A. Zeder, D.G. Bradley, E. Emshwiller, B.D. Smith (Eds.), *Documenting Domestication. New Genetic and Archaeological Paradigms*, University of California Press, Ltd, Berkeley, CA, 2006, pp. 294–305.
- [23] S. Naderi, H.R. Rezaei, F. Pompanon, M.G.B. Blum, R. Negrini, H.R. Naghash, Ö. Balkiz, M. Mashkour, O.E. Gaggiotti, P. Ajmone-Marsan, A. Kence, J.D. Vigne, P. Taberlet, The goat domestication process inferred from large-scale mitochondrial DNA analysis of wild and domestic individuals, *Proc. Natl. Acad. Sci. USA* 105 (2008) 17659–17664.
- [24] C.S. Troy, D.E. MacHugh, J.F. Bailey, D.A. Magee, R.T. Loftus, P. Cunningham, A.T. Chamberlain, B.C. Sykes, D.G. Bradley, Genetic evidence for Near-Eastern origins of European cattle, *Nature* 410 (2001) 1088–1091.
- [25] C. van Vuure, Retracing the aurochs: history, morphology and ecology of an extinct wild ox, Pensoft Publishers, Sofia, Bulgaria, 2005.
- [26] A. Achilli, S. Bonfiglio, A. Olivieri, A. Malusa, M. Pala, B.H. Kashani, U.A. Perego, P. Ajmone-Marsan, L. Liotta, O. Semino, H.J. Bandelt, L. Ferretti, A. Torroni, The multifaceted origin of taurine cattle reflected by the mitochondrial genome, *PLoS One* 4 (2009) e5753.
- [27] S. Bonfiglio, A. Achilli, A. Olivieri, R. Negrini, L. Colli, L. Liotta, P. Ajmone-Marsan, A. Torroni, L. Ferretti, The enigmatic origin of bovine mtDNA haplogroup R: sporadic interbreeding or an independent event of *Bos primigenius* domestication in Italy? *PLoS One* 5 (2010) e15760.
- [28] P. Ajmone-Marsan, J.F. Garcia, J.A. Lenstra, Globaldiv Consortium, On the origin of cattle: How aurochs became cattle and colonized the world, *Evol. Anthropol.* 19 (2010) 148–157.
- [29] I. Medugorac, A. Medugorac, I. Russ, C.E. Veith-Kensch, P. Taberlet, B. Luntz, H.M. Mix, M. Förster, Genetic diversity of European cattle breeds highlights the conservation value of traditional unselected breeds with high effective population size, *Mol. Ecol.* 18 (2009) 3394–3410.
- [30] T. Cymbron, R.T. Loftus, M.I. Malheiro, D.G. Bradley, Mitochondrial sequence variation suggests an African influence in Portuguese cattle, *Proc. Roy. Soc. London B Bio. Sci.* 266 (1999) 597–603.
- [31] M.M. Miretti, S. Dunner, M. Naves, E.P. Contel, J.A. Ferro, Predominant African-derived mtDNA in Caribbean and Brazilian Creole cattle is also found in Spanish cattle (*Bos taurus*), *J. Hered.* 95 (2004) 450–453.
- [32] C. Anderung, A. Bouwman, P. Persson, J.M. Carretero, A.I. Ortega, R. Elburg, C. Smith, J.L. Arsuaga, H. Ellegren, A. Gotherstrom, Prehistoric contacts over the Straits of Gibraltar indicated by genetic analysis of Iberian Bronze Age cattle, *Proc. Natl. Acad. Sci. USA* 102 (2005) 8431–8435.
- [33] A. Beja-Pereira, D. Caramelli, C. Lalueza-Fox, C. Vernesi, N. Ferrand, A. Casoli, F. Goyache, L.J. Royo, S. Conti, M. Lari, C. Triantaphyllidis, K. Ploumi, L. Sineo, F. Mallegni, P. Taberlet, G. Erhardt, L. Sampietro, J. Bertranpetit, G. Barbujani, G. Luikart, G. Bertorelle, The origin of European cattle: evidence from modern and ancient DNA, *Proc. Natl. Acad. Sci. USA* 103 (2006) 8113–8118.
- [34] M. Pellecchia, R. Negrini, L. Colli, M. Patrini, E. Milanese, A. Achilli, G. Bertorelle, L.L. Cavalli-Sforza, A. Piazza, A. Torroni, P. Ajmone-Marsan, The mystery of Etruscan origins: novel clues from *Bos taurus* mitochondrial DNA, *Proc. Roy. Soc. London B Bio. Sci.* 274 (2007) 1175–1179.
- [35] C. Diez-Tascon, R.P. Littlejohn, P.A.R. Almeida, A.M. Crawford, Genetic variation within the Merino sheep breed: analysis of closely related populations using microsatellites, *Anim. Genet.* 31 (2000) 243–251.
- [36] F. Rendo, M. Iriando, B.M. Jugo, L.I. Mazon, A. Aguirre, A. Vicario, A. Estonba, Tracking diversity and differentiation in six sheep breeds from the North Iberian Peninsula through DNA variation, *Small Ruminant Res.* 52 (2004) 195–202.
- [37] J. Cañón, D. García, M.A. García-Atance, G. Obexer-Ruff, J.A. Lenstra, P. Ajmone-Marsan, S. Dunner, E. Consortium, Geographical partitioning of goat diversity in Europe and the Middle East, *Anim. Genet.* 37 (2006) 327–334.

- [38] C. Maudet, G. Luikart, P. Taberlet, Genetic diversity and assignment tests among seven French cattle breeds based on microsatellite DNA analysis, *J. Anim. Sci.* 80 (2002) 942–950.
- [39] R. Frankham, J.D. Ballou, D.A. Briscoe, *Introduction to conservation genetics*, Cambridge University Press, Cambridge, UK, 2002.
- [40] X. Malher, F. Beaudeau, J.M. Philipot, Effects of sire and dam genotype for complex vertebral malformation (CVM) on risk of return-to-service in Holstein dairy cows and heifers, *Theriogenology* 65 (2006) 1215–1225.
- [41] J.E. Pryce, M.D. Royal, P.C. Garnsworthy, L.L. Mao, Fertility in the high-producing dairy cow, *Livest. Prod. Sci.* 86 (2004) 125–135.
- [42] I.R. Franklin, Evolutionary changes in small populations, in: M.E. Soulé, B.A. Wilcox (Eds.), *Conservation biology: an evolutionary-ecological perspective*, Sinauer, Sunderland, MA, 1980, pp. 135–149.
- [43] L.R.P. Neto, W. Barendse, Effect of SNP origin on analyses of genetic diversity in cattle, *Anim. Prod. Sci.* 50 (2010) 792–800.
- [44] U. Vali, A. Einarsson, L. Waits, H. Ellegren, To what extent do microsatellite markers reflect genome-wide genetic diversity in natural populations? *Mol. Ecol.* 17 (2008) 3808–3817.
- [45] The bovine hapmap consortium, Genome-wide survey of SNP variation uncovers the genetic structure of cattle breeds, *Science* 324 (2009) 528–532.
- [46] A.G. Clark, M.J. Hubisz, C.D. Bustamante, S.H. Williamson, R. Nielsen, Ascertainment bias in studies of human genome-wide polymorphism, *Genome Res.* 15 (2005) 1496–1502.
- [47] R. Nielsen, Population genetic analysis of ascertained SNP data, *Hum. Genomics* 1 (2004) 218–224.
- [48] C. Moritz, Defining “evolutionarily significant units” for conservation, *Trends Ecol. Evol.* 9 (1994) 373–375.
- [49] K.A. Crandall, O.R. Bininda-Emonds, G.M. Mace, R.K. Wayne, Considering evolutionary processes in conservation biology, *Trends Ecol. Evol.* 15 (2000) 290–295.
- [50] J. Shendure, H. Ji, Next-generation DNA sequencing, *Nat. Biotechnol.* 26 (2008) 1035–1045.
- [51] S. Naderi, H.-R. Rezaei, P. Taberlet, S. Zundel, S.A. Rafat, H.-R. Naghash, M. Abo-Shehata, M.A.A. El-Barody, O. Ertugrul, F. Pompanon, Econo-gene Consortium, Large-scale mitochondrial DNA analysis of the domestic goat reveals six maternal lineages with high haplotype diversity, *PLoS One* 2 (2007) e1012.
- [52] K.A. Weigel, Controlling inbreeding in modern breeding programs, *J. Dairy Sci.* 84 (E. Suppl.) (2001) E177–E184.
- [53] D. Boichard, L. Maignel, E. Verrier, Analyse généalogique des races bovines laitières françaises, *INRA Productions Animales* 9 (1996) 323–335.
- [54] A.C. Sørensen, M.K. Sørensen, P. Berg, Inbreeding in Danish dairy cattle breeds, *J. Dairy Sci.* 88 (2005) 1865–1872.
- [55] S. Koenig, H. Simianer, Approaches to the management of inbreeding and relationship in the German Holstein dairy cattle population, *Livest. Sci.* 103 (2006) 40–53.
- [56] IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4. (<http://www.iucnredlist.org>). Downloaded on 05 December 2010.