

Livestock Biodiversity

**Genetic resources for the farming
of the future**

Stephen J. G. Hall

MA, PhD

Department of Biological Sciences, University of Lincoln

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Preface

This book has been written in response to three stimuli. First, all over the world there is evidence that the diversity of domesticated animals is under threat and students, opinion leaders, researchers and policy makers should be aware of this and should be encouraged to do what they can to protect this component of global biodiversity. Second, it is now clear that the true functions and values of livestock are not merely the production of food and materials and the provision of draft power. Livestock have always had cultural and social significance, and they provide many services to society which are now beginning to be widely appreciated. These range from landscape conservation, to serving as a reliable investment where banking is poorly developed. These broader roles, how they relate to specific breeds, and how they change and develop, need to be better understood. Third, the conservation and sustainable development of livestock biodiversity has been seen as falling mainly within the range of interest of geneticists and animal breeders. While their insights and the new techniques they are developing are indispensable, there are other disciplines which have much to offer. The fruitful interactions of apparently rather different sciences have been seen in the emergence of conservation biology (Frankham *et al.*, 2002; Primack, 2002) in response to the crisis of floral and faunal extinctions. Similarly, livestock biodiversity needs inputs from several disciplines if it is to be conserved and developed sustainably. A recent review of the currently available scientific approaches is given by Simm *et al.* (2004).

This book aims to give an overview of the patterns and processes of evolution of livestock biodiversity, to emphasize its place in our cultural heritage and its value to the farming of today and of the future, to suggest future areas of research, to celebrate its richness and to advocate its conservation and sustainable utilization.

The study of livestock biodiversity embodies the kinds of issues that modern versatile graduates need to be able to tackle. This book is written at advanced undergraduate and junior postgraduate level for students of genetics, animal breeding and animal science, conservation biology and social and development studies. It is also intended for policy makers and as a background text for researchers in these general areas.

Stephen J.G. Hall

Acknowledgements

This book was begun while I was in Professor Don Broom's group in the Department of Clinical Veterinary Medicine, University of Cambridge. It was continued while I was at the Overseas Development Institute, London, and at De Montfort University, and has been completed at the Department of Biological Sciences, University of Lincoln.

The ideas have been developed during and after innumerable conversations with very many colleagues. I owe particular debts to Dr Roger Blench, Dr Juliet Clutton-Brock, Dr Martyn Murray and two referees. Without the interest, understanding and support of my parents, Dr and Mrs J.G. Hall, and of my wife Sue and daughters Nicola and Katie, the work would have been much more arduous.

The book is dedicated to the memory of Professor Peter Jewell, who was one of the pioneers of the conservation of rare breeds, as well as being a most valued friend, and inspiring mentor and colleague.

Introduction

Domestication of animals was a vital step in the development of human culture and many of the major issues facing the world at the beginning of the twenty-first century are related to livestock. The kinds of inter-species relationships so familiar in Nature – predation, parasitism, symbiosis, etc. – have been joined by another, domestication, under which animals have been shaped to meet human needs. In the 10 000 years since the major domestications began, thousands of distinctive taxa have emerged from a few relatively narrow genetic bases. Much of this biodiversity is now at risk.

What is the place of livestock biodiversity in the world today and why is it important for the future? The current belief is that the world should be able to feed its human population, which may total eight billion in 2020, provided fair distribution can be achieved and that intensification can continue. Increasing affluence, especially in the developing world, is expected to increase global meat demand from 209 million tonnes (in 1997) to 327 million tonnes in 2020; milk demand is expected to rise from 422 million to 648 million tonnes (de Haan *et al.*, 2001). The trends are also for a shift towards pigs and poultry in both developed and developing countries.

As crop production increases, land for pasture decreases, but the amount of straw and other residues increases. World annual crop production has been estimated at about 2750 million tonnes, and of crop residues 3750 million tonnes (Smil, 1999). The ruminant can remain confident of its food supply. In wealthy countries food quality and safety are important and, in some, animal welfare is as well. Perhaps the day will come when the animals of the factory farm are once more put out to grass but such free-range, welfare-oriented husbandry systems will only contribute a small proportion to the world's food supplies.

In many societies such as the European Union (EU), tracts of land are valued primarily for their scenic beauty and cultural significance – grazing livestock are often a key element in this maintenance (Hindmarch Pienkowski, 1998). In the Lake District of northern England, or in the parklands around historic houses, 50 years ago livestock were an important part of the food chain, but today they are often kept in order to cut the grass.

The thousands of breeds that exist were mostly developed in very different circumstances from those of today, but they are not anachronisms, they represent the genetic diversity that will enable the livestock farming of the future to respond to new challenges. These include emergent diseases, consumer dissatisfaction with current livestock systems, environmental disruption arising from climate change and shortage of grazing land in developing countries as a result of increasing crop

production. This diversity is under threat as high-performing breeds are freely available in a global market. For example Canada supplies 20% of the world's internationally traded dairy cattle semen and embryos, worth \$128 million annually (July 2001: www.dairyinfo.agr.ca/glance.pdf), and in 1999 importations of day-old chicks into the UK totalled 98 472 662 (www.parliament.the-stationery-office.co.uk). During the late 1990s about 1.6 million semen doses and 50 000 dairy cows were exported annually from the Netherlands (Siemes, 2001). In these circumstances local genotypes, produced in small numbers, find it difficult to compete.

Threats to wildlife biodiversity are easy to describe, explain and quantify. There is no arguing with photographs of poached rhino, or elephant, or gorillas, or torched forest, and the links between habitat loss, overexploitation and extinction are easy to explain. Threats to breeds are nowhere near as obvious. Repeated mating with another breed will change the genotype of a livestock population radically in a few generations, a very different concept of extinction from that which applies in wildlife. In many countries, traditional breeds are hardly known at all to policy makers or opinion leaders.

Agricultural policy makers will be seen by future generations as having abdicated their responsibilities if they fail to support conservation of livestock biodiversity, or find other organizations willing to do so. The Food and Agriculture Organization of the United Nations (FAO) has a 50-year record of promoting research into livestock biodiversity and of advocating its conservation, but there have been very few examples of internationally funded projects to support livestock biodiversity in the developing world and relatively few government-funded projects in richer nations. On the positive side, the FAO has helped to create a climate of awareness, which was recognized in the Convention on Biological Diversity, and this book tries to add to that achievement.

Part 1

The Nature of Livestock Biodiversity

Today's livestock biodiversity is the fruit of a two-stage process. First there was domestication, then there was breed differentiation. Both involved genetic change and are thus both evolutionary and cultural processes. Domestication of plants and animals was of fundamental importance for the development of the human cultures that are economically dominant today. Modern genetics has cast fresh light on this process: molecular genetics has been explicitly applied to the study of where and when domestication happened. Quantitative and population genetics have not – yet. How today's breeds arose is well known in some regions of the world and is almost a complete mystery in others.

Chapter 1

Biology of domestication

Introduction

What are the evolutionary processes that operate under domestication, and how do they differ from those observed in nature? What was the biology of the process of domestication, and how much of this can we infer from studies on present-day domesticated animals, to add to what is known from archaeology and from human sciences? Could the processes giving rise to new heritable variation have taken new forms under domestication?

Domestication and models of evolution

Humans probably existed for three million years as hunter-gatherers before the domestication of plants and animals began, about 10 000 years ago (Clutton-Brock, 1999). The effects of this cultural change, 400 human generations ago, on the evolution of our species would be difficult to demonstrate, but clearly the effects on the animals and plants which were then enfolded into our society were profound (Figures 1.1a, b).

Domestication and breed development are the evolutionary processes that are most visible to us and this is one reason why they have been used to help formulate evolutionary principles and to persuade people of the truth of these principles. Darwin used the existence of breeds and varieties in his arguments for evolution by natural selection. In order to convey the idea that heritable adaptation (and not merely individual developmental modification) could occur in nature, Darwin emphasized how humans could practise artificial selection to create animals and plants that were adapted to human use. There was an analogy here, suited to the public attitudes of his time, between man's activities and those of a 'benevolent, omniscient "super breeder" who, unlike human breeders, selects only for the benefit of the organism' (Richards, 1998).

This is the best known example of how knowledge of domestication helped to show how evolution could have taken place. Later, Sewall Wright's studies on Shorthorn cattle highlighted the importance of population structure in evolution. Currently, understanding of quantitative genetics, obtained from work on livestock, is being applied widely to studies on evolution in nature (for example Roff, 1997).

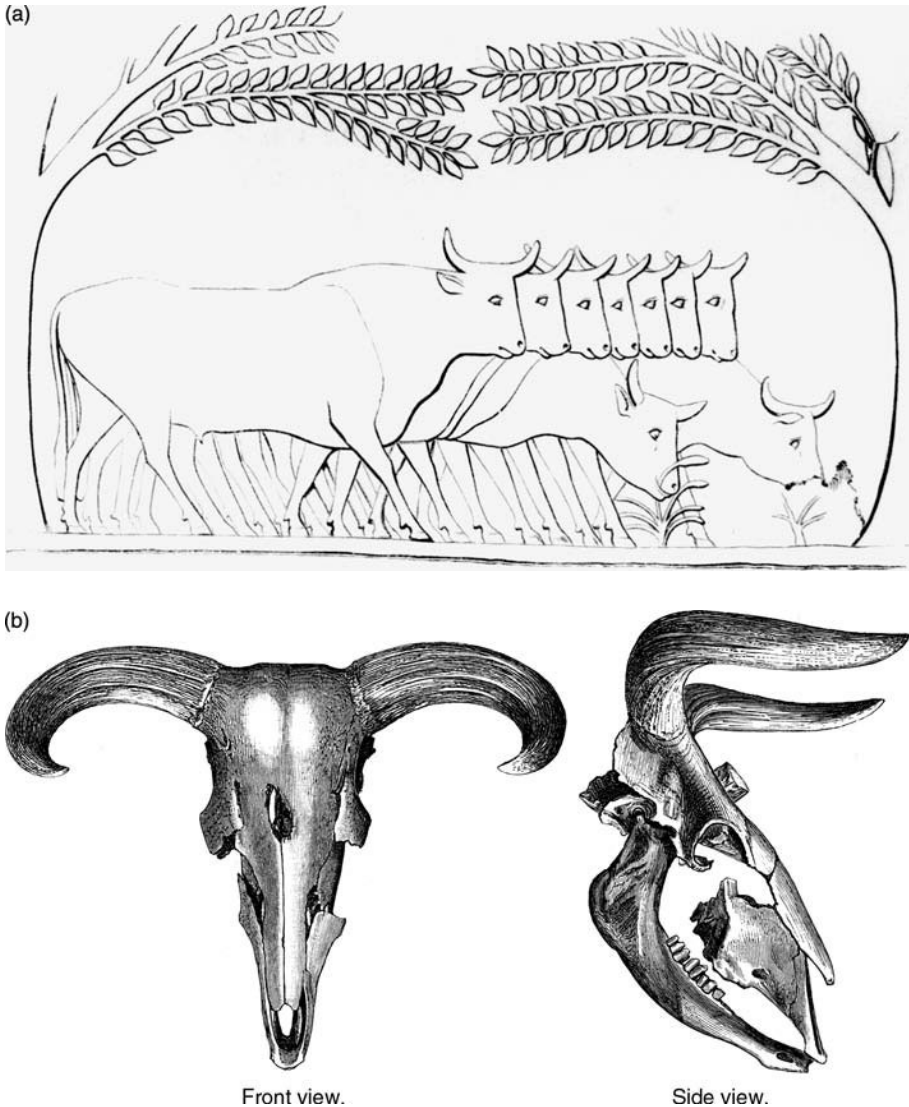


Figure 1.1 Domestication – a new relationship. This aurochs skull (b) (in the Haddon Museum, Cambridge University) still has a Neolithic stone axe embedded in it – relic of a violent encounter in what is now Burwell Fen, Cambridgeshire. The axe is depicted in the side view. In sharp contrast with the Egyptian cattle (a) in bas-relief in the temple of Hatshepsu, the themes are tranquillity, orderliness, uniformity and pride of possession. Both reproduced from McKenny Hughes (1896).

Rates of evolution under domestication

Domestication has been defined as ‘the process of enfoldng a species into human society and taking responsibility for its husbandry and control over its breeding’ (Clutton-Brock, 1992a).

Under domestication animals are subjected to breeding plans, which can be based on artificial selection, on relationship, or on phenotypic likeness (Lush, 1943). The breeds observed today have each emerged by an interaction of one or more of these processes with the operation of founder effects and inbreeding, and probably migration and natural selection.

Rapid evolutionary change is possible, perhaps even typical, when domesticated animals are artificially selected, and rates of evolution can be compared (Figure 1.2). If a phenotypic trait changes by a factor of e (2.718, the base of natural logarithms) in one million years its rate of evolution is defined as one darwin (Gingerich, 1983; Hendry & Kinnison, 1999). In animal breeding, annual rates of change in growth rate between 1 and 3% are possible (Simm, 1998, p.80; McKay *et al.*, 2000), i.e. around 380 000 darwins. Racing performance in Thoroughbred horses has improved at a rate of about 14 000–29 000 darwins (calculated from Eckhardt *et al.*, 1988). On a geological time scale, rates are mainly between 0.1 and 400 darwins, but within natural species or populations (microevolutionary scale) rates can be much higher, for example during a colonization event or recovery from a catastrophe. Evolution of dwarfism in island Red deer proceeded at a rate of 10 000 darwins (Lister, 1989).

Technological domestication

Nowadays many animals are farmed or kept in ways which do not involve their being enfolded into human society. If they can be described as domesticated it is only in the sense that their husbandry is fully under human control rather than that their relationship with humans is of any depth. Before the twentieth century chickens were essentially farmyard scavengers, pigs were kept mainly to deal with the

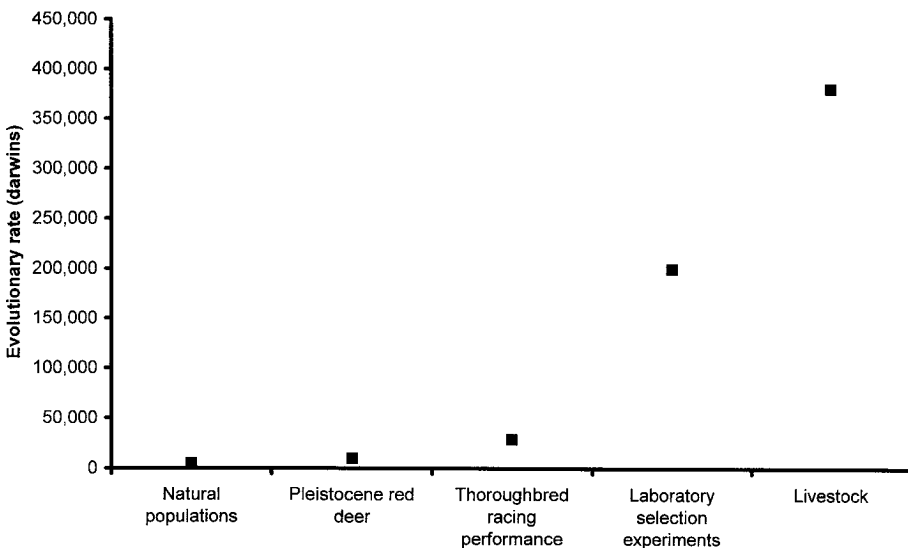


Figure 1.2 Evolutionary rates, when measured in darwins (see text), can be compared between populations.

leftovers of food production and processing and aquaculture was limited to herbivorous fish such as carp kept in ponds – all husbandry systems which involve fairly intimate human–animal interactions.

In recent years the availability of technology (housing and transport systems, feed formulation, meat processing and marketing) has enabled non-grazing livestock to be farmed intensively. More than 220 aquatic species are now farmed in a wide range of systems (Naylor *et al.*, 2000); farmed fish supplies totalled 29 million tonnes in 1997 compared with fisheries landings of about 95 million tonnes. The previously close human–animal interaction has been replaced by systems where animals are kept well apart from people. In poultry farming, certain attributes of a species which were not particularly valuable when it was being kept as a farmyard fowl have proved fundamental to the development of modern poultry industries (Table 1.1).

Molecular genetic insights into domestication

Our understanding of domestication comes from archaeology, and from knowledge of the behaviour and biology of humans and of the wild ancestors and present-day relatives of domesticated animals. Current knowledge and opinion is summarized by Hemmer (1990), Clutton-Brock (1999) and Price (2002). Providing new insights into the process, the molecular genetics of present day livestock is making it possible to test hypotheses generated by earlier work (see Chapter 7).

Table 1.1 Key features of the chicken making it highly suitable for modern intensive farming. From Hartmann (1989).

Feature	Consequence
High fecundity and short generation interval	Intense selection and rapid multiplication possible
Incubation can be mechanized	No reliance on broody hens. This is essential for commercial production, and enables selection against broodiness
Eggs remain fertile in storage	Family size can be modified for selection and increased flexibility of breeding
Depending on genotype, sex can be identified at hatching using sex-linked plumage characteristics	A relatively recent development permitting separate breeding programmes for egg and meat production. Previously all chicks had to be kept until old enough to be sexed. By then it was not economic to discard the males and they had to be reared for meat. Consequently selection programmes could not ignore meat qualities and specialist egg-producing breeds were not economically viable
Responsiveness of sexual maturation and egg laying to artificial light	Reduced seasonal variation in production and improved profitability
Apparent adaptability to novel feeding and housing conditions	Automatic feeding and high health, low labour-requirement housing possible

Early work on livestock breeds in the 1950s and 1960s, inspired by studies on human blood groups and other heritable variation in biochemical characteristics, showed how breeds could be grouped on the basis of shared descent, but mutation rates were too slow and allelic diversity too narrow to permit deductions relating to the evolutionary process. Today, mitochondrial DNA (mtDNA) lineages can be traced back in such a way that timings and locations of genetic bottlenecks suggestive of domestication can be deduced. Mitochondrial DNA is inherited in the female line; none is passed on by sperm, and there is no recombination so the only source of variation is mutation. Thus, for example, the divergence of the banteng *Bos javanicus* from the ancestral bovine stock can be dated to 2–4 million years ago (Kikkawa *et al.*, 1995). Between 610 000 and one million years ago (MacHugh *et al.*, 1997) the ancestors of today's two groups of true cattle, the zebu (humped) cattle of India and the Far East, and the taurine (humpless) cattle of the west and Near East, split. Whether or not zebu and taurine cattle truly represent distinct species (*Bos indicus* and *Bos taurus* respectively) has been thoroughly debated (Clutton-Brock, 1999); these findings clearly support the notion of separate domestications of two distinct races of aurochs to yield these distinct breed groups of cattle. Domestication of taurine cattle from their wild progenitor, the aurochs, is well attested in the Near East, and is also strongly implied in Africa (Bradley *et al.*, 1996; Mommens *et al.*, 1999). While most Chinese breeds descend from an interbreeding of Near Eastern taurine cattle with cattle derived from the Indian domestication of a distinct race of aurochs to form the zebu, there may also have been an independent domestication of zebu in China (Yu *et al.*, 1999). It is debated (Bailey *et al.*, 1996; Troy *et al.*, 2001) whether modern taurine cattle all descend from a single relatively small ancestral population of aurochs.

Microsatellites have been effective in resolving many questions on the relationships between present-day breeds (see Chapter 7) and may also shed light on the process of domestication. Present-day breeds geographically located near to where domestication took place have been claimed to still possess some of the allelic variation of the original domesticated population, which has been lost from breeds that are geographically further away. Microsatellite studies of Near Eastern cattle breeds (Loftus *et al.*, 1999) imply this. Similarly the reason why the Awassi (of Syria and nearby countries) is of all the sheep breeds examined by Byrne *et al.* (cited by Bruford, 2004) the most diverse in microsatellites, may be because it originated close to where the species was domesticated.

Incoming domesticated stocks may have been mated with resident wild conspecifics. In Europe, aurochs and domesticated cattle may have interbred, and indeed bones intermediate in size between the two types have been found in Poland (Lasota-Moskalewska & Kobryn, 1989). Davis and Payne (1993) report a bone deposit from third millennium BC England containing at least 184 skulls of domesticated cattle and one of an aurochs. This kind of immigration has been shown experimentally to have a beneficial effect on the reproductive fitness of inbred populations. Spielman and Frankham (1992) doubled reproductive fitness of small, inbred *Drosophila* populations that had declined significantly in fitness compared with an outbred control population by introduction of single immigrants. Lively *et al.* (1990) obtained

similar results for fish where inbred individuals had heavier parasite burdens than control animals, but these were reduced after new individuals with greater genetic variation were introduced into the inbred population.

Some breeds are evidently the result of hybridization between species. The Diqing cattle in China carry yak-type mtDNA (Yu *et al.*, 1999). Interestingly, this breed is adapted to a high altitude, cold environment, like that of the yak. Presumably there was introgression of yak genes after domestication (female cattle–yak hybrids can be fertile). In Indonesia, Bali cattle are considered to be domesticated banteng and indeed they do have banteng mtDNA. However there is zebu mtDNA in the Malaysian population of Bali cattle, confirming interspecies hybridization (Nijman *et al.*, 2003).

The two breed groups of water buffalo, the river type and the swamp type, have different chromosome numbers ($2n = 50$ and 48 , respectively). The F1 generation has $2n = 49$ and apparently produces gametes with either 24 or 25 chromosomes. In the river type, chromosomes 4 and 9 are distinct, while in the swamp type they have joined to form a large chromosome (Harisah *et al.*, 1989). The two types are interfertile but are very distinct functionally and in appearance, with the river type (relatively short, upturned horns) being primarily a dairy animal with several well-defined breeds, while the swamp type (long, swept-back horns) is used more for work and beef. The river type is native to the Indian subcontinent and spread westwards, reaching Egypt and Europe during the early Middle Ages (Clutton-Brock, 1999) while the swamp type is found throughout south-east Asia and is morphologically uniform throughout its range. They clearly diverged before domestication, which necessarily implies two domestication events, but there is not yet agreement on when this divergence happened (Flamand *et al.*, 2003).

Similar patterns can be found in other species. It is likely that there were three wild ancestors for sheep (Hiendleder *et al.*, 1998; Townsend, 2000). Current thinking is that each of these ancestors was a different lineage of the Asiatic mouflon *Ovis gmelini*. Pigs were clearly domesticated independently in western Asia and in China (Watanabe *et al.*, 1986; Huang *et al.*, 1999; Giuffra *et al.*, 2000; Kijas & Andersson, 2001). Goat mtDNA reveals a similar pattern, with three lineages implying separate domestication in west Asia and in eastern and southern Asia (Luikart *et al.*, 2001). Intercontinental transport has been important for goats and there has been such widespread mixing of lineages that today only about 10% of mtDNA can be ascribed to one continent or another; in cattle the proportion is 50% (MacHugh & Bradley, 2001).

Horses seem to have been domesticated in many different places in the grasslands of Asia (Vilà *et al.*, 2001; Jansen *et al.*, 2002). In contrast, the chicken seems to have been the result of only one domestication event (of a single subspecies of the red jungle fowl) which probably took place in Thailand (Fumihito *et al.*, 1994). There are two mtDNA lineages in rabbits, type A which is only found in wild rabbits in southern Spain, and type B which is found elsewhere in Spain and in all husbanded rabbits (Monnerot *et al.*, 1994). The two types probably diverged two million years ago. Goose breeds are derived from two species, the greylag *Anser anser* and the Chinese or swan goose *A. cygnoides*. Homologous chromosomes show

differences between these lineages and some breeds show heterozygosity in this respect (Romanov, 1999).

Changes in animals following domestication

Foxes *Vulpes vulpes* and *Alopex lagopus* have been kept on fur farms on a large scale since about 1950. They have been selected for behavioural adaptations to husbandry, one of the main ones being a generalized reduction of fear responses (Nimon & Broom, 2001). Behavioural development in individual mammals and birds, in the vast majority of cases, depends upon interactions with others. This dependence on learning means that humans can act as adoptive parents, and this is the basis for the taming of young animals. Probably, any young mammal or bird can be tamed, but on reaching adulthood a tamed individual of a non-domesticated species will be much less predictable behaviourally than a tamed adult of a domesticated species (Lickliter, 1991; Clutton-Brock, 1999).

Populations of animals often become genetically adapted to captivity (especially in zoos) and the extent of this is measured by their reproductive fitness (Frankham *et al.*, 2002). What is not clear is how the tamed state of the individual evolved into the domesticated state of the population. In a comprehensive review, Price (2002) defines domestication as ‘that process by which a population of animals becomes adapted to man and to the captive environment by some combination of genetic changes occurring over generations and environmentally induced developmental events recurring during each generation.’ Clearly, a definition must accommodate cultural, genetic and experiential aspects and avoid merely stating that phenotype reflects the action of genotype and environment. One mechanism might be that, in domesticated animals, genes conferring ‘tameability’ have become fixed, but many other speculations are possible.

Skeletal changes

After domestication animals generally became smaller than their wild progenitors and this is one of the main archaeological criteria of domestication (Clutton-Brock, 1999; Davis, 1987). Size reduction was not paralleled by size changes in contemporary wild species like gazelles, implying it was not an effect of a harsher climate (Davis, 1987, Chapter 6). Circumstantial evidence suggests that small size would be advantageous under domestication and thus would be selected for. Smaller animals may have been easier to manage, would reach puberty sooner, and larger flocks and herds could be kept. Allometry of bite size and body weight (Illius & Gordon, 1987) – the different body measurements do not necessarily change in the same proportion as body mass – means that smaller grazing animals are more efficient grazers than larger ones, and this could have enabled them to cope with the lack of night-time grazing that probably accompanied domestication. Corralling animals at night is a standard way of manuring cropland and of facilitating collection of dung, and it also protects livestock from thieves and predators.

This size reduction was not permanent because throughout history body sizes have increased again (Figure 1.3).

What could be the genetic basis for this process? Body size is influenced by large numbers of genes, each having a small effect (Hastings, 1996), and in livestock, heritabilities for adult body weight are moderate to high (Falconer & Mackay, 1996). By this it is meant that a large proportion of the variation in adult body weight has a genetic cause. When populations are small and immigration is restricted, variation in the genes for body size can become depleted (for example in the Soay sheep of St. Kilda, Scotland, where heritability of body weight is only 0.06; Milner *et al.*, 1999) and body weight would then be very dependent on the environment. The archaeological evidence of increasing body weight presumably reflects improved husbandry and, probably, the restoration of genetic variation due to crossbreeding among different, previously isolated stocks.

Body conformation has changed under domestication. The wild ancestors of cattle, sheep, pigs and goats would have displayed and fought using the power of their forequarters, and indeed their conformation suggests this. Farmed livestock also fight in this way (Jensen, 2002) but, under domestication, artificial selection has taken over

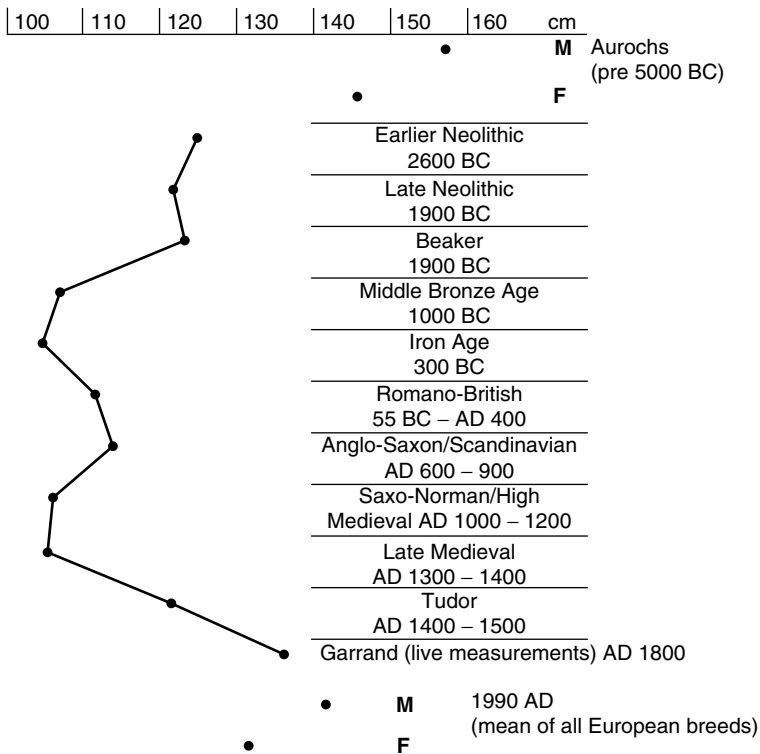


Figure 1.3 Mean withers heights (height at the shoulder) in British cattle, from several sources (Armistage, 1982; Grigson, 1982; Hall & Clutton-Brock, 1988; Simon & Buchenauer, 1993). The domesticated cattle introduced in Neolithic times are much shorter than the aurochs; heights increased during Roman times (probably reflecting evolution under better husbandry conditions), and again after the Middle Ages.

and has placed more emphasis on the hind quarters where the more palatable meat is located and where the growth constraints on muscle masses are less than on the shoulders (Figure 1.4).

Under domestication the mammalian skull shows marked changes in conformation, with the shortening of the jaws and facial region being very common, and resulting from a human preference for a flatter, more baby-like face (Clutton-Brock, 1999). It is striking how the teddy bear has also evolved in this way; people prefer them to have more baby-like features and there has been evolution of the teddy bear away from the original, more natural-featured phenotype (Hinde & Barden, 1985; Morris *et al.*, 1995). Skeletal tissue is known to be very plastic in response to subtle environmental changes. When pigs were run on treadmills, their leg bones became stronger and thicker, and so did their skulls (possibly as a result of changes in growth hormone concentrations; Gura, 2000). While there must be a genetic basis to the change of skull conformation under domestication, this has not been studied experimentally.

Many studies (Price, 2002) have suggested that captivity and domestication lead to the brain case becoming smaller, presumably reflecting adaptation to the captive environment. In 120 years of domestication the brain of mink has diminished by 20% from its original volume. The brains of the pig and the dog are said to be only 60% of their pre-domestication volume. Przewalski's horses in zoos have brains 14% smaller

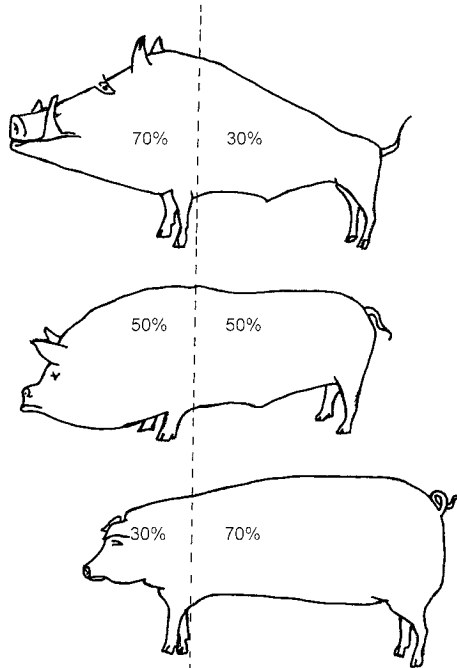


Figure 1.4 Pig conformation. In this caricature of pig conformation the distribution of body mass in the wild boar is contrasted with that in the old-fashioned pig, and in the modern meat pig (after Davidson & Coey, 1966). (Reproduced with permission from Asociación Argentina Productores de Porcinos.)

than those in the wild. However, Appleby (1999) says that if brain sizes of domestic pigs and wild boar are compared at the same age rather than at the same body weight, there is no difference. There is a need for a critical review of the effects of domestication on brain volume and skull shape, corrected for age and environmental effects.

Fat

Patterns of fat deposition may have changed as a result of domestication. Reduced predation pressure might encourage fat and this is clearly seen in birds (Gosler *et al.*, 1995), but demonstrations in mammals are lacking. With animals being prevented from migrating or seeking food elsewhere, under domestication there might have been selection for fat deposition as an aid to survival. Indeed, Ørskov (1998) suggested that in harsh environments it might be a better strategy to let ruminants store energy as fat on the body rather than for farmers to conserve feed to give to their animals later.

In western livestock breeds that have been selected for meat production, the fat is deposited either on or within the muscle, making the meat more palatable. In contrast, unimproved breeds or those which have been selected for maternal qualities rather than for meat production tend to store fat in internal depots, such as around the kidneys (Kempster, 1980; Mendizabal *et al.*, 1999). Fat-tailed and fat-rumped sheep have been selected to have exaggerated fat deposits (Figures 1.5, 1.6).

Meat with a higher fat content is better suited to cooking over an open fire than lean meat and Kyle (1987) speculated that one reason why deer were not fully



Figure 1.5 Sabi sheep. Ram of the Sabi fat-tailed sheep breed, in north-east Zimbabwe, 1997.



Figure 1.6 Sabi sheep. The circumference of the animal's tail was 24 cm at the base.

domesticated was because of the difficulty of producing palatable meat. Red deer only become fat when they are relatively old – while a well-grown stag may be 23% fat, at half the mature body weight young male deer are only 10% fat. At this stage of growth, lambs are 40% fat (Kay *et al.*, 1984) and horses are 13% fat (Robelin, 1986). Goats are lean and the fattest carcasses usually encountered are around 14% but the record (in the Katjang goat of Malaysia and Indonesia) is 25% (Devendra & Burns, 1983). Sheep can be 45% fat as adults (Butler-Hogg, 1984) while British cattle are around 20% fat (Butler-Hogg & Wood, 1982). A 9 kg force-fed goose can be up to 16% body fat, or 28% if the liver is included (Romanov, 1999).

Muscle

Meat comprises muscle fibres and connective tissue. In cattle, taurine breeds have been found to have tougher connective tissue and zebu breeds have tougher muscle fibres. The overall result is that meat from the latter is tougher (Gazzola *et al.*, 1999); another factor is that post-slaughter tenderization is biochemically inhibited in zebu (Warriss, 2000, p.104). This could reflect a basic physiological difference between the two ancestral stocks, or possibly a longer history of selection for meat tenderness in taurine breeds.

Muscle fibres are of two main types; red (Type 1, or slow-twitch oxidative, with aerobic metabolism) and white (Type 2a fast-twitch oxidative glycolytic and Type 2b fast-twitch, mainly with anaerobic glycolytic metabolism). White fibres do not need such an extensive capillary supply as red, and they might therefore be expected to proliferate when increased muscular bulk is selected. In pigs this is indeed the case, with domestic breeds having a higher percentage of white fibres than wild boar in the longissimus dorsi muscle (Weiler *et al.*, 1995). There is also plasticity, with exercise

leading to an increase in size of Type 1 fibres, though with excess growth hormone present giant Type 1 fibres are found, which indicates a degenerative condition.

Fatness and musculature are influenced by growth hormone concentration. Lean meat percentage is higher and backfat thickness lower in pigs with higher basal GH concentration, and domesticated pigs generally have higher basal GH than wild boar. The implication is that under heavy selection for muscular hypertrophy, metabolic imbalances and pathological conditions will become expressed in skeletal muscle. There are several different alleles of the gene coding for GH in pigs, as in other mammals, leading to differences in plasma GH concentrations. Knorr *et al.* (1997) made crosses between European wild boar and Piétrain, and between Meishan and Piétrain (the Meishan is a Chinese breed with the advantage of high prolificacy but also some disadvantages, including excess fat). GH variant was not related to fatness in the former, but it was in the latter cross. This implies the alleles in Meishan differ from those in Piétrain, while those in the wild boar and Piétrain are the same, and this is consistent with the separate domestication of Chinese pigs mentioned on page 8. Japanese Black cattle yield more tender beef than Holsteins; there is more intramuscular fat in the former reflecting a lower amplitude of GH secretory pulses, and a lower proportion of GH secreting cells in the adenohypophysis (Matsuzaki *et al.*, 2001).

Organ size

Effects of domestication upon organ size are very obvious in pigs. For example, the heart of the German Landrace is 0.29% of body weight, while that of the wild boar is 0.63%. The porcine heart has a poorer tolerance of exertion than that of other species and a high proportion of premature deaths of pigs is due to heart failure (Thielscher, 1987). The ability of pigs to go feral (see Chapter 6) implies that they have not, however, lost cardiac capacity irreversibly.

Lundstrom (1995) made crosses between Large White pigs and wild boar and found the best way to distinguish animals with different degrees of wild boar ancestry was by measuring the length of the small intestine. For animals with mainly wild boar ancestry this was about 16 m (about 2 m less than that of predominantly Large White pigs) and this lower length was associated with reduced growth rate and increased fat deposition.

Behaviour

Behavioural characteristics predisposed certain species to domestication (Clutton-Brock, 1999). On domestication the environment and social structure of animals changed dramatically and with it the opportunity or necessity of performing much of the behavioural repertoire (Jensen, 2002). Behaviours characteristic of the juvenile state continue to be expressed into adulthood, and this is especially obvious in dogs. There are many examples of behaviours that are important in the wild continuing to be expressed in captivity. Mason *et al.* (2001) have shown that in spite of having been 'bred in captivity for 70 generations', usually without access to water for swimming, mink show a stress response (elevated circulating cortisol) when deprived of the

opportunity to swim, and that the animals will ‘work’ (by opening a weighted door) to gain access to a water pool. Indeed, there is only one documented example of a behaviour ceasing to be expressed under domestication (Desforges & Wood-Gush, 1976): wild mallard ducks form pairs and develop territories while under the same conditions domesticated ducks do not. But there are many quantitative differences between wild and domesticated genotypes. Gustafsson *et al.* (1999) found that sows with a wild boar sire showed the same frequency and pattern of nest building behaviour as domestic sows but there were quantitative differences in maternal behaviour.

Behavioural strategies that are less energetically costly may have been favoured under domestication. Andersson *et al.* (2001) found that bantam chickens (domestic birds) used a less costly feeding strategy than their crosses with jungle fowl (wild type). The latter moved more between two separate patches of food, without eating more. Schuurman *et al.* (1999) report similar results from comparing Landrace and Landrace x wild boar pigs.

Domesticated salmon perform less nest building than wild salmon (Fleming *et al.*, 1996) and also differ in their behavioural responses to different environments (Fleming & Einum, 1997). Farmed fish were less cautious in their behaviour and were more aggressive in a tank while the wild type were more aggressive in running water.

Anti-predator behaviours, clearly vital in the wild, can continue to be important in the domesticated state. In Colorado, guard dogs kept with sheep flocks reduce predation by black bears and mountain lions. They also reduce predation by coyotes upon lambs but have no effect on predation upon ewes (Andelt & Hopper, 2000). This implies that ewes have an ability to defend themselves against coyotes, but not against the other two predators. In Norway, sheep breeds differ in susceptibility to predation by wolverines (Landa *et al.*, 1999) while as in Colorado they are defenceless against bears.

Intriguingly, heavily parasitized sheep behave in a less timid way than uninfected sheep (Fell, 1991). Studying the interaction of cattle and wildlife in the context of transmission of tuberculosis, Sauter and Morris (1995) found a possible relationship between social dominance, positive response to the tuberculin test, and likelihood of ‘investigating a sedated possum’. In general mammals carrying heavy parasite loads are more likely to be predated (Watve & Sukumar, 1995). Thus, under domestication, one of the selective forces favouring parasite resistance (differential predation) will be less effective than it was in the wild.

There exists genetic variation in various traits that are relevant to the domesticated state, for example taming, socialization to humans, and positive response to handling show much variation in lambs (Markowitz *et al.*, 1998).

Genetic processes under domestication: the origin of heritable variation

There are two ways of studying genetics. In the quantitative approach, no knowledge is assumed of the individual genes that influence a quantitative trait. The aim is to

provide information and predictions which will enable the animals of highest breeding value to be identified and used (i.e. the ones which are most superior to the population mean for the character(s) under selection). Quantitative genetics is at the basis of conventional animal breeding, for which it was developed and in which it has been highly successful.

The other approach is essentially one of molecular physiology, and interest is focused on the regulation of gene expression and on the chain of molecular events by which the phenotype is encoded. Examples include pig coat colours (see Chapter 7). The breeding of animals for performance characters has not yet benefited greatly from the molecular approach, but with the development of modern genomics the two approaches are likely to converge (Goddard, 2003).

Incorporated genetic material and mutations

New genetic variation arises from mutation and there are several reasons why mutation rates might be higher under domestication.

Environmental mutagens

Human populations characterized as ‘tropical zone/tribal/non-industrialized’ have higher mutation rates than ‘temperate zone/civilized/industrialized’ populations (Neel & Rothman, 1981). This has been suggested to be due to diet-related mutagens (prevalent when food is kept and cooked under poor conditions) and to certain diseases. Domesticated animals might be more exposed to such mutagens than wild animals because they are likely to be given food that has been stored or processed in some way.

Exposure to disease

The genome of some viruses (the retroviruses) consists entirely of RNA and they propagate themselves by transcribing the RNA into DNA that then acts as a template for synthesis of RNA (Nicholas, 1996a). This DNA template can become incorporated into the host genome and have a phenotypic effect. There are many examples in pigs (Chapter 3) and in other species. One might hypothesize that domesticated species have more genetic material of retroviral origin than wild species because of greater exposure to viral pathogens. There is no evidence of incorporation of bacterial genomes in vertebrates (Stanhope *et al.*, 2001).

Stressors

Domesticated animals can be regarded as pre-adapted (or not pre-adapted) to varying degrees to specific aspects of life with humans (Fraser *et al.*, 1997). An incompleteness of pre-adaptation leads to stress. Kohane & Parsons (1988) describe how mutation and recombination are more prevalent when animals are under stress, such as is the case in domestication. Parsons (1990) discussed the possible interaction

between environmental stress development and the genotype. This transmission is termed *epigenetic inheritance*. Under domestication unusual phenotypes arising in this way would be less liable to natural selection and a genetic background favouring their appearance would not be so strongly selected against as in the wild. Various molecular mechanisms could be possible, for example phenotypic variation among genetically identical individuals may be at least partly due to methylation of cytosine and to remodelling of chromatin, leading to alterations in gene expression (Rakyan *et al.*, 2001). Conventionally, these alterations have been believed not to be heritable but there have been many studies, often using experimental populations of *Drosophila*, which show that environmentally induced phenotypes can be transmitted to progeny.

Heterozygosity

In the context of a discussion on the evolutionary rate of microsatellites, Amos (1999) describes how microsatellites may have greater mutability when in the heterozygous state. Microsatellites consist of repeated sequences of DNA nucleotides of no obvious function; microsatellite alleles differ in the number of repeats and, therefore, in length. During meiosis the homologous chromosomes pair and heterozygous sites can undergo a repair process – parents whose microsatellite alleles differ considerably in length are more likely to produce offspring which carry mutants. This would create a positive feedback, with further heterozygosity being generated by these mutants, itself producing further mutation. In the case of microsatellites gains in length are more commonly found than reductions, and increased mutation rates would be expected to lead to longer microsatellite alleles.

There are some interesting species differences, with microsatellite alleles in sheep being more diverse (Byrne *et al.*, cited by Bruford, 2004) and longer than their homologues in cattle (Crawford *et al.*, 1998). Amos (1999) suggests heterozygotes would generally be more common in large populations. Microsatellite alleles are larger, with higher allele-size variances and with more genetic variation, in domestic sheep than in Rocky Mountain bighorn sheep (Forbes *et al.*, 1995) and populations of the latter are likely to be smaller than those of most breeds. Such a process need not be restricted to microsatellites. Amos (1999) also refers to hybridzymes, which are novel proteins arising in hybrid zones from alleles that are not found in either parental population. There are examples of this in small rodents (Sage *et al.*, 1993) but it remains to be seen if the population structure of livestock species is conducive to hybridzyme evolution.

Chromosomal characteristics

Chromosome number can vary within wild and domestic species. Acrocentric chromosomes (in which the centromere is at the end of the chromosome) can fuse to form a single metacentric chromosome (i.e. one in which the centromere is internal; Nicholas, 1987). In sheep there are some translocations associated with particular breeds and some Portuguese breeds of cattle effectively have $2n = 58$