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Animal Domestication: A Brief Overview

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Abstract

In the origin of modern humans, hunting of wild animals and gathering of wild plants in nature were the primary subsistence strategies. Yet, about 12,000 years ago, the domestication of plants and animals began. The two main goals of the present chapter are to briefly describe (i) how wild animals were domesticated and (ii) what are the main biological consequences for the major farmed species (cattle, pig, sheep, goat, and horse). During about 98% of their domestication history, domestic animals have been managed in a sustainable way by farmers, followed by a period of strong selection about 200 years ago to produce hundreds of well-defined breeds. A few decades ago, the selection pressures have further increased, leading to a few industrial breeds, which were introduced in numerous countries, most often at the expense of local breeds. Within a few decades, we thus might lose most of the highly valuable farm animal genetic resources that humans have gradually selected over the past millennia. Consequently, priorities should be given to preserve the genetic resources in marginal or rare breeds, and selection programs should aim at restoring the genetic diversity in industrial breeds.

Keywords: domestication, domesticated animals, genetics, industrial breed, local breed

1. Introduction

Since the origin of modern humans, *Homo sapiens*, about 200,000 years ago, hunting of wild animals and gathering of wild plants in nature were the primary subsistence strategies [1]. Yet, about 12,000 years ago, at the end of the most recent ice age and during the transition to the present interglacial period, domestication of plants and animals began [1–5]. This phenomenon occurred in at most nine areas of the world: the Fertile Crescent, China, Mesoamerica, Andes/Amazonia, Eastern United States, Sahel, tropical West Africa, Ethiopia, and New Guinea [4]. From these handful homelands of agriculture, a restricted number of domesticated species were progressively introduced across the globe as farmers migrate to new regions [4].

This is because the control of food production conferred to farmers huge demographic, technological, political, and military advantages over neighboring hunter-gatherers, allowing them to impose their lifestyle [4]. The history of the past millennia consists of tales of hunter-gatherer societies becoming driven out, infected, conquered, or exterminated by farming societies in all areas across the world suitable for farming [3, 4].

The domestication of plants and animals was part of a major transformation in the way of life of an increasing number of human societies, with deep social and spiritual changes, called the Neolithic transition [5, 6]. This also enabled a strong increase of the human population from about 1 million during the millennia before the advent of agriculture [7] to more than 7 billion today [8]. The increase of human population is spectacular during the past decades (**Figure 1**), with an additional 4 billion people since 1960 [8].

In 2010, the world agricultural production reaches more than 7.6 billion tons [7], representing a three-fold increase compared to 1961 (**Figure 2**). Globally, less than two-thirds of crop production (on a mass basis) are allocated to human food, versus 35% to animal feed, and 3% for bioenergy or other industrial products [9]. It is, however, important to highlight that global food production relied *in fine* on a tiny fraction of wild species domesticated in the past millennia, representing about 0.08% of known land plant species and 0.0002% of known land animal species [10]. Only about 15 plant species and less than 10 animal species supply more than 90% of worldwide agriculture production [11]. Four crops (wheat, rice, corn, and potato) account for more food production than all other crops combined [11]. Inversely, hunting and gathering have today become secondary (and most often recreational) activities that contribute little to global food security [12], one significant exception being the consumption of wild meat in a few regions, notably in Central Africa [13]. This implies that even though humans consumed diverse food products across the globe; they mostly come from the same domesticated plant and animal species. In the past decades, the standardization of food products has also strongly increased with the spread of few multinational food companies, such as McDonald's or Subway.

The other main consequences of domestication are that the bulk of global agriculture is today based on the culture or farming of a few alien domesticated species that had been

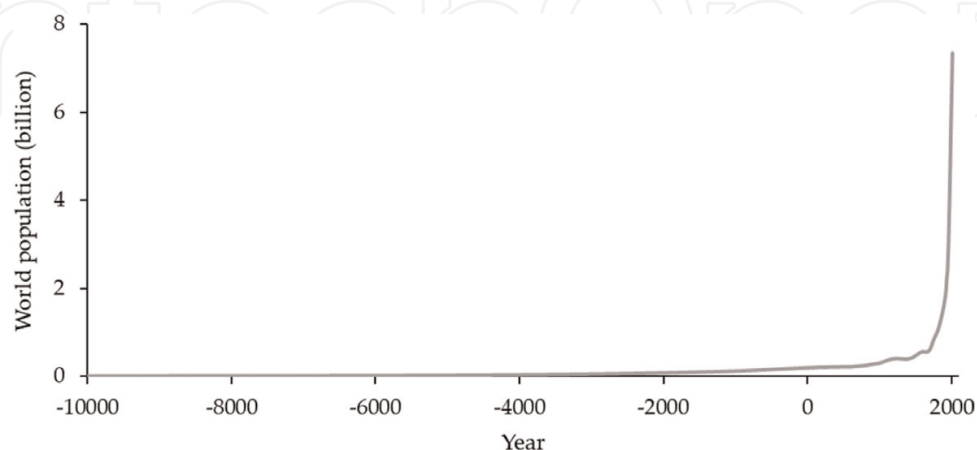


Figure 1. World population growth over time (modified from [8]).

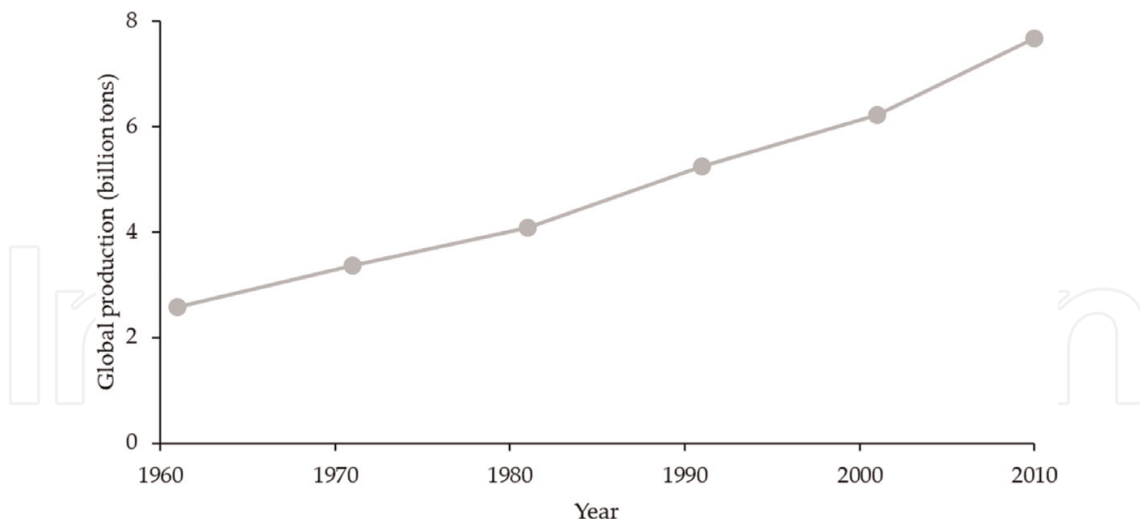


Figure 2. Global agricultural production, 1961–2010 (modified from [7]).

progressively introduced in all continents. This has contributed to widespread faunal and floral homogenization [14]. Nevertheless, because alien species are present for a very long period, they are generally not perceived as exogenous or introduced [15], but rather as part of the natural landscape [16–18]. This phenomenon has been described as the shifting baseline syndrome [19]. Agriculture is today responsible for the destruction or modification of nearly 40% of the land surface [20]. For instance, about 7 to 11 million km² of forest have been lost in the past 300 years due to land-use activities, primarily for agricultural expansion and timber extraction [20]. Besides, intensification of agriculture has also resulted in the degradation of water quality in numerous freshwater and coastal ecosystems due to the global use of fertilizers, pesticides, and antibiotics [9, 20]. Modern agriculture is thus generally considered to be the primary destructive force of biodiversity [17], which has led to the sixth mass extinction [21]. Some scientists even consider that truly wild nature (pristine zones from human impacts) does no longer exist on Earth [22]. In 2002, Crutzen [23] proposed to assign the term “Anthropocene” to the present geological epoch, supplementing the Holocene, once humans have become an important geochemical force and perhaps the dominant ecological force on the planet. The Anthropocene era could be said to have started in the late eighteenth century [23]. In conclusion, domestication corresponds to a pivotal change in the history not only of humanity but also of the biosphere [5, 6].

The two main goals of the present chapter are to briefly describe (i) how wild animals were domesticated and (ii) what are the main biological consequences for the major farmed species.

2. How were animals domesticated?

Domestication is a long and endless process by which animals become adapted to both humans and captive conditions ([24–26]; for an overview of definitions of domestication, see

[27]). Three main pathways of domestication have been proposed for land animals: a commensal pathway, a prey pathway, and a directed pathway [6, 28–30]. In the commensal pathway, the animals themselves played the largest role [29]. The animals first move into an anthropogenic habitat, most likely spurred by an attraction to human waste, and later develop a two-way partnership with humans [29]. Several domesticated species have followed this path, among which are dog (*Canis familiaris*), cat (*Felis catus*), or chicken (*Gallus domesticus*) [29]. In the prey pathway, humans have initiated domestication, perhaps as a response to depletion of local stocks of prey animals that humans had hunted for thousands of years [31], to enhance the yield or predictability of a resource (meat or hides) [29]. Over time and under certain circumstances, these game management strategies developed into actual herd management and, eventually, the controlled breeding of managed animals [28]. The main species that followed this pathway are sheep (*Ovis aries*), goat (*Capra hircus*), or cattle (*Bos taurus*) [29]. In the direct pathway, humans deliberately set out to domesticate a species [28, 31]. This pathway skips the early phases of habituation and management and starts with the capture of wild animals with the deliberate intention of controlling their reproduction [29]. This pathway occurred more rapidly and was accompanied by a dramatic bottleneck [29]. The main species are horse (*Equus caballus*), donkey (*Equus asinus*), and dromedary (*Camelus dromedarius*) [28].

Species that followed either commensal or prey pathways tend to possess more traits that make them appropriate candidates for domestication. Conversely, species on directed pathways likely possess barriers to domestication that require more knowledge on the part of humans to overcome [28, 31].

Whatever the pathway followed, captive animals began to be domesticated at some point. Yet, as for domestication, there is no consensus today about what a domesticated species is (see [27] for a review of the main definitions). Nevertheless, most authors considered that a domesticated species is a group of animals reproduced in captivity and modified from their wild congeners [27]. Yet, wild and domesticated animals should not be considered as complementaries (such as true/false, dead/alive) but rather as antonyms (such as long/short, fast/slow) because they represent the extremes of a process and not a simple dichotomy [32]. In other words, there is not a clear biological separation between wild and domesticated animals [33]. In addition, a domesticated animal is neither in a final nor a static status, and thus farmed species are still evolving today, particularly in response to changes in technology and husbandry practices, which themselves are evolving and constantly improving [34]. Conversely, domesticated species can sometimes return to nature, a process known as feralization [35].

3. How have animals evolved during domestication?

During domestication, five main genetic processes were involved [15, 28, 34], including inbreeding and genetic drift (two uncontrolled processes), natural selection in captivity and relaxation of natural selection (two partially controlled processes), and active selection (one controlled process) [34, 35]. The two uncontrolled processes are due to the limited size of the population (known as inbreeding) and the random changes in gene frequencies (genetic drift).

The two partially controlled processes are natural selection in captivity that accounts for selection imposed on captive populations that cannot be attributed to active (or artificial) selection and relaxation of natural selection expectably accompanying the transition from wild to captive environments [35]. At last, the fifth genetic process is controlled, known as active selection, because changes are directional [34, 35].

Domesticated animals have been profoundly modified during domestication. Indeed, the variation range of certain traits within a domesticated species occasionally exceeds that in whole families or even orders [36, 37]. Modifications resulting from domestication concern morphoanatomy, physiology, behavior, and genetics [31, 35, 38–40]. Behavior is probably the first to have been modified during domestication [35]. Nevertheless, behavioral traits neither appeared nor disappeared during domestication but rather are the response thresholds that changed [34, 35]. One of the most remarkable behavioral changes shared by all domesticates is their tolerance of proximity to (or complete lack of fear of) people [31, 37, 39]. Besides, because humans provide shelter, food, and protection against predators, domesticated animals most often express a lower incidence of antipredator behaviors and show lower motivation for foraging [34]. More generally, mood, emotion, agnostic and affiliative behavior, as well as social communication all have been modified in some way by domestication [39]. Most domesticated animals are also more precocious than their wild counterparts [34]. The activity of their reproductive system became enhanced and relatively uncoupled from the environmental photoperiod, and they all acquired the capacity to reproduce in any season and more often than once a year [37]. At last, the most spectacular and obvious changes concern morphology, among which are the animal size (dwarfs and giants), proportions (fewer vertebrae, shorter tails), color, length and texture of coat, wavy or curly hair, rolled tails, and floppy ears or other manifestations of neoteny (the retention of juvenile features into sexual maturity) [37, 39]. In most domesticated species, head or brain size has decreased [34]. The most illustrative example of such considerable changes is the morphological variations in dogs [37]. These morphological changes (“domestication syndrome”) may all be linked to strong selection for lowered reactivity to external stimuli [31]. At the beginning of the twentieth century, modern breeding programs were initiated, leading to dramatic changes in productivity, e.g., increase laying rate for laying hens or improved feed conservation ratio, meat yield, and growth rate in broiler chickens [41].

4. A brief history of the major domesticated animals

Even though the decision to consider farmed or captive animals as domesticated is subjective and arbitrary [35, 41], most authors agree that about 40 species around the world that directly or indirectly contribute to agriculture are domesticated; this number varies between 20 and 50 following the definitions used for a domesticated animal [36, 42–44]. Several of those domesticated species have a distinct scientific name than their wild ancestors [25].

The 14 most important domesticated mammal species are indicated in **Table 1**, among which the domestication of the “big five” (cattle, pig, sheep, goat, and horse) [3, 4] are further

Common name	Scientific names	Partial list of potential wild progenitors (in bold the main one)	Approximate date of domestication: BP	Number of breeds	Pathway to domestication
Sheep	<i>Ovis aries</i>	<i>O. orientalis</i> , <i>O. musimon</i>	9000	850	Prey pathway
Goat	<i>Capra hircus</i>	<i>C. aegagrus</i> , <i>C. falconeri</i>	9000	320	Prey pathway
Cow, cattle	<i>Bos taurus</i> and <i>B. indicus</i>	<i>B. primigenius</i> , <i>B. namadicus</i>	8000	815	Prey pathway
Pig	<i>Sus domesticus</i>	<i>S. scrofa</i> , <i>S. celebensis</i> , <i>S. barbatus</i>	8000	350	Commensal pathway
Horse	<i>Equus caballus</i>	<i>E. ferus</i> , <i>E. przewalski</i>	6000	350	Directed pathway
Dromedary	<i>Camelus dromedarius</i>	<i>C. dromedarius</i>	4500	50	Directed pathway
Bactrian camel	<i>Camelus bactrianus</i>	<i>C. ferus</i> , <i>C. bactrianus</i>	4500	6	Directed pathway
Llama and alpaca	<i>Lama glama</i> and <i>L. pacos</i>	<i>L. guanicoe</i> and <i>V. vicugna</i> (?)	6000	2 + 2	Prey pathway
Donkey or ass	<i>Equus asinus</i>	<i>E. africanus</i>	6000	70	Directed pathway
Reindeer	<i>Rangifer tarandus</i>	<i>R. tarandus</i>			
Water buffalo	<i>Bubalus bubalis</i>	<i>B. bubalis</i>	6000	70	Prey pathway
Yak	<i>Bos grunniens</i>	<i>B. grunniens</i>	4500		Prey pathway
Bali cattle	<i>Bos javanicus</i>	<i>B. javanicus</i>			Prey pathway (?)
Mithan	<i>Bos frontalis</i>	<i>B. frontalis</i>			Prey pathway (?)

BP, before present. If no information was found, cells were left empty. Note that the number of breeds per species varies between authors.

Table 1. List of the world’s 14 valuable big domestic mammals, including the major 5 (in bold) followed by the minor 9 [3, 4, 25, 28, 42, 44].

described below. For the five most valuable species, the domestication resulted in the creation of hundreds of breeds, particularly in the past centuries [42, 45, 46]. In France, the article D.653.9 of the rural code defines breed for ruminant species as “a group of animals that share sufficient common features to be considered homogeneous by one or several groups of breeders that agree on the broodstock renewal and induced changes, including the international level” [47]. Breeds have therefore both a biological sense (common features) and a social acceptance (group of breeders); the relative importance of the latter increased in the past years, for scientists as well as in the application of policies [47].

4.1. Cattle

The wild ancestor of cattle is a group of races of the now extinct aurochs *Bos primigenius* [48–50]. The aurochs, the last specimen of which died in a Polish park in 1627, had a very wide geographic distribution, which extended from East Asia to Europe and North Africa [42, 48, 50].

Traditionally, two major types of domestic cattle are considered: zebu (*Bos indicus*) which have a prominent thoracic hump and taurine (*Bos taurus*), which do not [40, 42, 49, 50]. However, these two species fully interbreed, and a meta-analysis of different microsatellite datasets revealed taurine-zebu admixture over Europe, southwest Asia, and Africa [40, 45, 49, 50]. Molecular evidence suggest that these two species came from two independent domestication events: zebu cattle were domesticated in the Indus valley region ca. 8000–7500 B.P., whereas taurine cattle were domesticated in Anatolia 10,500–10,000 B.P. [40, 42, 50–52]. However, Larson and Burger [29] recently suggested that only the latter was domesticated, while zebu may have resulted from the introgression of wild zebu populations into taurine cattle that were transported eastward. During several millennia, extensive gene flow among different groups of domestic cattle, as well as with aurochs until its extinction, was possible, leading to relatively high effective population sizes and preventing genetic drift at the regional scale [40, 48, 50, 51]. This might partly explain the relatively large cattle gene pool despite a likely bottleneck at the time of domestication [50]. Besides, it is also possible that other species were crossed with cattle in some areas of the world, including the yak (*Bos grunniens*) in Nepal or banteng (*Bos javanicus*) in Southeast Asia and Indonesia, which also contribute to maintain or increase genetic variability [40]. The large size of cattle and its low growth, as well as the early use for milk or traction, imply relatively low levels of directed selection during millennia [51]. However, this situation changed dramatically about 200 years ago with the emergence of breed concept [50]. The first cattle herd book was published in Britain in 1822 [49]. Since that time, stronger selection pressures have been applied to local populations followed by standardization of the desired conformation and performance, such as high milk yield for dairy cattle breeding programs [49]. This led to an isolation of breeds from each other (ca. 800 are now recognized; see **Table 2**), which could have caused a genetic drift and inbreeding and perhaps a fitness decrease [40, 46, 50]. Nevertheless, gene flow between neighboring regions did not completely stop, as deliberate upgrading was realized in order to increase production characteristics by using bulls of other populations from the same or a different country [45]. More recently, the number of males involved in reproduction schemes has drastically decreased with the expansion of artificial insemination, leading to another strong reduction of effective population size of breeds and inexorably to a genetic drift and loss of alleles [46, 50, 63]. For example, at the worldwide level, the Holstein cattle has an effective population size of about 50 [50]. This strong decrease of the effective population size might explain the strong reduction in fertility as well as the genetic diseases observed in this breed [50]. An even more extreme result was found in Japan, where the Japanese black cattle had an effective population size of 17.2 in between 1993 and 1997, despite a census size of 0.53 million reproductive cows [49]. Another extreme case of low genetic variability is a feral British breed, Chillingham cattle, for which 24 out of 25 microsatellite loci were found homozygous [46]. Inversely, numerous cattle breeds still have substantial nucleotide diversity, indicating a large ancestral effective population size [46]. In the past decades, a few of the most productive breeds were imported throughout the world at the expense of local, apparently less productive populations [45].

4.2. Pig

The wild ancestor of domestic pigs is boar *Sus scrofa* [42, 64]. Wild boars occurred throughout Eurasia and North Africa [42]. Multiple independent domestication events, mainly in Asia

Minor, Europe, and East Asia, have probably occurred, starting approximately 9000 years ago [40, 52, 64–66]; the earliest remains of domesticated pigs have been excavated at Çayönü in Southeast Anatolia [65]. Chinese breeds originated in East Asia, whereas European breeds are believed to have originated in Southwest Asia [42, 67]. These domestication events were separated not only by thousands of kilometers but also by thousands of years [65]. During millennia, it is likely that out-crossing of domestic pigs with wild boar was common in traditional pig husbandry across Europe [52, 67]. By the late middle ages, European and Asian domestic pigs were genetically very different because they were based on wild boar populations that diverged around 1 million years ago, and for thousands of years, they were submitted to selection pressures on very different traits [64, 68]. By the late eighteenth to early nineteenth century, strict organized breeding was adopted to improve and develop livestock breeds, particularly in Britain, as a reaction to increasing demand for meat in the wake of the industrial revolution [64, 66]. European breeders turned also their attention to Asia and imported Chinese pigs to improve their breeding stock [40, 64–66]. From the eighteenth century, pig breeds were selectively bred for specific production traits such as early maturation, rapid growth, and increased prolificacy. In addition, the coat color phenotype (which includes both skin and hair pigmentation) was another morphological trait often used during the selective breeding process. Substantial changes (body size, color, body shape, skull morphology, ear carriage, behavior, prolificacy, teat number, and other traits) occurred in breeds over a short period of time, resulting in the development of numerous distinct pig breed phenotypes [64–66]. From the twentieth century, with the recognition of the benefits of genetic improvement and changing consumer preferences, certain pig breeds experienced further strong selection for lean meat content, muscularity, and enhanced reproduction [64, 66]. To date, there are likely over 730 pig breeds or lines globally of which two thirds are in China and Europe and over 270 are considered as endangered or critical. Currently, 58 pig breeds are recorded as “transboundary” (occurring in more than one country) including 25 regional transboundary breeds and 33 international transboundary breeds [65]. The worldwide distribution of pigs is dominated by five international transboundary pig breeds from the United States (USA) or Europe, i.e., Large white (117 countries), Duroc (93 countries), Landrace (91 countries), Hampshire (54 countries), and Pietrain (35 countries) [65].

4.3. Sheep

The wild ancestors of the domestic sheep are probably the mouflon (*Ovis musimon*) and the urial (*Ovis orientalis*) [42, 49, 50]. Both archaeological and genetic data spot the domestication center of sheep in eastern Anatolia and North-West Iran [50] between 8500 [49] and 12,000 years ago [40]. The sheep mitochondrial DNA polymorphism diversity and single-nucleotide polymorphism (SNP) diversity seem to support an absence of a genetic bottleneck, and thus domestication occurred from a broad genetic base [50, 69]. Sheep were first farmed for access to meat before human-mediated specialization for wool and milk commenced ca. 4000–5000 years ago [69]. It has recently been shown that particular regions of the genome contain strong evidence for accelerated change in response to artificial selection, such as the removal of horns, likely to be one of the oldest morphological modifications that accompanied domestication and a trait now common across many modern breeds [69]. Furthermore, other genomic

regions under selection in sheep contain genes controlling pigmentation, reproduction, and body size [69]. In the last few hundred years, the division of animals into breeds, followed by the identification of superior rams and their disproportionate genetic contribution via artificial insemination, has lifted the pace of genetic gain for production traits [69]. Extensive haplotype sharing and generally low divergence time between breeds reveal that frequent genetic exchange has occurred during the development of modern breeds [69]. Approximately 75% of modern sheep breeds have retained an effective population size in excess of 300 [69]. The number of breeds is comprised between 850 and 1409 [49]. Yet, many sheep breeds originally selected for good performance in a specific, sometimes isolated, geographical area (e.g., the Shetland, Soay, or Herdwick breeds) are now considered rare. With generalist-type sheep taking over the larger part of intensive sheep production, maintaining genetic diversity by conserving these traditional breeds has become a challenge [50, 70].

4.4. Goat

The wild ancestor of goat is the bezoar, *Capra aegagrus* [40, 42, 49]. The first archaeological evidence of goat domestication traces back in the Fertile Crescent about 10,000 years ago [42, 49, 71]. A large-scale analysis of current bezoar mitochondrial DNA (mtDNA) polymorphism over its whole geographic distribution suggested that the domestication process occurred over a very large area encompassing eastern Anatolia and North-West Iran [50]. Additional primary centers of goat domestication, including the Indus Valley, Southern Levant, and China, have not been convincingly demonstrated yet [71]. Analysis of the goat mitochondrial DNA polymorphism of the main haplogroup (representing more than 90% of the haplotypes) strongly supports the absence of bottleneck at the domestication time in goats [50]. Besides, goat mtDNA polymorphism also suggests high historical gene flow among continents, which already occurred during the Neolithic expansion into Europe [49]. The extraordinary adaptability and hardiness of goats favored their rapid spread over the Old World [71]. Goats have successfully adapted to desert, mountainous, and tropical areas where other livestock species would not thrive [71]. Between the fifteenth and eighteenth centuries, goats were transported to America and Oceania [71]. Over the course of domestication, several morphological traits were modified, such as horn and ear shapes, the presence of wattles, long hair, and coat colors, which were driven probably by intentional selection as well as by genetic drift, isolation, and founder effects [71]. Throughout the ages, goats have been raised for milk production and cheese, meat, and skin and fiber commodities such as leather, mohair wool, and cashmere hair [71]. Breeds also show strong differences in their physiological capacity of adaptation to extreme conditions of temperature and humidity and differ in feed efficiency, behavior, and resistance to infectious and parasitic diseases [71]. Today, Asia and Africa contain 58.2 and 36.2%, respectively, of the 1 billion goats worldwide with much smaller populations in Europe (1.7%), America (3.5%), and Oceania (0.4%) [71]. China (187.8 million heads), India (133 million heads), Nigeria (71 million heads), Pakistan (66.6 million heads), and Bangladesh (55.9 million heads) are the top five goat producers [71]. In most countries, the sustained growth of the world goat population during the last 50 years (from 368 million heads in 1964 to 1006 million heads in 2014) has not involved a general improvement of the production and reproduction techniques associated with their management. Well-organized selection programs are in contrast restricted to a few highly

productive dairy breeds from Europe, North America, and Australia [71]. Despite its low caprine census, Europe produces 17.5 and 42.5% of the goat milk and cheese, respectively, consumed around the world, reflecting the benefits of raising highly selected dairy breeds such as the Saanen, Alpine, and Toggenburg under semi-intensive or intensive conditions [71]. The main traits under selection are milk production, protein and fat contents, somatic cell count, and udder morphology [71]. Globally, it has been proposed that 500–600 goat breeds exist; yet it is difficult to establish a reliable figure because several local populations are not managed via phenotypic standardization, herd book registration, and controlled reproduction [71]. Among these breeds, 86 have spread beyond their countries of origin and are considered cosmopolitan or transboundary breeds, whereas 19 have become extinct, and about 90 are critically endangered or just endangered (such as Arapawa, Bagot, Golden Guernsey, San Clemente, and Mallorquina), whereas 157 are not at risk [71]. Population decline of local goat breeds is mostly due to their replacement or uncontrolled crossbreeding with more productive foreign varieties, the progressive abandonment of low income rural activities, and the lack of genetic conservation programs [50, 71]. Some goat populations have escaped from captivity and became feral [71].

4.5. Horse

The wild ancestor of domestic horse is the now extinct, *Equus ferus* from central Asia [52]. The Asian wild horse, *Equus przewalskii* [42], also significantly contributed to the genetic makeup of domestic horses [72]. Even though there have been no confirmed sightings of wild Przewalski's horses since 1966, the species has been maintained in captivity for the last 90 years [42]. In addition to Przewalski's horse, a third divergent lineage corresponding to a wild population that inhabited the Holarctic region has also contributed to the genome of modern domestic horses [72]. Both archaeological and genetic evidence strongly support the onset of domestication of horse in the western Eurasian Steppes of Ukraine dating to 5500 years ago [42, 72]. Over the course of domestication, it has been argued that difficulties in maintaining domestic horse herd sizes during pastoral migrations led directly to restocking through the capture of wild females [52, 72]. Horses were not only used as a source of meat and milk; their stamina and quickness provide humans with rapid transportation, which has considerably changed the speed and magnitude of the circulation of goods and people, as well as cultural exchange, including the spread of Indo-European languages, religions, science, and art, and diseases [72]. With the introduction of the horse collar and horseshoes in agriculture, the horse was increasingly used for tilling soils, incrementing farmland productivity in medieval Europe, and remains today a crucial asset to the agriculture of the least-developed countries [72]. With a few notable exceptions, such as the Arabian, Mongolian, and Icelandic horses, breeds (**Table 1**) have been created in the last two centuries [72]. The earliest horse studbook, that of the Thoroughbred racing horses, was created in 1791 [72]. The population structure resulting from selective breeding is characterized by high interbreed and low intrabreed genetic diversity [72]. Domestic horses exhibit remarkable variation in coat coloration, including the bay or bay-dun wild-type phenotypes, other basic colors like chestnut and black, as well as dilution (e.g., cream and silver), and spotting patterns (e.g., leopard complex, tobiano, and sabino) [72]. Horse locomotion has also been recurrently selected, including their ability to perform alternate gaits, such as four-beat, lateral, or diagonal ambling [72]. Although some

horse breeds, such as the Thoroughbred racing horses, are still extremely popular, a significant part of this great diversity is currently endangered: 87 horse breeds are already extinct, and among the remaining 905, almost a quarter are categorized as at risk [72].

5. Final considerations

Ever since Darwin, the study of domestication has puzzled scientists [39]. Hundreds of articles are published each year [33, 39], as well as books, among which some are listed in **Table 2**. Despite this interest, both the words “domestication” and “domestic animal” remain confusing and poorly defined [32]. For domestication, this is mainly due to the inherent difficulty in assigning static terms to a process involving long-term and continuous change [32]. For “domestic animal,” this is because this sort of dichotomous perspective wild/domestic is false and obscures the existence of transitional forms [32, 36, 73–75]. This is why the concept of “domestication level” was proposed for fish to describe more accurately the diversity of production methods as a continuum [52], from fishing up to the rearing of genetically improved animals [24, 25, 41, 76, 77]. This concept could be applied to other animals [26, 27] and may help describing the evolution of farmed species through both space and time in the future [36, 73].

Traditionally, the process of domestication was assumed to be initiated by humans, involving strong bottlenecks in the domestic population (corresponding to founder events due to the

Authors or editors	Date	Title	Ref.
Darwin CR	1859	On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life	[53]
Darwin CR	1868	The Variation of Animals and Plants under Domestication	[54]
Clutton-Brock J	1987	The Natural History of Domesticated Mammals	[55]
Digard JP	1990	L’homme et les animaux domestiques: Anthropologie d’une passion	[36]
Diamond J	1997	Guns, Germs, and Steel: The Fates of Human Societies	[3]
Guillaume J	2010	Ils ont domestiqué plantes et animaux: Prélude à la civilisation	[56]
Clutton-Brock J	2012	Animals as Domesticates: A World View Through History	[44]
Gepts et al.	2012	Biodiversity in Agriculture: Domestication, Evolution, and Sustainability	[57]
Vigne JD	2012	Les débuts de l’élevage	[58]
Wuerthner et al.	2014	Keeping the Wild: Against the Domestication of Earth	[59]
Francis RC	2015	Domesticated: Evolution in a Man-Made World	[60]
Alves and Albuquerque	2018	Ethnozoology: Animals In Our Lives	[61]
Scanes and Toukhsati	2018	Animals and Human Society	[62]

Table 2. Few examples of books focusing on animal domestications.

selection of only a few individuals at the beginning of the process) and reproductive isolation between wild and domestic forms [52, 67]. However, a growing body of archaeological, genetic, and ethnohistorical evidence suggests that long-term gene flow between wild and domestic stocks was much more common than previously expected, and selective breeding of females was largely absent during the early phases of animal domestication [52, 67]. Therefore, complete separation between wild and domestic populations was relatively late and region-specific [52]. These findings challenge assumptions about severe genetic bottlenecks during domestication and interpretations of genetic variability in terms of multiple instances of domestication and raise new questions regarding ways in which behavioral and phenotypic domestication traits were developed and maintained [52, 72]. The identity of the wild progenitor (or progenitors) of most domestic mammals remains also unclear because (i) the potential wild progenitors are often able to interbreed and produce fertile offspring with the domesticated congeners and (ii) many domestic animals can produce viable offspring with a host of wild, closely related sister taxa [32]. Therefore, the intuitive notion that each modern domestic animal (when discussed as a global population) is descended solely from a single wild species is almost certainly incorrect, and the genetic ancestry of domestics is likely to be relatively complex [32, 40].

Domesticated species are the result of a long and endless process that started millennia ago (**Table 1**). During about 98% of their domestication history, farm animals have been managed in a sustainable way by farmers, which lead to animals well adapted to local conditions [49, 50]. Yet, the situation changed dramatically 200 years ago as animals began to be selected for the same phenotypic characteristics to produce hundreds of well-defined breeds (**Table 1**), and reproduction among breeds was seriously reduced, leading to the fragmentation of the initial gene pool [49, 50, 70]. A few decades ago, the selection pressures were increased further, particularly with the use of artificial insemination, leading to a few industrial breeds with very high performances [49, 50, 70]. In the United States, the average milk production/cow of dairy cows increased by 1287 kg between 1993 and 2002, and 708 kg of this increase, or 55%, was due to genetics [78]. Interestingly, until the mid-1980s, most of the increase in milk yield was the result of improved management, in particular better application of nutritional standards and improved quality of rough age [78]. Since then, genetics became the major factor as a result of effective use of artificial insemination, intense selection based on progeny testing of bulls, and worldwide distribution of semen from bulls with high genetic merit for production [78]. This results in that, despite their total number of individuals, numerous industrial breeds have low effective population sizes [49, 50, 70]. This might explain that apart from a highly favorable increase in production, present-day selection for high production efficiency in livestock species in many cases was accompanied by undesirable side effects for several physiological, immunological, and reproduction traits [78, 79]. A new breeding goal aimed at improving fitness and tolerance of metabolic stress is necessary to prevent the decrease in the quality of life of farmed species and instead, perhaps, enhance it [70, 78–80]. More generally, an alternative to breeding for specific traits is to target “robustness” and “resilience,” with the former focusing on current variation among environments and the latter on future variation [81]. Management strategies should be used to address short-term challenges from changing environments, and genetic selection should be used to address long-term problems [81]. Another solution might

be to crossbreed domesticated animals either with their wild ancestor (if they still exist) or with wild relatives; it is therefore also urgent to properly assess the potential of the wild relatives as genetic resources for agriculture, and because most are endangered, actions should be implemented to preserve them [50]. Local breeds (present in only one country) in marginal areas are also seriously endangered [49, 50, 80]. For instance, in Europe more than 40% of livestock breeds are currently estimated to be endangered [82]. Farmers are often forced to abandon their traditional breeds and to raise more competitive industrial breeds [40, 83]. As a consequence, many locally adapted breeds have already disappeared [49, 50, 82]. Such a phenomenon can be very fast, and a valuable traditional breed can be lost within a decade [50]. Furthermore, even in less-developed countries, the introgression of genes from industrial breeds seriously compromises the long-term persistence of genetic resources in locally well-adapted breeds [49, 50, 83]. 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 [50]. According to the FAO, about 300 of 6000 breeds of farm animals have become extinct over the past 15 years, and 1350 currently face extinction in the near future [42, 50].

In conclusion, within a few decades, we might lose most of the highly valuable farm animal genetic resources that humans have gradually selected over the past millennia [45, 49, 50, 72]. Subsidies should therefore be urgently given to help farmers who contribute to the *in situ* preservation of genetic resources in marginal or rare breeds [80], and selection programs should aim at restoring the genetic diversity in industrial breeds [49, 50].

Conflict of interest

The author declares no conflict of interest.

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