Chapter 1

Wildlife Conservation: Is Domestication a Solution?

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Additional information is available at the end of the chapter

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Abstract

Biodiversity is facing a major crisis, which is most often described as the sixth mass extinction or Anthropocene extinction. Several solutions have been proposed to save threatened animal species, among which *ex situ* conservation or captive breeding, which is the essential part of a process called domestication. The main goals of the present chapter are to define clearly what domestication is, describe what the possible consequences are and discuss whether it can truly play a significant role to save threatened animal species. Domestication appears as a possible tool to help saving threatened species. Nevertheless, the time in captive conditions has to be minimized in order to modify as less as possible wild individuals. Therefore, zoos and aquariums can play a crucial role in helping to save the most endangered species and then restore their populations in the wild, but only if they are involved in both *in situ* and *ex situ* conservation programs. More importantly, domestication should be considered as part of the solution, but not the only one, to save threatened species. The protection of wild animals *in situ*, the restoration of habitats and the development of reserves should first be considered.

Keywords: wildlife, domestication levels, endangered species, mammals, fish

1. Introduction

Of the 4 billion species estimated to have evolved on the Earth surface over the last 3.5 billion years, some 99 % are gone [1]. This illustrates how very common extinction is [1]. However, the rate of extinction of species is uneven over the course of evolution and particularly paleontologists recognize five mass extinctions as times when the Earth loses more than three-quarters of its species in a geologically short interval (typically less than 2 million years) [1]. Those big five mass extinctions are near the end of the Ordovician, Devonian, Permian, Triassic and Cretaceous periods [1]. Common features of the big five suggest that key synergies may involve unusual climate dynamics (e.g., global warming or cooling), atmospheric composition (e.g., modification of H_2S and CO_2 levels) and abnormally high-intensity ecological stressors (e.g., anoxic episodes) that affect many different lineages, among which Mammalia, Aves, Actinopterygii, Bivalvia, or Decapoda [1]. Today, it is now well accepted that biodiversity is facing a major crisis, which is most often described as the sixth mass extinction [1] or Anthropocene extinction because human impacts are at least as important as natural processes [2, 3]. One of the most obvious evidence of this biodiversity crisis is the much higher species extinction rates calculated over the past centuries than those estimated from the fossil record [1, 4]. Current extinction rates are estimated to be 1,000 higher than natural background rates of extinction (about 0.1 extinction per million species per year) and future rates are likely to be 10,000 higher [4].

Among the most charismatic endangered species for which extinction status has been formally evaluated by the International Union for Conservation of Nature (IUCN) are land and marine mammals [5]. In land, various species of equids, gomphotheres, ground sloths, glyptodonts and mammoths have already disappeared during the late Pleistocene due to humans [6, 7]. Besides, there are today numerous species that are on the brink of extinction in the wild, such as the giant panda (*Ailuropoda melanoleuca*), the black rhinoceros (*Rhinoceros bicornis*), or the tiger (*Panthera tigris*) [5]. For instance, it is estimated that there are now less than 2500 mature giant pandas in the wild, with no more than 250 mature individuals in each population [5]. The endangered and threatened marine mammals include various species of whales, manatees, dugongs, sea cows and monk seals [8–10]. Among these, only very few seem to have become globally extinct due to human activities, such as the Steller's sea cow (*Hydrodamalis gigas*) and the West Indian monk seal (*Mustela macrodon*) [10]. Numerous other animal species have also strongly declined or collapsed in the past decades due to human activities, among which many marine commercial fish [8, 9, 11]. For instance, the northern and Grand Banks Atlantic cod (*Gadus morhua*) populations have declined by more than 90 % relative to their recorded highs [11].

At global scale, the biodiversity crisis is chiefly due to overexploitation, pollution, introduction of alien species, degradation/destruction of habitats and climate change [1, 8–10, 12, 13]. Yet, hunting (or fishing) was probably the first and main reason why species became extinct in both land and marine ecosystems [7–9]. For instance, millions of large mammals, among which mammoth (*Mammuthus* sp.) or giant sloth (e.g., *Megalonyx jeffersonii*), became extinct chiefly due to hunting and then to habitat alteration [7]. In coastal ecosystems, ecological extinction caused by overexploitation (known as overfishing) clearly precedes all other pervasive anthropogenic impacts [9]. Consequently, the decline of large vertebrates as well as shellfish is first due to overfishing globally and other human impacts all come later in the standard sequence of historical events [9]. Nevertheless, habitat loss and the introduction of alien species are also causing the extinctions of many species today [13]. Indeed, habitat loss can cause species extinction when the entire habitat occupied by locally endemic species is destroyed [13]. The introduction of alien species can also cause or facilitate extinctions of native species by initiating species interactions (e.g., predation, competition) that lead to declines in the abundance and distribution of native species [13].

In the past century, two main solutions have been proposed to try to save some of the most threatened animal species, which are the creation of protected areas such as national parks [14, 15] or more recently marine reserves [16] for *in situ* conservation and *ex situ* conservation or captive breeding, which is sometimes followed by reintroduction into the wild [17, 18]. The latter solution implies the reproduction of wild animals in captivity, which is the essential part of a process called domestication. The main goals of the present chapter are thus to define clearly what domestication is, describe what the possible consequences are and discuss whether it can truly play a significant role to save threatened animal species.

2. Domestication, what does it mean?

Even though domestication is probably studied for centuries [19, 20], there is still no consensus about its definition [21–23]. Some examples [22–28] are provided in the **Table 1**. The lack of consensus on a single definition is partly due to the inherent difficulty in assigning static terms to a process involving long-term and continuous change [22]. In the present chapter, domestication is defined as a long and endless process during which captive animals become gradually adapted to both humans and captive conditions [29]. Therefore, as soon as animals are transferred from wild to captive conditions, domestication starts (**Figure 1**). If the process either voluntary or involuntary stops at this level, it corresponds to taming, i.e., to behavioral changes of a wild animal over its lifetime; yet no genetic modifications will be transmitted to the subsequent generations [28]. Once the whole life cycle is controlled in captivity (captive breeding), the process can proceed further up to the establishment of well-defined breeds displaying desired traits.

During domestication, five main genetic processes are involved in the evolution of animals [29–31]. These include two uncontrolled processes that are inbreeding and genetic drift. They result from the small size of the founder population (sometimes containing only few individuals) and create random modifications in gene frequencies. Then, the two partially controlled processes are natural selection in captivity, which results from the selection imposed on captive populations that is not due to active selection and relaxation of natural selection in captivity that can be expected to accompany the transfer from wild to captivity. The first partially controlled process, natural selection in captivity, eliminates animals incapable to reproduce in captivity and inversely favors animals that can produce a high number of offspring in the environment provided by humans [30]. In the absence of artificial selection, natural selection provides the basic selective mechanism for genetic change in captive populations [21]. The intensity of natural selection in captivity depends on the extent to which the environment allows for the development and expression of species-typical biological characteristics and on the number of generations in captivity [21]. As species possess relatively few preadaptations to captivity, natural selection is most intense during the first generations following the transition from wild to captive environments [21]. The second partially controlled process, relaxed natural selection, consists of a reduction of the selection pressure [30]. Certain behaviors important for survival in nature but not in captivity, such as food finding, predator avoidance, as well as other morphological traits (plumage or coat color), lose much of their adaptive significance in captivity [21, 30]. As a result, both genetic and phenotypic variability for these traits can thus be more variable as domestication proceeds [21, 30]. At last, the fifth genetic process is controlled, known as active selection, because changes are directional [21, 29, 30]. Artificial selection, which is the only selective mechanisms unique to domestication, involves humans selecting the breeding animals and results in the creation of different breeds [30].

Definitions	References
Domestication of wild species to produce food means that the breeding, care and feeding of organisms are more or less controlled by humans.	[24]
Domestication is defined as that process by which a population of animals becomes adapted to man and to the captive environment by some combinations of genetic changes occurring over generations and environmentally induced developmental events recurring during each generation.	[25]
Domestication involves wild animals being transformed into something more useful to humans.	[26]
The word domestication is often confusing and poorly defined, primarily because of the inherent difficulty in assigning state terms to a process involving long-term and continuous change.	[22]
The original meaning of the term domestication is the gradual adaptation of an organism to living conditions that are determined by some form of human intervention.	[27]
Domestication should not be conflated with taming. Taming is conditioned behavioral modification of an individual; domestication is permanent genetic modification of a bred lineage that leads to, among other things, a heritable predisposition toward human association.	[28]
Domestication is a continued multigenerational, mutualistic association in which one individual significantly influences the reproduction and care of another individual in order to secure a more predictable source of a resource of interest and through which the partner organism gains advantage over organisms that are not include in this relationship, thus benefiting and often improving the fitness of both the domesticator and the domesticate.	[23]

Table 1. Examples of definitions of domestication for animal species, modified after [38].

Over the course of domestication, captive animals will become domesticated (**Figure 1**). Yet, as for domestication, there is still no consensus on what a domesticated animal species is. According to most definitions [22, 32–34, 38], a domesticated species is a group of animals bred in captivity and modified from their wild ancestors (**Table 2**). However, wild/domesticated should not be considered as complementary such as true/false or dead/alive, because they represent the two extremes of a process and not a simple dichotomy [22]. In other words, no clear threshold separates wild from domesticated animals [35]. Besides, domesticated animal is neither a definitive status nor a final end point of domestication as these animals are still evolving today [30] and can sometimes return to the wild (**Figure 1**), a process known as feralization [21, 36]. According to authors, feral animals are either merely free-living individuals [36] or populations of animals (reproduce in the wild) that originated from domestic stock [21] or animals undergoing the domestication process in reverse [21]. This latter definition implies that feral animals, which are no longer exposed to artificial selection by humans or natural selection imposed by the captive environment, will therefore evolve through generations to become "wild" once more [21]. Depending on the species and the number of generations in captivity, feralization might not be possible (animals will die rapidly in nature) or will take a long period of time for animals to return to "wild" form; yet they will not go back to the original "wild" ancestor genotype and phenotype. One of the best example is cats (*Felis catus*) [28], whose domestication started about 4000 years ago from the African wildcat (*Felis silvestris lybica*) and that establishes numerous feral populations worldwide [37]. However, because feral cats are directly responsible for a large percentage of global extinctions, particularly on islands, numerous eradication programs (using trapping, hunting, poisoning and introduction of viral diseases) have been carried out in the last 30 years to preserve biodiversity, particularly seabirds [37].

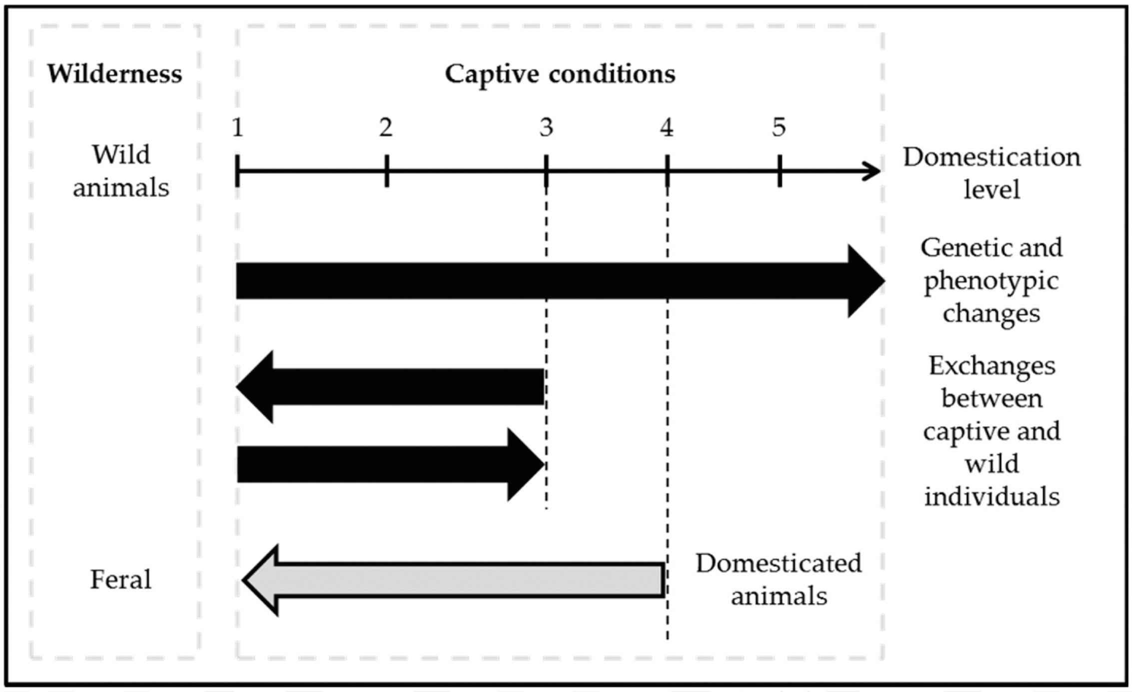

Figure 1. Evolution of a wild animal species throughout the process of domestication. As soon as wild animals are transferred to captivity (level 1), the process starts. The numbers correspond to the domestication levels described in **Table 3**. During domestication, wild animals will evolve both genetically and phenotypically, particularly when exchanges with wild congeners do no longer exist (level 4). Therefore, to minimize changes, captive animals should remain at the first three levels. Once animals have reached the level 4, they are generally considered domesticated. Domesticated animals can return to the wild and are then known as feral. The differences between feral and wild animals will depend mainly on the time spent in captivity and particularly the number of generations without exchanges with wild congeners.

In order to go beyond the usual dichotomy of wild versus domesticated animal species that was particularly not relevant for food fish production, Teletchea and Fontaine [38] created a classification based on both the level of control of the life cycle of a species in captivity and the link with wild individuals. This classification displays five levels (**Figure 1**, **Table 3**). Most authors would probably agree that at the level 4, captive animals are domesticated, particularly when they sufficiently differ from their wild ancestors [39]. Then, we applied this new concept to the fish species farmed for human consumption in order to better describe the various fish production strategies. Among the 250 species recorded in the FAO database in 2009, 70 % were classified into levels 1, 2 and 3 representing a transitory form of fish production dependent on the availability of the wild resource. In contrast, 75 species were classified at the levels 4 and 5 [38]. Yet, when a species is classified at a given level, this does not imply that the entire aquaculture production is at that level; different populations (or batches of fish) belonging to the same species can indeed display different domestication levels, even within same farm [39].

Definitions	References
A domestic animal can be defined as one that has been bred in captivity for purposes of economic profit to a human community that maintains total control over its breeding, organization of territory and food supply.	[32]
A domesticated animal species is a species bred in captivity and thereby modified from its wild ancestors in ways making it more useful to humans who control its reproduction and its food supply.	[33]
A truly domesticated species is valued and kept for a given objective, its breeding is controlled by humans, its behavior is different from its wild ancestors, its morphology and physiology display variations never observed in the wild and certain individuals at least would no longer be able to survive without human protection.	[34]
"Wild" and "domestic" represent the extremes of a process and not a simple dichotomy.	[22]
To be considered domesticated, the fish life cycle must be fully closed in captivity, independent of wild sources (domestication levels 4 and 5).	[38]

Table 2. Examples of definitions for domesticated animals, modified after [38].

Domestication level	Definitions
5	Selective breeding program is used focusing on specific goals
4	Entire life cycle closed in captivity without wild inputs
3	Entire life cycle closed in captivity with wild inputs
2	Part of the life cycle closed in captivity: several bottlenecks
1	First trials of acclimatization to the captive environment
0	Capture of wild animals (hunting or fishing)

Table 3. Domestication levels, modified after [29, 38].

In conclusion, domestication is a long and endless process during which animals become more adapted to both human and captive conditions. According to the species considered, some

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have started this process long time ago and have thus reached the level 5 for many years or centuries, while others have just entered into it (level 1 or 2). The possible consequences are further described below for both mammals and fishes.

3. What are the main consequences of domestication?

3.1. Domestication of mammals

Domestication on land started around 12,000 years ago in at most nine areas over the world [23, 28, 33, 40]. These nine homelands of food production were Fertile Crescent, China, Mesoamerica andes/Amazonia, eastern USA, Sahel, tropical West Africa, Ethiopia and New Guinea [33]. From these primary homelands, domesticated animals were moved throughout the world, first according to an east-west axis and then a north-south axis (mainly because less evolutionary change or adaptation of domesticates was necessary for locations at the same latitudes compared to those at different latitudes) [33]. These initial introductions ultimately became the essential source of foodstuffs worldwide, resulting in that today human meat-eating diet depends on this tiny fraction of wild land mammals that were domesticated over the past millennia [26, 33, 40]. Five domesticated mammals provide the bulk of animal products (milk, meat) that are consumed across the globe. The "big five" are cow (*Bos taurus* and *B. indicus*), pig (*Sus domesticus*), sheep (*Ovis aries*), goat (*Capra hircus*) and horse (*Equus caballus*) [33].

Domestication was one of the most significant cultural and evolutionary transitions of human history [23, 28, 33, 40]. Indeed, it constitutes a core component of a major change in the way of life of an increasing number of human societies throughout the world, in a process called Neolithisation [28]. Almost everywhere in the world, hunger-gatherer communities were progressively replaced by farming societies as food production gave farmers enormous demographic, technological, political and military advantages [33]. Domestication also results in a fundamental change in the evolution of the biosphere, mainly due to the development of agriculture, which is now responsible for the transformation of approximately 40 % of the Earth's surface [41]. Today, humans are such a major geological and environmental force, at least as important as natural processes, that some considers that Earth has entered a new distinct period, called Anthropocene [3].

Over the course of evolution, wild animals were profoundly modified, including behavior, physiology, morphology and genetic [21, 23, 28, 30, 42]. One of the first modifications during domestication is behavior [21]. Yet, behavior traits did not appear or disappear, but the threshold of their expression changed [21, 30]. One of the most obvious behavioral changes manifest by all domesticates is the remarkable tolerance of proximity to (or complete lack of fear of) human [23, 28, 43]. Besides, as humans provide both protection against predators and feed, domesticated animals express a lower incidence of antipredator behaviors and show lower motivation for foraging, respectively [30]. More generally, mood, emotion, agnostic and affiliative behavior and social communication all have been modified in some way by domestication [28, 30]. Besides, most domesticated animals are more precocious than their wild counterparts [30] and the activity of their reproductive system became enhanced and relatively uncoupled from the environmental photoperiod and they all, unlike their wild ancestors, acquired the capacity to breed in any season and more often than once a year [28, 43]. At last, the most spectacular changes are probably morphological, including the overall body size (dwarfs and giants) and its proportions (fewer vertebrae, shorter tails); color, length and texture of the coat; or other manifestations of neoteny (the retention of juvenile features into sexual maturity) [28, 43]. The variation range of certain traits within a domestic species occasionally exceeds that within whole families or order, such as for dog (*Canis familiaris*) [43]. Some of these specific trait attributes (white spotting, floppy ears and curly tails) have been aptly called the morphological markers of domestication [43]. In most species, head or brain size has decreased [30]. These morphological changes may all be linked to strong selection for lowered reactivity to external stimuli [23]. More recently, the tools of molecular genetics, such as microsatellites or quantitative trait loci (QTL), have been used to investigate to what extent gene frequencies have changed between wild and domestic animals and among breeds [30, 42]. It appears that, except for certain breeds, domestic animals present a very high genetic diversity [39]. This is mainly due to the fact that exchanges between wild and captive/domestic animals were frequent in the earliest phase of domestication and probably lasted several centuries. Hence, the complete separation between wild and captive populations was relatively late and region specific [39]. It is only when breed formation started in the mid-eighteenth century, followed by the application of modern breeding methods, such as artificial insemination, in the past decades, that effective population size (N_e, which is estimated on the basis of the size of both the female and the male breeding populations) declined, resulting in strong genetic bottlenecks in certain breeds [39].

In conclusion, domestication is a very powerful process that has enabled humans to produce various domestic animals that now constitute the bulk of what we eat, i.e., cattle, pig, horse, goat and sheep. During this very long and complex process [29, 39], which started around 12,000 years ago, domesticated animals have been intensely changed resulting in numerous breeds with their own specific characteristics [42]. Besides, their numbers have increased tremendously: about 1 billion individuals for each of the big five [38]. Today, a clear dichotomy seems to exist between wild and domesticated mammalian species, which explains why researchers gave a new scientific name to some domesticated mammals [38, 42]. Nevertheless, when domesticates are sympatric with populations of the parent wild species (if the latter still exist), they can generally reproduce together [28]. Therefore, under the conceptual framework of the biological species concept, domesticated populations should not be considered as distinct species from their wild ancestors [28].

The comparison between domesticated animals and their wild ancestors is useful to study how domestication has modified animals, yet these comparisons cannot help to understand changes that happen in the first generations of domestication [30]. Only very few studies have been performed on mammalian species to evaluate early changes, among which one of the best known is on silver fox (*Vulpes vulpes*) at the Institute of Cytology and Genetics, Novosibirsk, Russia [30, 43]. During more than 50 years, about 10,500 foxes were used as parents and 50,000 offspring foxes were selected for tamability or amenability to domestication [43]. In the behavioral test, the experimenter approached the home cage, tried to open it and monitored the expression of the response [43]. The pressure of selection was very severe as less than 10 % of the tamest individuals were used as parents of the next generation [43]. As a result of such strong selection, the offspring exhibiting the aggressive and fear avoidance responses were eliminated in just two to three generations of selection [43]. After 18 generations, reproduction (capacity to breed at any time throughout the year), coat color pattern as well as other morphological traits (floppy ears, curly tails), relationships with humans and several behavioral traits (frequency of wagging, specific vocalizations, posture of the body and its communicative parts such as tails, ears and others) were very close to those of the domestic dog [30, 43]. This example demonstrates that domestication can modify very quickly captive animals [36]. Nevertheless, in this case, animals were artificially selected for tameness, which probably increased the rate of evolution of these traits in the population [30]. Besides, this study did not allow to specifically studying the transition from nature to captivity [21] as silver foxes initially used had been farm-bred for about 50 years before the experiment [43].

3.2. Fish species

Compared to land animals, the domestication of fish for human consumption has started recently [29, 38, 39, 44, 45]. Except for few species, such as the common carp (*Cyprinus carpio*) or Nile tilapia (*Oreochromis niloticus*), most trials of domesticating new fish species dated back to the early 1980s [27, 34, 39]. Consequently, there are still lots of exchanges between wild and farmed individuals and thus captive fish have only slightly changed from their wild conspecifics [46–48]. This represents a unique opportunity to study how animals evolve during the transition from wild to captive conditions, as well as during the first generations of domestication [29]. Yet, compared to the knowledge on the behavioral, physiological, morphological and genetic consequences of domestication among land vertebrates, there is very little information on the consequences of domestication in fish [49]. Besides, much knowledge acquired has been on salmonids due to their economic importance for both human consumption and sport fisheries (e.g., [50–52]).

In general, behavioral traits are among the first traits to be affected by the domestication process [46, 53]. Yet, depending on the species and captive conditions (population density, food supply, aquaria, or streams) used, it has been found that both agonistic (aggressive) and schooling behaviors could be modified (decreased or increased) during domestication [49]. While comparing wild-caught and domesticated sea bass (*Dicentrarchus labrax*) juveniles, which is one of the top farmed species in Europe [29, 45], Benhaïm et al. [53] found no differences in spatial learning. Yet, swimming behavior parameters (angular velocity, total distance traveled and velocity mean) were significantly different between the two groups. It was also found that several life-history traits have changed significantly in two salmonid species, Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) reared at the hatchery at Älvkarleby, central Sweden, over the period 1968–1991 [50]. For instance, the body size of the 2-year-old smolts increased for both species and sexes. Both female and male trout adults had larger body size. Eggs were significantly larger for both species, particularly for Atlantic salmon, indicating that female salmon invest more in egg size with increasing body size. The time spent in sea has decreased for both female and male sea trout, but not for Atlantic salmon [50]. At last, several studies have been recently published that try to detect genomic differences in recently domesticated species, such as the Atlantic salmon [51]. In their study, these authors analyzed a genome-wide set of single nucleotide polymorphisms (SNPs) in three domesticated Atlantic salmon (from five to nine generations in captivity without wild inputs) and their wild conspecifics to identify loci underlying domestication. They found that the genetic differentiation between the two wild and domesticated was low and domesticated strains harbored similar level of genetic diversity compared to their wild conspecifics. Their study indicates that detecting selection in the first generations of domestication could be tricky unless selection is strong and the traits under selection show simple inheritance patterns [51]. Because a genome-wide response to selection can take many generations, as found for the Atlantic salmon, Christie et al. [52] hypothesized that the earliest changes associated with domestication may first manifest as heritable changes to global patterns of gene expression. They compared patterns of gene expression in offspring of first-generation hatchery and wild steelhead trout (*Oncorhynchus mykiss*) collected directly from the Hood River, Oregon, reared in the same environment. More than 700 genes were differentially expressed between the two groups that could not be explained by either maternal effects or by chance differences in the background levels of gene expression among unrelated families. Therefore, this is the first study to demonstrate that earliest stages of domestication are characterized by large changes in heritable patterns of gene expression, which are probably linked to adaptation to highly crowded conditions, as those genes were involved in pathways in wound healing, immunity and metabolism [52].

4. Can domestication truly help wildlife conservation?

4.1. Fisheries enhancements

Fisheries enhancements are a set of management approaches involving the use of aquaculture technologies to enhance, conserve, or restore fisheries in natural ecosystems, which are ecosystems not primarily controlled by humans, whether truly natural or modified by human activity [54–56]. Among those various aquaculture technologies, the most common form of enhancement is the release of hatchery-reared aquatic animals into natural habitats [49, 56]. Aquaculture-based enhancements have been practiced on a large scale since the mid-nineteenth century [54] and are now widely used in both inland and coastal fisheries across the world [56, 57]. For instance, state fisheries management release over 1.7 billion fish hatchery annually in the USA [56]. Besides fisheries regulation and habitat restoration, fisheries enhancements of populations are the third principal means by which fisheries can be sustained and improved [54]. Aquaculture-based enhancements can, at least in principle, increase yield through manipulation of population and/or food-web structure, aid the conservation and rebuilding of depleted or threatened populations and provide partial mitigation for ecosystem effects of fishing [54]. However, in practice, the contribution of enhancements to global fisheries has remained small [54], contrasting with the exponential growth of aquaculture in the past few decades [38]. Indeed, only a few “success stories” have been described in the literature, such as the Japanese and New Zealand scallop enhancements, Alaska salmon enhancement and Asian culture-based lake fisheries [54].

Fish cultured for fisheries enhancements enter the process of domestication as soon as they are moved from wild to captive conditions [55], which corresponds to the domestication level 1 (**Table 1**). Therefore, even though no artificial selection (selective breeding focusing on specific goals) is applied, wild fish can still be modified due to inadvertent responses to the culture environment, leading to what Lorenzen et al. [55] called "captive types." In order to mitigate as much as possible the effect of domestication and promote "wild-like types," attention should be paid to both sampling of fish for the founder population (sufficient diversity of genetic and life-history phenotypes to allow re-establishment of viable populations in the wild) and its subsequent management in captivity [55]. The most effective way of minimizing both loss of genetic diversity and the effects of domestication is to minimize the time spent in captivity [55] and release the fish at an early stage (eggs or larvae) to reduce environmental effects of the hatchery [57]. In other words, only one part of the life cycle should be controlled in captivity (level 2 in **Table 1**). Besides, the post-release performance of captive-reared fishes can be improved by modifying the captive environment of hatchery to try to mimic key aspects of natural conditions [57]. Relatively simple modifications of the captive environment, among which physical enrichment (modifications or additions of physical structure to the tanks, such as shelters) and reduced rearing density, can help produce a more wild-like fish that will perform better in the wild [57]. Yet, where populations must be maintained in captivity for multiple generations (thus reaching level 3 and perhaps level 4), there is an inherent trade-offs between the goals of maintaining diversity (avoid inbreeding and genetic drift) and minimizing adaptation because the potential for genetic adaptation is directly proportional to the heritable genetic diversity [55]. If adequate genetic diversity is maintained, it should provide sufficient reserve for feralization [55]. A recent study on Atlantic salmon demonstrated experimentally that the exposure of captive-reared fish to natural river environments during early life resulted in a twofold increase in the survivorship of offspring of wild-exposed parents compared to the offspring of captive parents [58]. The authors proposed that for lowering the possible effect of domestication, parental exposure to captivity should be minimized and exposure to the wild should be maximized but even for short period of time and within generations [58].

Salmonids are certainly the fish taxa for which most information is available on the efficiency of captive breeding programs to conserve genetic diversity and fitness of natural populations or to re-establish self-sustaining populations in the wild [59]. It appears that for most captive breeding programs, genetic diversity within populations can be sufficiently maintained in captivity for several generations. However, the captive environment may lead to unavoidable genetic changes and/or wild fitness changes in quantitative traits (despite large N_e). Decrease in fitness may potentially arise even within one generation, or after one or two generations in captivity, due to modifications, among others, of behavior, swimming performance, developmental time to hatch, embryo size, maternal reproductive investment, body morphology and age at maturity. More importantly, there is currently little empirical evidence that captive-reared lines of salmonids can be reintroduced as self-sustaining populations, particularly if the factors contributing to their initial decline are not concurrently addressed. A minimum of 15–20 years will likely be necessary to potentially achieve the conservation goal of reestablishing a self-sustaining salmonid population in the wild [59]. More recently, a comparison between first-generation hatchery-reared juvenile Atlantic salmon either released into four different river environments or kept at the hatchery showed strong differences between the two groups [60]. Hatchery fish that survived in the wild became more streamlined and more symmetrical and developed longer heads and thicker caudal peduncles and their caudal fins and opercula regenerated [60]. More importantly, this study demonstrates that hatcheries generate fish that are phenotypically mismatched to the natural environment, which may explain why they typically perform poorly in the wild [60]. Another study explored the long-term consequences of stocking captive-bred Atlantic salmon in France [61]. Based on the analysis of 11 microsatellite loci for 1428 salmon sampled from 1965 to 2006 in 25 populations, they found that the overall genetic structure among populations dramatically decreased over the period studied [61]. Depending on population, admixture rates either increased, remained stable, or decreased in samples collected between 1998 and 2006 compared to samples from 1965 to 1987, suggesting either rising, long-lasting, or short-term impacts of stocking [61]. They recommended favoring the use of native in priority as these fish may represent the most appropriate basis to restore a locally adapted population and then wild individuals (nondomesticated over several generations) to limit detrimental introgressive hybridization [61].

In conclusion, fisheries enhancement and particularly the release of captive-bred fish, might be helpful in conserving or restoring fish population [54–56, 59]. Yet, clear goals should be formulated for fish culture and domestication strategies [62], bearing in mind that different uses of fish (e.g., fish consumption versus wildlife conservation) call for very different approaches [38, 55]. At last, it should be stressed that hatchery releases should only be considered in cases where there are no realistic ways to save or maintain sensitive natural populations [57]. As a long-term strategy, habitat restoration should always be the first choice in fish conservation efforts to allow the “natural” recolonization of rivers or lakes by fish from which it has been extirpated [61].

4.2. *Ex situ* conservation: the role of zoos and aquariums

As described for fish, captive breeding of land animals is the act of bringing rare or endangered species into captivity with the hope of rearing sustained captive populations for eventual reintroduction into the wild [17]. In the past century, *ex situ* conservation programs and reintroductions of captive-bred animals have become widespread measures to protect various endangered species [18]. Successful reintroductions are exemplified by the Guam rail (*Gallirallus owstoni*), black-footed ferret (*Mustela nigripes*), California condor (*Gymnogyps californianus*) and Przewalski’s horse (*Equus przewalskii*) [17, 63]. Yet, only about 10–15 % of reintroduction programs of captive-born populations were considered successful (with success judged as a self-sustaining and viable population) [17]. Although poor habitat quality is one common denominator in failed reintroductions, altered behaviors (e.g., courtship rituals, foraging/hunting routine, nest-site selection), depleted genetic diversity, or a combination of these factors also limit population growth trajectories [17, 63]. Besides, it was also found that success of translocations of wild-caught individuals that were never in captivity was much higher than those of reintroduction programs of captive-born populations, which demonstrate, as for fish species, that the best approach to minimize genetic adaptation and ensure the success of reintroduction is to reduce the time a species spends in captivity [17].

For some species reintroduction may not be an option owing to the state of their natural environment [17, 18, 64, 65]. In this case, the role of zoos and aquariums has changed from historical menageries that collect and exhibit exotic animals to modern institutions around the world that actively contribute to conservation, scientific research and public education [66–70]. Since the 1980s, many zoological gardens coordinate their breeding programs in "European Endangered Species Programs" (EEPs) and "Species Survival Plans" (SSPs) [18]. In 1993, the first World Zoo and Aquarium Conservation Strategy (WZACS) was published, which proposes clear goals for zoos and aquariums, including the need to support both *in situ* and *ex situ* conservation projects [18].

Because the goal is now to maintain a species in captivity for an extended period of time before a possible reintroduction into the wild, management strategies have to evolve [17]. Some authors proposed to attempt to minimize generations first by delaying reproduction and then by cryopreservation of germplasm [17]. Besides, because captive populations are often started with a low number of founders, either because it is difficult to collect more individuals or because there simply are no longer available, inbreeding depression is a common phenomenon in zoo populations [18]. A recent analysis showed that 67 % of *ex situ* populations in the Association of Zoos and Aquariums (AZA) institutions have a population size of less than 100 individuals and the mean N_e of Species Survival Plan (SSP) populations is 41 [18]. A perusal of studbooks from various captive mammals shows that a single founder often produces a disproportionality higher number of offspring than the remaining founders leading to a higher genetic contribution to the subsequent generations [71]. Most of the cooperatively managed breeding programs in the world possess too few captive individuals, among which too few are in proper conditions for breeding, with most often undocumented ancestries and/or too little collaboration with scientifically designated breeding recommendations [72]. These problems are leading to declining populations or decreasing gene diversity or both [72]. This demonstrates that zoo stocks still require a lot of restructuring in order to make captive breeding a more valuable contribution to species conservation [18]. In order to evaluate which methods (random mating, minimizing mean kinship and selection for docility) are the best to maintain genetic diversity in captive breeding populations, Willoughby et al. [63] evaluated genetic changes in captive populations of white-footed mice (*Peromyscus leucopus*) using microsatellites and mitochondrial DNA. After 20 generations, minimizing mean kinship resulted in slowest loss of microsatellite genetic diversity than the two others. They concluded that this method should be preferred for captive breeding, even though this method does not fully mitigate the effect of drift, as illustrated by the loss of about half of the microsatellite alleles [63]. At a much larger scale, Chargé et al. [64] found, even for a species, the Houbara bustard (*Chlamydotis undulata*), in which several thousand individuals are under a strict genetic management following worldwide used recommendations, genetic changes in several life-history traits (mean values of gamete production, body mass and courtship display rate) [64].

This example highlights the, still unresolved, question of the success of recognized guidelines for genetic management of captive populations, which in zoo are much smaller, to prevent genetic changes [64]. Other authors proposed that if there are still sufficient individuals in the wild, the immigration of individuals from the wild at a rate of one migrant per one to two generations could allow decreasing inbreeding as well as minimizing adaptation to captivity [17, 18]. Another solution that is already in practice is to exchange animals between zoos and aquariums [67, 72]. Yet, increasing regulation/restrictions on importations have reduced the ethical and logistically feasibility of importations as significant numerical support to zoo and aquarium populations [67]. At last, maintaining genetic diversity of captive populations is not sufficient as a number of difficulties in captive breeding can affect the survival of a captive population (and the success of a reintroduction program, if ever occurs). Among these known difficulties, the requirements for physical health and behavioral anomalies (e.g., stereotypic movements, lethargy, social incompatibility) have received much attention [73] and both zoos and aquariums are under increasing scrutiny for the quality of their animal management and care [67].

Today, more than 8000 species are maintained in the world's zoos and aquariums and have probably help saving the most endangered ones. Yet, in the recent decades, an increasing number of "wild" animal species are bred in captivity (tigers, gorillas and polar bears), with no longer exchanges with wild congeners [28]. Consequently, even though these species might probably not be considered as domesticated by most authors, they have reached the level 4 and therefore they could progressively diverged strongly and rapidly from their wild counterparts in few generations [36]. This could perhaps prevent possible reintroductions in the future (if habitat is restored) or at least decrease the chance of successful reintroductions. Therefore, the general objective of zoos and aquariums should not be to produce self-sufficient population, but rather to engage in the management of broader metapopulation, with carefully considered exchange between populations across a spectrum of *ex situ* to *in situ* [72]. The zoos of the future will be justified by how well they contribute positively to overall species conservation efforts, not by how well they can minimize harm to wildlife populations [72].

5. Conclusions

In 2002, Crutzen [74] coined the term Anthropocene to clearly express that since the late eighteenth century, Earth has entered a new geological epoch, dominated by human. During the past three centuries, the human population has indeed increased tenfold to more than 7 billion and the effects of humans on the global environment have escalated [74]. The most obvious environmental changes include increase of greenhouse gas concentrations, ocean acidification, alteration of global and regional nitrogen cycles, the creation of novel minerals, the transport of materials from place to place and human appropriation of net primary production [3]. During this period of time, biodiversity has been drastically modified throughout the globe due to habitat alteration/destruction, introduction of alien species and extinction of species [75]. Some even considered that truly wild nature (pristine areas) does no longer exist [14].

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In this context, domestication (*ex situ* conservation) has appeared as a possible solution to save or perhaps restore populations of endangered species. Even though domestication is probably the sole solution in extreme cases, it is neither necessary nor sufficient for conserving or restoring wildlife. Indeed, numerous wild species have recovered from extreme low levels without domestication. One of best example is the rebuilding of some depleted marine fish populations by merging diverse management actions, including catch restrictions, gear modification and closed areas [76]. Obviously, the time to recovery will depend on the life-history traits of the species as well as the efficiency of conservation actions [77]. Yet, even a long-lived mammal that was heavily exploited, the humpback whale (*Megaptera novaeangliae*), which has benefited from protection from commercial whaling (since 1955), has improved from vulnerable to least concern [77]. Nevertheless, domestication has probably contributed to save some species on the brink of extinction, among which large terrestrial mammals. In the future, zoos and aquariums can play a crucial role in helping to save the most endangered species and then restore their populations in the wild, but only if they are involved in both *in situ* and *ex situ* conservation programs [72]. Otherwise, they will progressively host domesticated animals and no longer wild-type animals, which have little chance to reproduce and survive in the wild. Such a possible Noah's ark approach (focusing on a tiny proportion of wild species given the limited holding and exhibition space within and among institutions [67]) highlights that if we really want to preserve wildlife, the most important is to protect species in the wild (e.g., by reducing overfishing and poaching) as well as their environment (e.g., avoid introducing or eradicating alien species, preserve or restore "natural" habitats by establishing reserves) [14, 75, 77–79]. Stopping biodiversity decrease will thus need harmonized efforts to protect and efficiently manage critical sites, complemented by large-scale action to lower additional destruction and degradation of habitats and to encourage the sustainable use of productive ecosystems in a way that is supportive to biodiversity [77]. This implies also setting limits to human demand on nature [14]. Otherwise, natural landscapes will be progressively replaced by "working landscapes" inhabited either by domesticated or feral animals, but no longer wild animals. At the global scale, this means that we would have domesticated not only animal (and plant) species, but probably the entire Earth [15].

In conclusion, domestication appears as a powerful tool that could be useful to save threatened species. Nevertheless, the time in captive conditions has to be minimized in order to modify as less as possible wild individuals (**Figure 1**). More importantly, domestication should be considered as part of the solution, but not the only one, to save threatened species. The protection of wild animals *in situ*, the restoration of habitats and the development of reserves should first be considered.

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