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Is Fish Domestication Going Too Fast?

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Abstract

Domestication is a very strong process that has enabled humans to produce both plants and animals with desired traits. For land animals, this process started about 12,000 years ago and resulted in that today hundreds of well-defined breeds are available for the five most important farmed mammal species (cattle, pig, horse, sheep and goat). For aquatic animals, this process started much earlier, and the bulk of domestication of new species dated back only to the early 1980s. Nevertheless, there are now numerous fish species for which the life cycle is already closed in captivity and some domesticated fish have been genetically improved. This implies that what probably took hundreds of years in mammals (*i.e.*, to control the life cycle in captivity and then to improve captive individuals) has been accomplished in only tens of years for some fish species. Based on the main problems observed today in farmed mammals, the possible consequences of this fast domestication of fish are discussed.

Keywords

Domestication, Farmed Animals, Mammals, Fish, Global Change

1. Introduction

Domestication is, by definition, a long and endless process during which animals become progressively adapted to both captive conditions and humans [1]-[5]. This process implies first to control part of the life cycle of the targeted species in captivity [1] [3]. Then, once the entire life cycle is closed in captivity, the process can proceed further up to the establishment of well-defined breeds displaying specific traits [2] [4].

In order to better describe the diversity of farm practices applied today, particularly in aquaculture, Teletchea and Fontaine [6] have recently proposed a new classification with five levels of domestication. The first level corresponds to the initial trials of acclimatization of wild animals to captive environment. In other words, as soon as wild animals are transferred to captivity, domestication starts. Nevertheless, if the process stops at this level, it corresponds only to taming, *i.e.*, to the modification of behavior of a wild animal during its lifetime; yet no genetic modification will be transmitted to the offspring [1]. Then, once part of the life cycle is controlled in captivity, the level 2 is reached. Major bottlenecks have to be overcome in order to close the life cycle in captivity, among which the most important is breeding in captivity [6]. Then, once the entire life cycle is controlled, but there are still wild inputs into the captive stocks, the level 3 is reached. The level 4 also implies that the entire life cycle is closed in captivity, but wild animals are no longer brought into the captive stocks. Most authors would probably consider that at the level 4, captive animals are domesticated, particularly when they sufficiently differ from their wild congeners [4]-[6]. The level 5 is reached when specific breeding programs have been developed to improve one or several traits, which results in well-defined breeds [6]. Importantly, reaching any level does not necessarily imply that the entire species is at that level; different populations (or groups of individuals) within the same species can indeed display different domestication levels, even within the same geographic area or in a given farm [6].

Within the framework of this new classification, the first goal of the present study is to briefly describe the history of domestication of land animals and then assess the main problems encountered today in the five major farmed species. Then, the second goal is to summarize the history of fish domestication and discuss whether it is too fast compared to land animals.

2. Domestication of Land Animals: What Consequences?

2.1. Brief History of Domestication of Land Animals

In land, domestication started about 12,000 years ago for the five main farmed mammal species that represents today the bulk of what we eat: cow (*Bostaurus* and *B. indicus*), sheep (*Ovisaries*), goat (*Capra hircus*), pig (*Sus scrofa*) and horse (*Equus caballus*) [7]-[11]. Domestication was acrucial step in human history, known as the Neolithic transition, which results in a progressive shift from hunting-gathering to farming, and eventually in-human population explosion that has continued unabated to this day [7] [9] [11].

Following the seminal research of Darwin, strongly influenced by European animal breeding practices during the 19th century, domestication studies have most often emphasized the crucial role of humans by focusing on genetic isolation of captive animals from wild congeners and directed or controlled breeding of individuals [12], which corresponds to the domestication level 4 and 5, respectively. Therefore, it was generally considered that the creation of separate breeding populations of animals completely isolated from their wild progenitors was essential for domestication [12] [13]. Besides, it was assumed that domestication occurred only once at a specific place for each domesticated species and involved a strong population bottleneck that significantly reduced genetic diversity [14].

New archeological, genetic and ethnohistorical findings suggest, however, that exchanges between wild and captive/domestic animals were frequent in the earliest phase of domestication and probably lasted several centuries [12]. This implies that complete separation between wild and captive populations was relatively late and region-specific [12]. According to Teletchea and Fontaine's classification [6], this means that currently domestic animals remained at the domestication levels 2 to 3 for a very long period of time, and only reached the level 4 quite recently (variable according to species and breeds). This is particularly true for animals used for transport, such as donkey (*Equusasinus*), horse or Bactrian camel (*Camelusbactrianus*) [12]. Yet, this also might be the case for other domesticated species, including animals kept for meat and secondary products, such as milk or wool [12]. There is, indeed, strong evidence for gene flow for a long period of time between pig, sheep, goat, and cattle, and their wild relative in areas of common distribution [12].

2.2. Evolution of Genetic Diversity during Animal Domestication

A common misconception about domestic animals is that they are highly inbred [14] [15]. This might be true only if one considers certain breeds, but as a whole, domestic species are characterized by a high degree of genetic diversity [14] [15]. This is chiefly due to the fact that effective population size (N_e), which is estimated on the basis of the size of both the female and the male breeding populations [16], were large during most part of the domestication process [15], for reasons explained above.

However, particularly when breed formation started in the mid-18th century [17], followed by the application of modern breeding methods, such as artificial insemination, in the past decades, N_e declined, resulting in strong genetic bottlenecks in certain breeds [15] [18]. For instance, estimates of current N_e in several commercial taurine cattle breeds are now very low (≤150) and those breeds generally display low genetic variability [15]. One extreme case is a feral British breed, Chillingham cattle, in which 24 out of 25 microsatellites loci were found to be homozygous [15]. Nevertheless, genetic isolation was rarely absolute for most breeds, and gene flow did not stop, even after when cattle [19] or sheep [20] were partitioned into breeds. For cattle, the history of breeds, indeed, mentions deliberate upgrading in order to improve production characteristics by using bulls of other populations from the same or a different country [19].

In the past decades, highly productive breeds (e.g., Holstein-Friesian for dairy cattle [17]) have progressively replaced or crossbred local breeds (present in only one country) to the point that they have effectively disappeared [16] [17] [21] [22]. According to the FAO, one-fifth of the 7600 breeds reported worldwide, belonging to 34 mammalian and avian species, are at risk, and 62 breeds already became extinct in the past years [16]. However, growing concerns about the erosion of genetic resources of farm animals and general skepticism regarding the side effects of technological progress, have promoted initiatives to conserve local breeds [17] [21] [22]. These local breeds, which have often developed adaptations to local, sometimes extreme conditions, belong to our cultural heritage and are of local cultural importance, even if most are only one or two centuries old [17].

2.3. Main Negative Effects of Domestication/Selection

In last decades, genetic selection has considerably increased production performances of farmed species [23] [24]. However, in the meantime, negative side effects have become more apparent [23] [24]. Animals that have been genetically selected for high production efficiency could also present some undesirable side effects for several reproduction, health and metabolic traits (**Table 1**). For instance, after less than a century of animal breeding, the double muscling phenotype (a trait selected for meat production), which is nearly fixed in Belgian Blue cattle, also results in that calves are now delivered by caesarean section [15].

Therefore, the goals of breeding programs have to be redefined including not only production traits, but also economical traits, such as veterinary costs (e.g., resulting from higher diseases), as well as the welfare of animals, which is becoming an important issue, particularly in European countries [23] [24].

3. Domestication of Fish Species

3.1. Brief History of Fish Domestication

Compared to land animals, the domestication of fish species is much more recent [6] [25] [26]. Except for few species, among which common carp (*Cyprinus carpio*) and Nile tilapia (*Oreochromis niloticus*), the bulk of domestication trials dated back to the early 1980s [6] [25] [27]. Nevertheless, several species have already reached the level 5 [28]-[31], even though globally less than 10% of the aquaculture production comes from selectively bred farm stocks [28] [29]. A survey on the selective breeding programmes developed in European countries is provided in **Table 2**. One of the best examples of rapid domestication is the Atlantic salmon (*Salmo salar*), whose first trials (level 1) started in the early 1970s in Norway [28] [32]. Less than four decades later, almost 100% of all farmed salmon worldwide have reached the level 5, and are sourced from a relatively small number of companies that utilize the original Norwegian fish, or a mixture of local and imported strains in Scotland, Chile and Iceland [28].

Table 1. Possible negative side effects of selection for high production efficiency in two farmed species (adapted from [23] [24]).

Species	Breeding goals	Possible negative side effects of selection		
		Reproduction	Health	Metabolism
Pig	High growth rate and/or minimum back fat thickness	Prolonged interval from weaning to farrowing Delayed onset of puberty Shorter pro-oestrus More frequent vulvar symptoms	More leg weakness	
Dairy cattle	High milk yield	Breeding later Longer calving interval Higher number of inseminations per conception	More digestive disorders More skin or skeletal disorders More udder edema Higher risk of mastitis	Lower energy balance Loss of body condition score

Table 2. Survey of European fish species that have reached the level 5, classified according to their global aquaculture production in 2014 (from [28] [31]). Importantly, this does not imply that the entire production is based on improved stocks [31], particularly for common carp. Generations: number of generations under selection in the oldest breeding program (if known).

Species	Common name	Generations	Production (tons)
Solea solea	Common sole		88
Gadus morhua	Atlantic cod	>3	1696
Salmo trutta	Sea trout		4389
Argyrosomus regius	Meagre		11,770
Scophthalmus maximus	Turbot	5	71,851
Dicentrarchus labrax	European seabass	8	156,450
Sparus aurata	Gilthead seabream	7	158,389
Oncorhynchus mykiss	Rainbow trout	14	812,940
Salmo salar	Atlantic salmon	11	2,326,288
Cyprinus carpio	Common carp		4,159,177

3.2. Selective Breeding Programs in Fish: Which Goals?

Selective breeding programs in fish have most often focused on improving growth rate [33]-[35]. The genetic gain averaged about 10% - 14% per generation, which is about four to five-fold greater than what is usually obtained in breeding programs for land species [33] [34]. This is mainly due to: a higher genetic variance in fish compared to farm animals, the high fecundity of fish allows for higher selection intensity than in farm animals, and selection has just started in fish, thus problems with reallocation of limited resources has not yet occurred [35]. Other traits have also been included more recently in some breeding programs, such as disease resistance, feed conversion ratio, or flesh quality [33] [34]. However, it was found that without proper management, numerous breeding programs resulted in a rapid loss of genetic diversity as a consequence of inbreeding, leading to a decline of productivity and ultimately the abandon of the program [29] [34] [36]. As most farmed fish species are at an early stage of domestication (levels 2 or 3) or selection (levels 5, but only a few generations), precautions should, therefore, be taken to avoid inbreeding as well as the apparition of similar undesirable side effects (e.g., reduced reproductive performance [28]), as described above for certain livestock breeds [34]. This requires that breeding programs include not only market (e.g., growth rate, flesh quality), but also non-market values (e.g., ethical, welfare), as well as reproductive traits (e.g., fecundity, egg/larvae quality traits) [28] [35]. Also, the size of N_e should be sufficiently large and genetically diverse when starting and then running a breeding program [29] [35]. At last, it is important to consider the possible introduction of genetic variability from outside the breeding stock (wild fish or domesticated fish from other farms [29]) to avoid as much as possible long-term inbreeding and loss of genetic variability [35]. This will probably affect performance, but will help increasing or maintaining the genetic variability on the long term [36].

4. Conclusion

Domestication is a very strong process that has allowed humans to produce various domesticated plants and animals with a large range of desired traits. In land, domestication started about 12,000 years ago and captive animals remained at the levels 2 or 3 for a very long period of time. Thereafter, during the past centuries, domesticated animals reached the levels 4 and then 5 when breeds were created. This results in that today, domesticated animals display a high genetic variability, and strong negative side effects of domestication are restricted to some highly inbred breeds. For aquatic animals, the domestication is much more recent, and the time required to evolve from level 1 to level 5 could be as short as one or two decades in some species. Therefore, what took probably hundreds of years in mammals, took only few years in some fish species. This might result in a strong decrease of the genetic variability of domesticated stocks, particularly when compared to their wild congeners, and ultimately to the apparition of some negative side effects much quicker than in mammals. Therefore, caution should be taken when implementing breeding programs to adequately balance the demand for improving rapidly fish production performances and the conservation of sufficient genetic variability and capacity of fish to adapt to diverse environment, particularly in the current context of climate change.

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