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Effects of Domestication on Fish Behaviour

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Abstract

Domestication is a process by which humans select some phenotypes of wild animal species (i.e., morphological traits or growth), but as all traits are linked, the selection of a particular one has consequences on others. In that context, behavioural traits may be affected by human selection. In this chapter, through classical behavioural traits, such as swimming capacities, foraging, social interactions, or reproduction, and also personality or cognitive abilities, what domestication modifies in fish behavioural traits is shown. The information is taken only from studies that make a clear comparison between domesticated and wild animals; the major difficulty was that the domesticated status was not clearly determined. Whatever the behavioural trait considered, domestication affects some of them even after only one generation. These data deserve to be taken into consideration when humans try, not only to domesticate new species but also to release domesticated species into their natural habitats. In this last case, alteration of behavioural traits could make the fish incapable to adapt to their new wild environment and alter their foraging or reproductive performances. Moreover, fish behaviour in farm is currently recognised as an essential component of the welfare and all behavioural modifications must be considered.

Keywords: behavioural traits, hatchery-reared fish, wild fish, performances, behavioural responses

1. Introduction

Behaviour is an animal phenotype and could be considered as a variable of adjustment for an animal to changes of environmental factors. Domestication gives new environmental conditions to animals; they have to adapt to these restricted surroundings. In general, captive conditions are less complex than those of a natural environment but even with less complexity, the environmental conditions of farms or other rearing structures could appear as new for animals. So they

have to adapt. As a phenotype, behaviour is certainly the mean and the most useful to survive under the new conditions. So during the domestication process, behaviour allows the animal to adapt to its new environmental conditions. Through domestication, the artificial selection is a process of changing characteristics of animals by artificial means such as directional selection, familial selection [1] or genomic selection [2], and the domestication may impact the behaviour even after only one generation [3, 4].

Behavioural traits are among the first traits to be affected by domestication [5, 6]. Behaviour is more easily moulded than morphology or chemical composition and thus the costs of behavioural modification are more efficiently adjusted to environmental variations. In his book, Jensen [7] described the effects of domestication in vertebrates, mainly on birds and mammals but there was nothing on fishes. Before that, there were three major reviews [3, 4, 8] on the influence of aquaculture and domestication on fish behaviour. In these papers, the authors summarised most of the available information on the effects of domestication on different traits of fish behaviour. The major aim of these reviews was to consider the importance of behavioural modifications due to domestication on the economic interest of the culture of fishes and on the welfare of animals in fish farms. In this chapter, I focus on the behavioural traits that have been modified by domestication without consideration to either economic objectives or animal welfare.

There are many difficulties to analyse papers dealing with the effects on domestication. First, it is not easy to identify precisely neither the number of generations in captivity nor the link between captive and wild animals. It is easy when it concerns the first generation obtained in captivity, but it is more complex when we address to 'individuals reared in hatcheries' for several years. Most often, we do not know if there was time introduction of wild animal (e.g. males) during the domestication process. Second, in most studies comparing wild and domesticated strains, we have very few information on the characteristics of the wild animals and on those of their native sites. It is important because there is an important variability of the behavioural trait parameters between different populations. Third, in general, fish performances of behavioural traits are tested under laboratory conditions except for displacements for which some experiments were realised in natural water areas. So whatever the experimental sites, the foreigner population (wild or domesticated) needs a period of acclimation to its new rearing conditions. These could introduce a bias in the results.

Behaviour is the basis of all relationships between the animal and its environment and concerns with several behavioural traits: swimming, foraging, predator avoidance, relationships with conspecifics and reproduction. Moreover, it is now known that individuals exhibit behavioural or physiological characteristics, which, if they are consistent over time, define a coping style or personality [9]. As through domestication, human beings select some individuals among a population, this could modify the equilibrium between the different behavioural profiles (or coping styles) of the individuals of a population. Now, some researches integrate this individual component and highlight the effects of domestication on individual behaviour as it has recently been done considering the learning and other cognitive abilities of fish.

In this chapter, I will review some of these behavioural traits in hatchery-reared fishes that have often been altered in a characteristic manner by domestication.

2. Swimming behaviour

Swimming is a general behavioural trait, which is used in different situations: foraging activity, predator avoidance, stress responses or reproduction. For fish, one of the most determinant traits that are able to improve foraging is the swimming ability. In rearing conditions, swimming is no longer as important as in nature; in general, fish have less space at their disposal, but if domestication selects individuals on their morphological and physiological characteristics, this could influence directly their swimming performances.

This behaviour trait has been tested on fishes in response to a predator attack. It is the case for juveniles (between 55 and 125 days old) of the sea bass (*Dicentrarchus labrax*); wild individuals showed a greater angular velocity and a stop distance to a new object more important than reared fishes [10]. These responses decrease with habituation in both groups. It means that wild individuals have a greater reactivity and a longer escape distance from an unknown object in their environment.

In the context of swimming behaviour, one of the more common tested parameter is the C-start response: this is the ability of an individual to rest from a novel environmental situation; it is characterised by a rapid reaction of the body with a C posture and after an S followed by a rapid (less than 10 ms) displacement. It measures the physical ability of a fish to react to a stress situation by using its physical abilities to swim. It has been tested in different environmental situations: pollution [11], water temperature [12], hypoxia [13] or the influence of conspecific presence by comparing solitary and grouped individuals [14]. In all cases, wild fishes showed a greater velocity and more rapid swimming abilities, so it seems that domestication decreases the swimming performances of the fish. This decrease could be parallel to physiological events. Comparisons of swimming and metabolic physiology were done in aquaculture-reared California yellowtail (*Seriola dorsalis*) in comparison to wild individuals. Incremental swimming velocity trials showed that aquaculture-reared fish had a significantly slower mean maximum sustainable swimming speed (4.16 ± 0.62 Body Length s^{-1}) in comparison to that of wild fish (4.80 ± 0.52 BL s^{-1}). In addition, oxygen consumption was significantly higher in aquaculture-reared fish (7.31 ± 2.32 vs. 3.94 ± 1.60 mg O_2 kg^{-1} min^{-1} at $18^\circ C$) in comparison to wild-caught yellowtail (15.80 ± 5.78 mg O_2 kg^{-1} min^{-1}) [15].

This could alter other behaviours, which depend directly on swimming (i.e. foraging, survival). One point that concerns with swimming performances is the ability for reared individuals to be released in wild sites. This is the case for the European grayling (*Thymallus thymallus*) that were tagged with radio-transmitters and tracked in the Blanice River, River Elbe catchment (Czech Republic) [16]. Wild and hatchery-reared fish increased their diel movements and home range with environmental variables (light intensity, flow, temperature and turbidity), but hatchery-reared fish displayed greater total migration distance than did

wild fish, which was caused mainly by their higher dispersal. Patterns in space use and activity were compared for wild and hatchery-reared Mulloway (*Argyrosomus japonicus*) using acoustic telemetry. Adult individuals were followed during 288 h in a river. Hatchery-reared fish used significantly larger areas with higher rate of activity than wild fish, but their movement ranges were more variable [17] than those of wild fish. By comparing initial movement, habitat use, growth and mortality between stocked hatchery and wild fish of juveniles of Florida Bass (*Micropterus floridanus*) with a radio telemetry experiment, Thomson et al. [18] showed that tagged hatchery fish exhibited greater movement (75 and 124 m/d, respectively), greater proportion of locations offshore (8 and 23%, respectively), but slower growth (1.73 and 0.41% of their body weight gained per day, respectively), and higher predation (47 and 0%, respectively) than wild fish.

These results showed that domestication can not only be influenced through selecting the physical characteristics of the individuals, but also through their swimming performances and consequently the foraging and space use by hatchery-reared individuals when released in wild conditions.

3. Foraging behaviour

Foraging is not only the activity, which consists to take off resources in the environment, that is, prey, but also the choice of the best site or the most favourable period where and when to forage. The animal must be at the good place at the best moment. This aim seems easy for animals in controlled environments where the food is abundant and regular; but this fact could be a disadvantage when aquaculture-reared fish are released in natural environment in order to supply the low level of the wild stocks.

Fishes change their foraging habits with domestication. Zebra fish (*Danio rerio*) and coho salmon (*Oncorhynchus kisutch*) change the place where they forage after domestication after just one generation. Domestic fishes swim at the surface of the water column instead of the lower part for wild animals [19, 20]. One of the consequences is that farmed animals had a higher rate of prey capture than their wild congeners [21, 22]. These changes in foraging behaviour could be the result of changes in the relation of the fishes with its environment: as the predation rate was lower for farmed fishes, they adopt a more risky behaviour near the surface; the farmed conditions modified also the social relationships between individuals and could result in a lower influence of dominance in the foraging behaviour [23].

Perhaps, the main difference is that the natural environment provides a lot of different situations to which fishes have to adapt. It seems that the environmental complexity of natural environments may facilitate training to different situations [24], with a more important prey variability [25–27] or opportunity of social learning [28]. Consequences could be measured when farmed fishes were realised into natural environment: they use less of natural objects such as stones or leaves for digestion than wild animals [25] or they make no difference between prey of different profitability [26] and they do not choice an unknown prey [27].

The conditions of foraging allow the fish to get a certain amount of resources from the environment and could explain important differences between hatchery-reared and wild

individuals in terms of survival and growth. If we compare the survival rate of aquaculture-reared or wild Chinook salmon fry (*Oncorhynchus tshawytscha*) facing predation by rainbow trout (*Oncorhynchus mykiss*) or sculpin (*Cottus rhotheus*) under experimental conditions, wild fry had a survival advantage within the two next years of experiment [29]. So it is possible that the domestication can affect the vulnerability of juveniles of salmon after only one generation in a culture system. But it is not always the case. For example, the survival of Atlantic salmon (*Salmo salar*) in the Baltic Sea was examined in relation to the origin, and prey fish abundance (here herring *Clupea harengus* and sprat *Sprattus sprattus*). The study was based on recapture data for tagged hatchery-reared, and wild smolts demonstrated a combined influence of origin and environmental factors on survival; prey fish abundance had no influence on the survival of reared or wild smolt groups [30]. The results suggest that some larger smolt of the reared groups compared with the wild groups compensated for their lower ability to live in the wild.

4. Predator avoidance behaviour

The anti-predator behaviour is highly sensitive to artificial rearing and so to domestication [12, 31–36]. Anti-predator behaviour is thought to change during domestication, along with other traits. One prediction is that domestication should reduce behavioural responses to predation risk. This prediction was supported by a lot of studies most of the time on salmonids, on rainbow trout (*Oncorhynchus mykiss*) [31, 32], on brown trout (*Salmo trutta*) [12] and on Atlantic salmon (*Salmo salar*) [35, 37].

In wild population, decreased activity, spatial avoidance of risky areas and the use of refuges reduce the rate of mortality caused by predators [38, 39]. This natural reaction of a fish faced to a high level of predation seems to disappear after two or three generations reared under artificial conditions; that is, after two generations, the common trout becomes non-sensitive to the predation risk; animals were active during the daylight and not during the night as their wild conspecifics [40]. As a consequence, domestication would decrease the level of defences against predators, as the reared animals would not experiment contacts with predators or some other life history traits should be affected by domestication and consequently affect the response of the animal to predator risk. For example, wild fishes react more rapidly to a predator than reared fishes [41, 42]. Wild animals may use natural refuges in their environment they know to escape from predation [43]. Moreover, wild individuals seem more careful to predators than reared fishes in the common carp (*Cyprinus carpio*); but these results are under suspicion because ‘wild’ animals are in fact reared individuals, which were returned back to natural conditions [44]. Domestication may also affect the reaction to a novel object in the environment; reared fishes approach more easily to a novel object and take more risks [36, 45]. This difference in behaviour is linked to physiological variations (heart activity, mobility, swimming abilities...) [35, 37]: but the results are not so clear and in a large number of cases, the responses of reared fishes to predators are variable [19, 46].

Some more recent results confirm the complexity of the relationships between this behavioural trait (anti-predator behaviour) and domestication. For example, the anti-predator behaviour of juvenile Atlantic salmon of conventional hatchery compared with that of wild-caught juveniles from the same population, tested in two unfamiliar environments, did not

differ between the two strains in the spontaneous escape response [47], but after this first reaction, hatchery-reared juveniles stayed less time in association with the shelter than the wild animals. The same result has been found in the grass carp (*Ctenopharyngodon idella*); in the frame of restocking programs using hatchery-reared individuals, it is important to test the anti-predator behaviour. This behaviour was compared with that of wild-caught animals. The two groups exhibited a clear anti-predator behaviour; however, the hatchery-reared individuals showed lower aggregation and spent time in the risky areas and most of them were predated [48]. These variations between domesticated and wild strains in the display of the anti-predator behaviour are well documented in rainbow trout (*Oncorhynchus mykiss*). Comparisons between wild and hatchery population between clonal lines of rainbow trout derived from either wild and hatchery-reared populations identified several genes associated with behavioural variations between lines [49]. These genetic variations underlying anti-predator behaviours may be used in conservation programs for monitoring alleles of loci affecting predation in natural populations.

As behaviour is a phenotype corresponding to the plasticity of the responses of animal to the set of environmental conditions, it is interesting to understand how development can affect the behaviour of different genotypes. Now, the existence of transgenic species offers a good tool to study this problem. By comparing wild-type siblings and transgenic individuals, Sundström et al. [50] found that wild and transgenic animals behave in the manner under natural like conditions; but until now, there are not a sufficient number of studies to conclude that genetically modified organisms are not affected by the complexity of natural conditions.

5. Social behaviour

Social behaviour is particularly developed in fishes, such as shoal [51], which is a part of the social life and is present in more than 25,000 species [52]. Shoal is important and ensures protection against a potential predator (a particular prey is undetectable in the group), but also it increases the foraging efficiency (the amount of food per individual is higher in groups than for solitary fishes whatever their diet). Shoal — defined as a group of individuals [51] — may be influenced by environmental factors, and domestication is one of these factors; reared conditions modify the fish environment. It limits the available space for fishes that could have for consequences a non-response of the fishes to environmental stimuli [53]; in reared conditions, food is distributed *ad libitum*, and such situation modifies the foraging behaviour limiting the exploration of the environment [54] and the predator avoidance [12, 32, 55]. In domesticated fishes, there is less variability of the age and size of the individuals, and so, the relations between fishes are modified and the results are counterbalanced; in some studies, they show that there is an increase of the aggressiveness between individuals [56, 57], and in other studies, they find that the aggressiveness is higher in domesticated populations [55, 58]. Growth in rearing situations is influenced by intra-specific competition [59, 60].

One of the most important components of the social relations between individuals is the agonistic behaviour. Comparisons between wild and reared fishes show that new agonistic behaviours do not appear due to domestication [61]; agonistic behaviours are the same for both wild-reared individuals. In general, agonistic behaviours appear for the competition for resources: prediction is that agonistic behaviours must be less numerous when the

quantity of resources increases. Domestication introduces the selection of individuals with a rapid growth; the consequences on the level of agonistic behaviours between individuals inside the groups are very dependent of the situation. Globally, it has been demonstrated that an effect on agonistic behaviours exists [62]. Agonistic behaviour can increase for domesticated fishes [58, 63, 64] or decrease [56] or be stable [57]. For example, the brown trout sea-ranched individuals have a higher growth rate and have no difference of activity with wild animals, but intensity of agonistic behaviours was higher in wild individuals [65]. These results could be interpreted as a consequence of the rearing conditions; in wild populations, agonistic behaviour has a function for space sharing, food accessibility [66], foraging efficiency and predator avoidance [67, 68]. So selection in rearing conditions leads to the individuals that have the most rapid growth but with particular behavioural traits (i.e. the most aggressive fishes); it is a known phenomenon, analysed as phenotypic selection (or economic selection by culturists) [69]. This implies that fishes are selected on their size and growth rate, and the dominance effect, which could be the result of competitive relationships, disappears if we introduce the size as variable [23]. But the dominance depends on the environment; this could be linked to the residence effect, which exists in wild fishes and not in reared ones [70]. In any case, competitive behaviours are the same; they vary in quality and intensity between wild and reared fishes [71]; for example, the high density for reared fishes in tanks could induce less territoriality and so a lower aggressiveness during dyadic confrontations [70, 72]. Competition and dominance have been tested in the salmon (*Oncorhynchus tshawytscha*) and the results showed that wild fishes were more aggressive than fishes from the first generation (F1) reared in aquaculture [73]. In general, the consequence of dominance is better growth rates for the dominant individuals whatever their origin (wild or reared). More recently, a relationship was found on the influence of domestication on brain size and aggressive behavioural changes. A study on rainbow trout lines highlighted that some behaviours such as 'freeze' and 'escape' are associated with a high level of domestication instead of 'display' and 'yawn' behaviours, which are linked to wild lines [74]. Moreover, these authors found that the total brain size and olfactory volume were associated with domestication.

An important consequence of the level of aggressiveness between individuals is the existence of cannibalism [75]. It could appear either within the same cohort or between different cohorts. Cannibalism is a natural phenomenon, which is for regulating natural populations in many fish species. In cultured fishes, cannibalism has a negative effect on the populations; some individuals switch from food given by humans to the attacks and consumption of conspecifics.

6. Reproduction

There is very few data on the influence of domestication or different lineages on the reproductive behaviour of fishes? This is the consequence that the reproductive behaviour in reared fishes received very little interest. It is the consequence that humans biased reproduction in reared fish populations; in fact, it is always handed by humans, and there is neither mate choice nor normal reproductive behavioural sequence. So, comparisons of reproductive behaviours between wild and reared fishes are based on behavioural differences between reared fishes that returned to natural environment and wild animals.

Studies focused on the choice of the spawn area; reared animals had more difficulties to find the good place to spawn with environmental features [76]. But the results are not so clear. Reared fishes may arrive earlier on the spawning zones than wild animals [77]. Fishes show different strategies with regard to their origin (wild or reared) [30, 78].

Most of the studies on the influence of domestication on the reproductive behaviour are done on salmonids because this is the group of species with the highest pressure for restocking the natural populations with hatchery-reared individuals, so it is absolutely necessary to evaluate their reproductive performances under natural environment. Coho Salmon (*Oncorhynchus kisutch*) produced by hatcheries have lower fitness in the wild than naturally produced salmon, but the factors underlying this difference remain an active area of research [71]. Neff et al. [79] used genetic parentage analysis of juveniles produced by experimentally mixed groups of wild and hatchery coho salmon to quantify male paternity. In all contexts, wild animals showed a higher paternity rate than hatchery-reared individuals.

7. Personality

The concept of behavioural syndrome (synonyms = personality, temperament, behavioural differences) is defined as a collection of behavioural traits, which are constant over time and environmental situations [80]. It does not mean that these traits do not evolve with time for example, but that the combination of them is constant. This concept has been widely used in fishes. These behavioural syndromes may be dependent from the environmental situations (i.e. high or low density) and have different performances (i.e. boldness or shyness are the most efficient). This concept has been used for cultured fishes (*Salmonidae*) in order to select the most advantageous behavioural traits for the rearing of fishes in captivity. The human selection on economic criteria (size, growth) may be biased and this selection leads to keep the individuals that have the highest boldness (as in *Salmonidae*). But these results are not so clear, and in some cases, the selection of the individuals, which have the highest boldness, leads also to the selection of the most aggressive animals, i.e. salmon reared in farm for many generations are more aggressive and bold than individuals hatched in farm but from wild parents [72, 81]. Now, it is possible by comparing wild and domesticated strains, to show the existence of QTL for personality trait such as boldness. By testing the boldness of Zebra fish (*Danio rerio*), Wright et al. [54] showed that there are strong behavioural differences between a wild-derived strain of fish and a laboratory strain AB. Based on anti-predator behaviour, their results indicated a QTL for boldness on chromosomes 9 and 16 and suggest another genomic region that influences anti-predator behaviour on chromosome 21. So, these results confirm the possibility of QTL mapping of behavioural traits in zebra fish and the consequences of selection during domestication.

These behavioural differences between captive of reared fish and their wild conspecifics could be used in the frame recovery programmes for threatened and endangered species. By comparing the boldness and prey acquisition behaviours of wild bull trout (*Salvelinus confluentus*) and reared ones, Brignon et al. [82] showed that wild fish and captive reared fish from complex habitats exhibited a greater level of boldness and prey acquisition ability, than fish reared in conventional captive environments. These results suggested that rearing

fish in more complex captive environments could create a more wild-like phenotype than conventional rearing practices.

In this frame of animal personality, or coping style, an important effect of the domestication is the reduction of emotional reactivity or responsiveness to a fear-evoking stimulus [83]; the emotional reactivity of wild fishes is better than those of reared individuals [84]. The emotional reactivity of an animal is necessary for provoking a flight response when there is a potential danger; it could be linked to a survival response. It seems that after domestication, fishes lost very rapidly, in only one generation, the stress response. This change in behaviour is probably directly linked to physiological changes: in the rainbow trout, two different lineages were selected on the basis of their rate of cortisol as responsiveness to stress. Individuals, which showed a low rate of cortisol, had a lower response to stress; they developed a better foraging behaviour but had a bad response to a potential danger. These individuals were well adapted to the environmental conditions of fish farms, but not the natural environment [85]. This is a general problem; the selection by humans of particular lineages of fishes based on their potentiality of growth and development has an influence on other life traits especially on behavioural traits. In the sea bass, the repetitive application of stress elements (pursuit of the fishes with a net, luminous changes, application of predator lure) modifies the foraging habits of wild fishes but also of reared ones. This could be interpreted as a habituation to the situation, which becomes less stressful [86].

8. Learning-cognition

If the domestication process leads to a change in behavioural traits, empirical evidence for a difference in cognitive performance, however, is scarce. In the framework of animal personalities, differences in behaviour may arise during ontogeny through learning and bolder, and more aggressive animals (usually, the wild form) should learn faster. Such examples exist in vertebrates especially in mammals; by comparing wild cavies and domestic guinea pigs (*Cavia porcellus*) in behavioural tests. Domestic guinea pigs were less bold and aggressive than their wild congeners, but learnt an association faster [87]. Such studies exist also in fish but are scarce, and now, results are not clearly established, leading an important field of research. For example, Klefoth et al. [88] tested two common genotypes of common carp, *Cyprinus carpio* L., differing in degree of domestication (a highly domesticated mirror carp and a less domesticated scaled carp) exposed to fishing. Domesticated mirror carp were more vulnerable to angling gear than scaled carp in both environments; these results were related to a bolder-foraging behaviour for the latter. Independently of genotype, fish become more difficult to catch, indicating learned hook avoidance, based on the boldness, so scaled carp get an advantage with a lower vulnerability to fishing. The study of Rodewald et al. [89] showed that after their release in natural environment, hatchery-reared salmon had a lower foraging rate than wild individuals. They showed that this difference was the consequence of higher abilities of learning the new environment and especially the presence of potential prey by the wild fish. Such studies should be initiated before the reintroduction of hatchery stock in the natural habitat, to ensure the success of the operation.

9. Conclusion

'Domestication is that process by which a population of animals becomes adapted to man and to captive environment by genetic changes occurring over generation and environmentally-induced developmental events recurring in each generation [90]'. It affects all functions of the organisms and, in particular, behaviour. There are behavioural differences between wild and reared fishes (see **Table 1**), but these differences are more quantitative than qualitative; no new behaviours appear with domestication.

The selection of individuals for economic reasons leads to the selection of fishes on morphological or developmental traits (growth, size). These traits are directly linked to other biological traits (i.e. behaviour) and their selection may lead to select fishes, which present some behaviours affecting the life in groups of high density and so the development of each individual (increase in aggressive and agonistic interactions between individuals, higher levels of cannibalism). One solution to prevent that is to identify as soon as possible in the fish development the behavioural profiles of the individuals under different domestication levels [91]. These studies lead to better knowledge of the fish larvae, which are difficult to test given their high sensitivity to environmental conditions.

In this review, we saw that all behavioural traits may be impacted by domestication even after only one generation. For some traits, the results are clear and follow the same trend; the response to a predator is affected by domestication whatever the domesticated species and the reared environment. But in some cases, it is more difficult to find a common trend: foraging is affected but it depends on the type of food, and on the feeding conditions. It is the same for aggressiveness in the hatchery-reared individuals; it could decrease in that way we can put a high number of predators together if we give them a sufficient amount of food, but on the other hand, the high fish density in tank can produce a high level of aggressiveness between individuals leading to cannibalism event if the food is abundant. It is also true for other behavioural traits such as personality or cognitive capabilities; until now, there is a lack of studies on the influence of domestication on these behavioural traits and it is not possible to conclude. What we know is that the human selection on morphological or physiological traits of some individuals (even through a genetic program) has a direct influence on behavioural traits.

This has two implications: first, it is necessary to study behavioural traits in the case of domestication of new species in order to determine the best environmental conditions of rearing, and second, these behavioural trait modifications must be into account when release of domesticated animals into natural habitats is considered. For these two points, we have to keep in mind that the consequences of behavioural selection traits through domestication correspond to the selection of a particular behavioural trait belonging to the natural behavioural range of the species under rearing environmental conditions; this might lead to a new species, the other behavioural traits of the species range disappearing. It is known under a genetic-environment process by which the epigenetic landscape is modified by the environment constraints influencing directly the genetic program [92, 93].

Behavioural traits	Type of responses to environmental constraints	Effects of domestication	References
Swimming behaviour	Response to a predator attack	Wild is more reactive than hatchery	[10]
	Response to a novel environment	Wild exhibits higher swimming abilities	[11, 12, 13, 14]
	Capacity to be released in the wild	Wild exhibits lower dispersal	[16, 17, 18]
Foraging behaviour	Changing the foraging strategy	Hatchery exploits all the water column	[19, 20]
		Hatchery has a higher capture rate	[21, 22]
	Prey profitability	Wild has better rate than hatchery	[26]
	Consequences on survival	Wild shows a higher rate of survival	[29]
Predator avoidance	Reaction in front of a predator	Wild is more rapid	[41, 42]
	Reaction to a potential predator	Hatchery takes more risks	[36, 45]
	Spontaneous escape responses	No difference between wild and hatchery	[47]
	Use of shelter	Wild has a higher rate	[47, 48]
Social behaviour	Aggressiveness	Hatchery is more aggressive than wild	[56, 57]
		It is higher for hatchery	[55, 58]
	Agonistic behaviour	It is higher for hatchery	[58, 63, 64]
		It is higher for wild	[56, 65]
		There is no difference	[57]
	Competitive behaviour	Territoriality is higher in wild	[70, 72]
		Dominance is higher in wild	[73]
Reproduction	Cannibalism	No information?	
	Abilities to reproduce after realising	Paternity rate higher for wild	[79]
	Choice of place to spawn	Better for wild	[76]
		No difference	[77]
	Fitness in natural sites	Higher for wild	[71]
Personality	Boldness	Higher for hatchery	[72, 80]
		Wild higher than for wild	[82]
	QTL mapping	There is no difference in prey acquisition	[54]
	Stress	Wild is more stressful than hatchery	[83, 84]

Behavioural traits	Type of responses to environmental constraints	Effects of domestication	References
Cognitive abilities	Learning	Wild is less bolder-foraging than hatchery	[88]
	Releasing	Wild learns new environment faster	[89]

Table 1. Summary of the different results found for this review. The behavioural traits were divided in behavioural acts and their responses to domestication process in fish were briefly described. Wild referred to animals coming from wild strains and hatchery for fish larvae reared under farm or laboratory conditions.

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