Genetics of adaptation and domestication in livestock[☆]

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Abstract

In this review, we assess the current state of knowledge on domestication of the major livestock species. We present first some historical background on location and dates of domestication of livestock. The characteristics that favoured domestication are described, especially gregariousness, precocity of young and diet. We then describe the genetic processes involved during domestication, i.e. uncontrolled processes such as inbreeding and genetic drift, partially controlled processes such as relaxation of natural selection and natural selection in captivity and controlled processes such as active selection. Details are also given on how the resource allocation theory explains changes occurring during domestication. The methods used to assess the extent to which domestication has changed animals (comparisons of wild and domestic stocks, longitudinal analysis and molecular genetics) are also listed. Finally, major behavioural modifications observed during domestication are described, including relationships with humans and predators, and social, feeding, reproductive and maternal behaviours as well as morphological changes.
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1. Introduction

Several definitions of domestication can be found in the literature. Among them, Price (1984) defined domestication as "the process by which captive

animals adapt to man and the environment he provides". Adaptation is achieved through genetic changes over generations, which involves an evolutionary process, and also through environment stimulation and experiences during an animal's lifetime, which involve ontogenetic processes (Price, 1984). Domestication is the first step of selection and has to be distinguished from taming, in that domestication means that breeding (by choice of the reproducers and isolation from wild counterparts), care (shelter, food, protection against predators) and feeding of animals are more or less controlled by humans (Hale, 1969). Therefore, simply rearing animals in an adequate environment for a species (as for oysters or mussels) cannot be considered as domestication.

Very few species have been domesticated. In the case of livestock, among 148 non-carnivorous mammal species weighing more than 45 kg, only 14 have been domesticated (Diamond, 1999). Thirteen of these species come from Europe or Asia and only one from America (the llama). The proportion is even lower in birds, with 10 of around 10,000 species being domesticated. Finally, domestication of fish is beginning in a few species. There is huge variability in indicators of successful domestication such as spread area and size of the domesticated population and extent of the control of humans on production or reproduction. Depending on these indicators, domestication of the species is uncontested (e.g. cattle) or still debated (e.g. the carp). For example, among cattle, common cattle and zebu (*Bos* genera) are spread throughout the world and domesticated populations include more than 1200 million animals (Lenstra and Bradley, 1999). In contrast, the numbers of domesticated silver fox and Bison are low. The domesticated population of the latter is even less than the wild population (i.e. 15,000 domesticated vs. 25,000 wild). The area of domestication is restricted for reindeer and rabbits. Finally, human control of

production and reproduction of fish is only moderate. However, these minor species in which domestication is not complete can provide us with very useful information on the domestication processes and have therefore been included in this review.

While domestication events occurred at different places and times, the history of domestication has spread over the last 14,000 years before present (YBP, Belyaev, 1979). The first species to be domesticated was the dog (14,000 YBP), which humans used first for hunting and as watchdogs (Braastad and Bakken, 2002). Domestication of livestock began with the major current domesticated species used as food sources and labour animals from 8000 to 10,000 YBP (see Fig. 1a and b), sheep and goats apparently being the first (Craig, 1981). Domestication of these species occurred mostly in the Middle East and Asia (Bruford et al., 2003, Fig. 1b). Horses, donkeys, water buffalos and llamas were domesticated later, around 6000 YBP. In the case of the horse, it appears that domestication occurred simultaneously in various places (Bruford et al., 2003). For some minor species such as the gayal, the date of domestication remains unclear (Lenstra and Bradley, 1999). The main bird species were domesticated after mammals, domestication of chickens and geese being between 5500 and 3000 YBP (Wood-Gush, 1958; Leclercq, 1990) while fish species were not domesticated until the Romans domesticated the carp (Balon, 1995; Vandeputte and Prunet, 2002). Evidence of domestication of other species comes from the end of middle ages, with the domestication of rabbits and turkeys (Brant, 1998; Morton, 2002). Most recently, i.e. in the last 150 years, a period of domestication has occurred in order to fulfil specific product needs, such as fur (e.g., fox and mink) and alternative sources of meat (e.g., ostrich and salmon, Jensen, 2002a).

The small number of domesticated species can possibly be explained by the characteristics required

Fig. 1. (a) Dating of the domestication of the major livestock species. References used for the figure: Anonymous, 1997; Avignon, 1981; Balon, 1995; Belshaw, 1985; Brant, 1998; Bruford et al., 2003; Diamond, 1999; Giuffra et al., 2000; Guy and Buckland, 2002; Hale et al., 1969; Hall, 2002; Jensen, 2002a,b; Keeling, 2002; Leclercq, 1990; MacDonnell, 2002; MacHugh et al., 1997; Mills et al., 1997; Morton, 2002; Price, 2002; Rutter, 2002; Vandeputte and Prunet, 2002; Wood-Gush, 1958; Zeder and Hesse, 2000; Zeuner, 1963. (b) Sites of domestication of the major livestock species. References used for the figure: Anonymous, 1997; Avignon, 1981; Balon, 1995; Belshaw, 1985; Brant, 1998; Bruford et al., 2003; Diamond, 1999; Giuffra et al., 2000; Guy and Buckland, 2002; Hale et al., 1969; Hall, 2002; Jensen, 2002a,b; Keeling, 2002; Leclercq, 1990; MacDonnell, 2002; MacHugh et al., 1997; Mills et al., 1997; Morton, 2002; Price, 2002; Rutter, 2002; Vandeputte and Prunet, 2002; Wood-Gush, 1958; Zeder and Hesse, 2000; Zeuner, 1963.
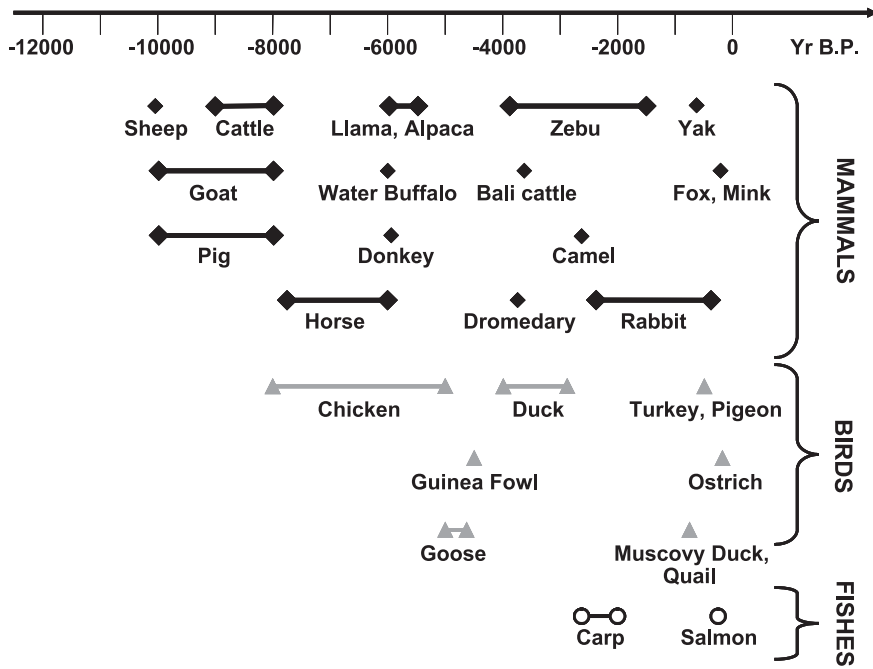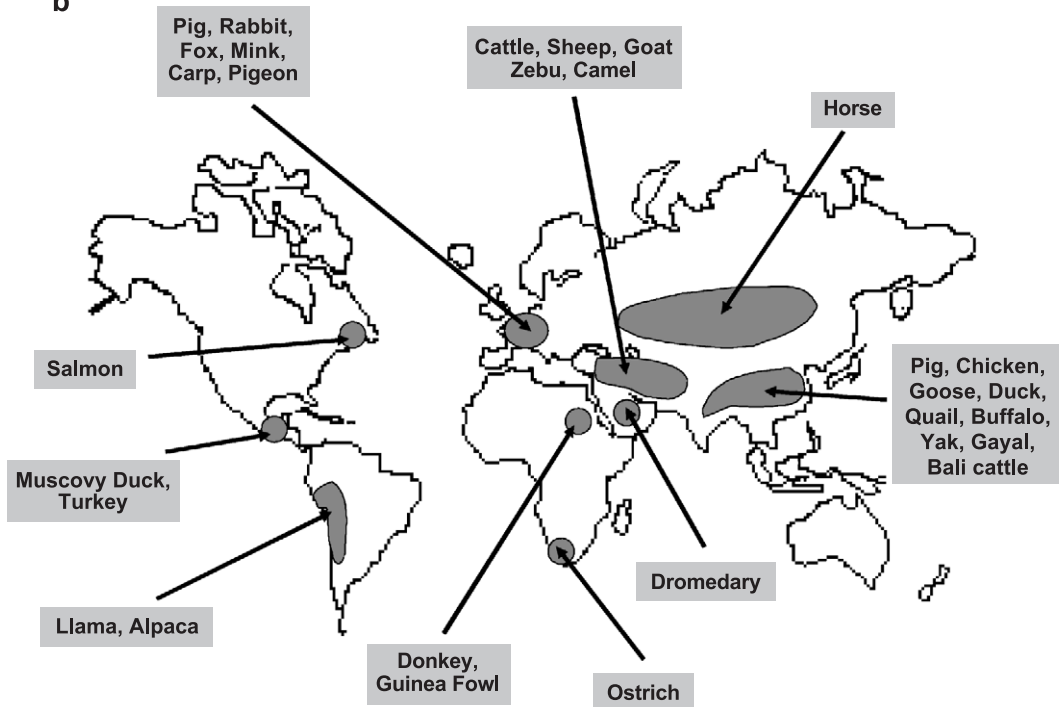
for domestication, including traits such as diet, reproduction, social relationships and behaviour towards man. Among these characteristics, the most important are a strong gregariousness (Diamond, 1999), feeding regimes that can be easily supplied by humans, which may explain why carnivores are scarce among domestic species, and precocious young (Diamond, 2002). It is also probably the reason why most of the earlier domesticated species are ungulate mammals and gallinaceous birds, as they are gregarious, herbivorous or omnivorous and have precocious young (Jensen, 2002a). In addition, reproduction is easier in captivity if males are dominant, if sexual signals consist of movements and postures instead of colour or morphology and if mating is extra-pair mating (Price, 1999). In contrast, reluctance to breed in captivity (e.g., the panda) or long birth spacing (e.g., the elephant) are unfavourable (Diamond, 2002). Large groups with a hierarchical dominance structure enable humans to adopt the role of the dominant animal within the herd (Jensen, 2002a). In contrast, large territories and solitary habits (e.g. deer) are unfavourable. Parent–young interactions that include a sensitive period between mother and offspring (e.g. imprinting for birds) and precocious young are advantageous in the domestication process. High maternal ability increases animal autonomy and is thus also a desirable trait in a wide range of environments. Most domesticated species also show behavioural plasticity that enables them to adapt to captivity constraints and to a wide range of environments. This may be one reason why gazelles have not been domesticated, as they panic in enclosures (Diamond, 1999). They should also show low reactions to humans (e.g., short flight distance) and low fear reactions (Price, 1999; Diamond, 2002). Great agility (e.g. the antelope) makes it difficult to handle animals, and is thus to be avoided.

Most of the behavioural characteristics mentioned above are present in the earliest domesticated species. However, in most cases, the presence or absence of some of these characteristics cannot be a predictor of the domestication or non-domestication of a species. For example, even the absence of many of these characteristics does not preclude domestication of the pigeon. Pigeons have a long flight distance to man, are fearful, require a specific habitat, and are extremely agile. Moreover, males live in family groups, are territorial, and form pairs with females. However, despite these drawbacks, the pigeon has nevertheless been domesticated. At the other extreme, the highly aggressive behaviour of rhinos toward man is a sufficient reason to explain why they have not been domesticated, although it may not be the only one (Diamond, 1999).

2. Genetic basis of livestock domestication

2.1. Genetic processes

Three main genetic processes are involved in the evolution of animals during domestication: inbreeding, genetic drift and selection (Ollivier, 1981). The first two are dispersive processes resulting from the limited size of the population and leading to random variations in gene frequencies (Beaumont et al., 2002). At the opposite end of the spectrum, artificial selection is a controlled process. Relaxation of natural selection and natural selection in captivity are partially controlled by humans, through determining environmental conditions.

Relaxed natural selection consists of a reduction of the selection pressure. It applies to traits that are important in nature but not in captivity, such as food finding, seasonal reproduction, plumage or coat colour, and predator avoidance. Domestic animals can thus be more variable for these traits than their wild counterparts (Price and King, 1968). This is, for example, the case in withdrawal reactions to humans in sheep, which are very variable among both highly and less domesticated breeds (Lankin, 1997).

Artificial selection and natural selection in captivity modify traits in a given and foreseeable direction. Natural selection eliminates animals unable to reproduce in captivity, and favours animals which can wean a high proportion of young in the environment provided by humans. For example, Kawahara (1972) reported a 50–67% increase in laying rate in wild Japanese quails after three generations of breeding in captivity.

Artificial selection involves humans selecting the breeding animals and is a process specific to domestic species. It has resulted in the creation of different breeds (Beaumont et al., 2002). The efficiency of artificial selection has greatly improved since quanti-

tative genetics has been used to increase selection pressure.

While all these genetic processes can be involved to different extents and in various directions, the resource allocation theory could be helpful to predict the changes resulting from domestication.

2.2. Resource allocation theory

The resource allocation theory argues that under selection within a particular environment, the resources used by the animal are optimally distributed between the important traits for breeding and production within that environment (Beilharz et al., 1993). This implies that any additional selection-mediated increase in performance of a production-related trait, without a concurrent increase in resources, must lead to declines in other traits, due to a re-allocation of resources. The decrease in these traits is proportional to the heritability of the "allocation factor", defined as the proportion of resources devoted to production vs. fitness (Van der Waaij et al., 2002).

When animals are undergoing domestication, two phenomena may happen. First, some traits such as ability to compete in sexual competition or aptitude to hide from predators will have a decreased weighting in total fitness because humans choose the breeders and provide shelter. This may explain why white colour or plumage is less frequent in wild animals, as this colour makes them too easy for predators to locate (Beilharz et al., 1993; Gross, 1998). Secondly, by active selection, the weighting given to some other components will be increased. When the domestication process begins, the relative importance of ability to reproduce in captivity or tameness increases. Subsequently, with active selection, the weighting given to production will increase. After a certain time, as equilibrium is expected to be reached within a given environment, highly specialised animals may have difficulty in adapting to changes in their breeding conditions, as no buffer is left to respond to unexpected changes. Finally, if the weighting given to production is disproportionate, resources are diverted from other traits, such as health or reproduction. This may explain why high-producing dairy cows often have reproduction problems (as reviewed by Rauw et al., 1998).

3. Methods to investigate consequences of domestication

3.1. Comparisons of wild and domestic stocks

The most commonly used method to study how domestication has changed animals is to compare wild and domestic animals of the same species in captivity and in the wild environment. However, it is sometimes difficult to find wild representatives or breeds, except for fish, for which the domesticated animal is more difficult to find than the wild. For instance, in sheep the wild bighorn is thought to represent the remnant of formerly domesticated sheep that have escaped from humans (Rutter, 2002). Even when wild references exist, there is usually not a single form, and a representative sample must be utilized (Price, 2002). The difficulty in utilizing a representative sample usually leads to studies based on comparison between two domesticated stocks differing in the intensity of their relationships with humans. For example, Boissy et al. (1996) compared Romanov with Lacaune sheep, to evaluate variability in flight distance to humans. However, these comparisons cannot help to understand changes that happen in the first generations of domestication. In addition, such studies have to take into account the presence of genotype–environment interactions. For example, Limousine cattle show a greater flight distance than Jersey cattle when reared in their usual environments (extensive and intensive, respectively), but the difference disappears if both breeds are reared in similar extensive conditions (Fisher et al., 2001).

3.2. Longitudinal analysis of wild animals kept in captivity

Longitudinal analysis is an approach involving looking for phenotypic changes in wild populations kept in captivity (Price, 2002). The representativeness of the wild reference is not as important as in breed comparisons, as the purpose is to quantify the rate of evolution with time. For example, Kawahara (1972) kept a wild population of Japanese quail in captivity for 15 years. As a result of natural selection in captivity, the laying rate rapidly increased in the wild population, as quails not reproducing in captivity were eliminated. Kawahara et al. (1974) also showed the

effects of inbreeding, as genetic variability of all traits decreased, although polymorphism and heterozygosity remained greater in the wild population than in a domestic population bred in the same conditions (Kimura, 1989). Belyaev (1979) kept silver foxes in captivity and observed major modifications of behaviour and morphology. After 18 generations, fur colour, relationships with humans, and social attitudes were very close to those of the domestic dog. However, in this case, animals were artificially selected for tameness, which probably increased the rate of evolution of these traits in the population.

3.3. Results brought by molecular genetics

Molecular genetics information contributes to better understanding of the history of domestication (see Bruford et al., 2003 for a review). Giuffra et al. (2000) used mtDNA to prove that pig domestication occurred independently in both Asia and Europe, followed by an introgression of Asian pigs into European breeds. Molecular tools may help to quantify the introgression of escaped domestic fish into wild populations (Garant et al., 2003).

More recently, the tools of molecular genetics have been used to investigate to what extent gene frequencies have changed between wild and domestic animals. Identifying quantitative trait loci (QTL) involved in the determinism of traits related to the capacity of adaptation allows investigation of sources of genetic variability. When possible, studying a cross between wild and domestic animals will allow investigation of the effects of domestication. For example, in a second generation cross between wild Jungle Fowl and the domestic White Leghorn, Schütz et al. (2002) and Kerje et al. (2003) found two major QTL located on chromosome 1 showing a high pleiotropic effect on behaviour in stress-related traits (duration of tonic immobility, distance moved in open-field test, reaction to restraint test), growth and egg production, comb size in males and females (Pizzari et al., 2004) and in the size of the testes. Together with two other QTL, they explained 80% of variation in adult growth in males and 50% in females.

As for comparison of breeds, the wild reference is often difficult to find. Therefore, crosses between two domestic breeds differing by their intensity of relationship with humans have been used in the majority of QTL studies. For example, Fisher et al. (2001) detected QTLs influencing flight distance to man with a cross of Limousine and Jersey cattle. Similarly, Schmutz et al. (2001) found QTLs involved in the determinism of movement score and habituation in cattle, most of them showing a pleiotropic effect on both traits. However, crosses between two domestic breeds do not allow identification of genes that were fixed at the beginning of the domestication process. This is probably the reason why QTL detected in the White Leghorn×Red Jungle Fowl experiment have not been found in crosses between domestic lines (Schütz et al., 2002; Kerje et al., 2003).

4. Which traits have been modified during domestication?

Domestication has resulted in modifications of many traits determining the capacity of adaptation of animals, including behaviour, and also other traits, such as physiology and morphology. The aim of this section is not to give a complete overview of all these changes, but rather to provide elements to understand which changes occurred during domestication. With regard to morphology, as a result of relaxation of natural selection on predation, the proportion of white colour has increased in domestic populations (see review by Gross, 1998). Pied baldness also appeared in Belyaev's tame foxes (1979), probably due to a pleiotropic effect of a lower level of thyroxine in less fearful animals (Diamond, 1999). Size has been consciously increased in small species, in order to increase meat quantity, but reduced in large species to make them easier to handle. Aurochs were thus twice as tall as Celtic cattle (Clutton-Brock, 1992). Size modification is not homogeneous. For example, fat content has increased in fish (Gross, 1998) and fat location has been modified in cattle. It is stored under the skin and around the kidneys in wild animals, and in muscle and around the tail in domestic animals (Clutton-Brock, 1992). In most domestic species, head or brain size has decreased (Gross, 1998; Diamond, 2002).

With regard to behaviour, it can be argued that domestication has mostly resulted in quantitative rather than qualitative changes. Behaviours traits did

not appear or disappear, but the thresholds of their expression changed (Price, 1999). Pigs and wild boars show little difference in their behaviour, and domestic pigs placed in a natural environment express similar behaviour patterns to their wild counterparts (Jensen, 2002b). Therefore, if the opportunity is offered to them, domesticated species can probably in most cases revert to the behaviour observed in related wild species, as the genetic variability is still present in domesticated populations.

4.1. Relationships with humans

One of the first processes of domestication was to ensure that animals were less fearful of humans, and domesticated animals are thus much tamer than wild animals (Lankin, 1997; Gross, 1998). The genetic basis of these changes is supported by a number of studies. For example, Belyaev (1979) selected wild silver foxes according to tameness and showed that this trait was partly genetically controlled. After 18 generations of selection, foxes had reduced cortisol levels and reduced fear when exposed to humans (Harri et al., 2003). In Belyaev's tame foxes, baseline serum cortisol level was much lower than in wild foxes (36 vs. 160 nmol l^{-1}), and the stress-induced cortisol response was lower than in wild foxes (87 vs. 234 nmol l^{-1}). They also presented reactions to humans very similar to those of dogs, i.e. increased attachment and sociability towards humans (Belyaev, 1979). Breed comparisons in ruminants have shown that flight distance from humans is much greater in Romanov sheep used in extensive rearing with little contact with humans than in Lacaune sheep reared in more intensive production systems with closer contact with humans (4.0 m vs. 2.3 m, Boissy et al., 1996). Lacaune animals also stayed close to humans for longer than Romanov animals (98 s vs. 30 s). Heritability of docility has been estimated to be moderate in Limousine cattle (0.22–0.32, Morris et al., 1994; Le Neindre et al., 1995, 2002).

Fear of humans can be selected, as shown in different experiments in quails, chickens and turkeys by the use of behavioural criteria (duration of tonic immobility) or corticosterone level after stress challenges (Brown and Nestor, 1973; Mills and Faure, 1991; Satterlee and Johnson, 1988). Sheep selected for calm behaviour in open-field situations showed a

threefold shorter flight distance to man than nervous animals (Le Neindre et al., 1998).

4.2. Behaviour towards predators

As domestication involves human protection of animals from predators, they express a lower incidence of antipredator behaviours, probably due to relaxed selection on these traits. Consequently, it might be expected that there would be greater losses than wild animals when faced with predation. A few studies in birds have confirmed this hypothesis. Hill and Robertson (1988) showed that captive-reared pheasants were three times more susceptible to predation than wild birds. White Leghorn chickens also showed less antipredator behaviour than Jungle Fowl. The former had less activity after predator exposure, but fewer attempts to induce tonic immobility and longer duration of tonic immobility (Schütz et al., 2001; 2002). Berejikian (1995) demonstrated that wild steelhead trout were less susceptible to predation than farmed trout if they were naïve (death rates 12% and 23% in wild and farmed, respectively), and also if they had experienced predation before (death rate 9% and 17% in wild and farmed, respectively). These differential susceptibilities may be linked to greater risk-taking by domesticated animals. Domesticated masu salmon for example take feed closer to the surface, where they are more susceptible to predation (Reinhardt, 2001), and show a shorter latency to feeding after introduction of chemical alarm signals (Yamamoto and Reinhardt, 2003). Juveniles of steelhead trout have also been found to take more risks with natural predators than their wild counterparts (Johnsson and Abrahams, 1991).

4.3. Feeding behaviour

As feed is provided at least to some degree by humans to captive domesticated animals, they are not required to seek or identify quality differences in food to the extent required by wild animals. Differences observed between wild and domesticated animals are consistent with this hypothesis. Domesticated animals show lower motivation for foraging. For instance, a comparison of Jungle fowl and White Leghorns showed that the latter preferred free food (67% vs.

33%) to food mixed with litter (Schütz and Jensen, 2001). Likewise, wild geese have been reported to be more active than domestic geese, due to their greater need to search for food (Molnar et al., 2002).

Differences observed between wild and domesticated birds may also be partly attributable to selection for high performance in the latter, which leads to selection of birds with less contra-freeloading behaviour, defined as the aptitude of the animal to work for food even if free food is available, probably to increase information about possible alternative food sources. In fact, in their comparison of wild jungle fowl with domesticated White Leghorns, Schütz and Jensen (2001) also included domesticated Bantams that had not undergone artificial selection for production traits and noted that the proportion of animals preferring food mixed with litter instead of free food was the same in both unselected breeds (Bantams and Jungle fowl). However, selection on performance does not fully explain the differences, as a similar comparison of unselected domestic Bantams with Bantams×Wild jungle fowl crossbreds by Andersson et al. (2001) demonstrated that the crossbreds had a more costly foraging strategy, visiting more feed patches (7.4 vs. 4.0), staying less time at each visit (42 s vs. 100 s), and eating the same quantity as the Bantams.

Domesticated animals also seem less able to adapt their foraging strategies to a variable environment. Gustafsson et al. (1999) compared domesticated pigs (Landrace×Great Yorkshire) and Landrace×wild boar crossbreds. When barriers were placed between patches where food was offered, both types of animals reacted similarly, but the reactions of Landrace×Wild boar were more rapid. The difference would probably have been greater if domesticated pigs had been compared to pure wild boars. Andersson et al. (2001) obtained similar results in poultry, with wild-type birds being willing to increase energy usage to gain food while domesticated birds were not. In this case, it could not have resulted from confusion with selection on body weight as no artificial selection had been applied to the Bantams.

4.4. Reproductive behaviour

Most domesticated animals are more precocious than their wild counterparts. The difference can

partly be attributed to active selection, e.g. laying hens have been selected for an increased laying rate and thus an earlier age at first egg laying. Saeki and Inoue (1979) showed that White Leghorn and Red Jungle fowl hens laid their first egg at 159 d and 298 d, respectively. The number of eggs laid by the Red Jungle hens was also much lower, as 87.5% of them showed broodiness (0.0% in White Leghorns). However, even without voluntary selection, dramatic changes may occur, especially after a large number of generations. For instance, in an experiment involving wild Japanese quails reared in captivity, Kawahara (1972) observed a large decrease in age at first egg laying as early as the third generation of captivity. Although this difference can be partly attributed to sampling variations, it must also reflect some genetic changes. Loss of seasonality and moulting is also characteristic of domesticated animals (Belyaev, 1979) as humans ensure survival of the young even at the unfavourable birth season. Probably as a consequence of active selection, domesticated animals may consequently have much poorer performance when placed in wild conditions than their wild counterparts. For example, the reproductive success of domesticated salmon is only 16% of that of their wild counterparts (Fleming et al., 2000) in natural conditions, due to decreased early survival and reproductive competitivity.

4.5. Social behaviour

Most domesticated species are naturally social animals that live in large, highly organised groups with a stable social hierarchy. While these characteristics have favoured domestication, domestication in turn results in interference with social relationships as humans control both reproduction and production. Whereas few populations of cattle in the world are really feral, observation of domestic cattle that are free ranging with minimal human interference can provide useful information on what the social structure and behaviour of the ancestors of our domestic animals might have been. Clutton-Brock et al. (1976) concluded that the hierarchical organisation of free-ranging cattle on the Isle of Rhum is similar to that of animals raised under human control. Young males progressively form groups of bachelors which are less

cohesive than the female groups. At the same age, females remain very close to their mothers (Kimura and Ihobe, 1985). This probably enables the building of a matriarchal relationship with specific affinities between females (Lazo, 1994). For domesticated animals, the structure of the social group often includes only animals of the same sex or age. Territorial behaviour is not possible, so that territorial species tend to evolve to hierarchical groups with dominant animals. Social interactions are also reduced in captivity. The goose, for example, shows less aggression in captivity (Molnar et al., 2002). Differences in aggressivity between wild and captive masu salmon are more controversial, and may be attributed to a strong interaction between genotype and environment, as the young salmon's behaviour varies with location (Yamamoto and Reinhardt, 2003).

Differences in social behaviour have a partly genetic basis. First, differences have been observed between breeds. For example, mooing is more frequent in Aubrac than in Holstein breeds when animals are isolated from others (Boissy and Le Neindre, 1990). Moreover, it has been possible to select Japanese quail on social reinstatement behaviour (Mills and Faure, 1991). In contrast, some breeds have been selected for increased aggressivity, e.g. fighting fowls or Hérens cows. In the latter animal, aggressivity is only directed at other cows, and not at humans.

4.6. Maternal behaviour

In the wild and in extensive rearing conditions, maternal behaviour is essential to the survival of young, and it is possibly poorer in domesticated animals, although there are few comparisons of wild and domesticated animals. Gustafsson et al. (1999) and Spinka et al. (2000) observed few differences in the maternal behaviour of domestic sows and wild boar and domesticated sow crossbreds. Domesticated sows invested more energy in the present litter compared to the crossbreds that appeared to save resources to invest in a future litter. Such a small difference between wild and domesticated maternal behaviour may suggest that maternal behaviour is relatively robust in pigs (Nowak et al., 2000), although the difference would probably be greater between pure domesticated and pure wild sows. This

is possibly not the case in sheep and rabbits, as Lindsay (1988) and Selzer et al. (2000) observed differences in the maternal behaviours of wild and domesticated animals of these two species. More information is available to assess the genetic basis of this trait, as differences in maternal behaviour have been shown to exist within cattle and sheep breeds. Le Neindre et al. (1998) showed that Salers cows suckled their calves longer than Friesian cows (27.0 s vs. 23.3 s,), licked their calves longer (7.2 min vs. 2.3 min) and were less accepting of being suckled by a strange calf (10% vs. 50%), thus optimizing milk availability for their own calves. In sheep, Boissy et al. (1996) showed that a higher proportion of Romanov ewes licked their lambs (96%) compared to Lacaune ewes (75%), and that they reaction was greater to lamb removal (48 high pitch bleats vs. 33). Maternal behaviour has been estimated to be moderately heritable in Limousine cows (h^2=0.31, Grignard, 2001).

5. Conclusion

Domestication is an evolutive process during which many behaviour traits have changed from the wild types to the existing domesticated populations. It is however difficult to trace back how those selections really occurred, and for some species, the wild counterparts no longer exist. Domestication is probably still occurring and populations of domestic animals are still evolving. These changes lead animals to be better adapted to their captive lives and to the presence of humans. Especially during the last few centuries active selection has been implemented on some specific production traits. As a consequence of these investments in specific production traits and due to the limitation of total resources, domesticated animals have adapted to their environments but may be less able to adapt to new or variable environments. It therefore seems interesting to improve the capacity of adaptation which would allow selection for "adaptable" animals, thus ensuring the animal's ability to maintain their welfare. However, traits that evaluate adaptability are difficult to design and work is still needed to find suitable ways to measure such traits. Studying them could help to improve our knowledge and reveal practical implications. It will be very

important to evaluate the social acceptability of selection for such traits before it can be implemented on a large scale.

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