A Discussion of Genetic, Morphological and Behavioural Changes Observed in Domesticated Animals, Namely Livestock, and their Affect on Fitness.

Julia Quick

November 2007

A Discussion of Genetic, Morphological and Behavioural Changes Observed in Domesticated Animals, Namely Livestock and their Affect on Fitness

Domestication is an important development in human history and a pre-requisite to the development of civilisation. It provides us with our food today, plant and animal alike.

The origins of domestication involved behavioural changes in both humans and animals. The efficiency of previous hunter-gatherer methods used by humans began to decrease during the Pleistocene era due to climate changes, causing decreases in numbers of big-game species that were first-choice prey (Diamond, 2002). To offset this, people broadened their diets. This, together with the new tendency of humans to colonize permanent settlements brought on the farming era.

There is no official definition of Domestication, and many different opinions have been held as to the exact guidelines to use to decide whether an animal is truly domesticated or simply tamed. Below are some contributions I have come across;
"…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 (in the case of animals) its food supply." (Diamond, 2002)
"…that process by which a population of animals become adapted to humans and to the captive environment by the combination of genetic changes occurring over generations and environmentally induced developmental events re-occurring during each generation" (Newman, 1994; Price, 1984)
"…the process whereby animals reproduce in and adapt to an anthropogenic environment (by genetic change and environmentally induced developmental changes) and are separated to some degree from wild populations for the purposes of human exploitation." (Arbuckle, 2002).
The lines have been blurred because people place emphasis on different factors being important, for example some opinions focus solely on the phenotypic and genetic differences and changes that occur in the animal, and some recognise the symbiosis that must occur between animal and human, particularly the social changes that must take place for us to be able to keep animals.

The main genetic process by which phenotypic and genetic changes typical of domestication are brought about is through Artificial Selection. This is basically humans only breeding specific individuals that are more suited to their needs of production, increasing economic efficiency. For example, Chickens are selected to be larger, Cattle to be smaller, and Sheep to lose their bristly outer kemp but keep their soft inner wool (Diamond, 2002). However inadvertently, secondary traits are also being selected for that carry through generations, and it is these that will bring about evolutionary behavioural and physiological changes in species, and these traits are also what separates domestication from taming. These are mainly a product of the environmental control wielded by humans. An optimum environment of protection from predators, feeding, disease control and housing is provided. This also means that animals must already posses some characteristics in the wild to be suitable for domestication, for example food choice should be cheap and readily available in bulk – making herbivores popular; socially they should be naturally comfortable with many individuals in close proximity to allow herding; and reproductive cycles should be relatively short to maximise productivity.

However the controlled environments designed to maximise output of the animals have been shown to have adverse effects. By providing all an individual needs, you never expose it to situations where it has to fend for itself, survive through hardships or compete for mates. In short, life becomes less challenging. Therefore its sensory and motor abilities that have evolved to allow the animal through harsh conditions such as lack of food or predator avoidance, are no longer used or needed. Loss of this higher sensory processing can reduce overall fitness compared to a species' wild counterparts.

As most domesticated populations probably began as a small number of individuals, inbreeding is a likely side effect. This in itself can reduce fitness before any phenotypic changes are observed by reducing genetic variability and increasing homozygosity, potentially uncovering deleterious recessive alleles. This may leave the herd more susceptible to disease and stress, and less able to cope with variations in their habitat. For example, as a cause of increased inbreeding co-efficient, higher numbers of cow and calf deaths have been recorded in captivity compared to the wild, and reduced numbers of calves weaned per cow (Newman, 1994; Brinks and Knapp 1975). This also shows in farmed fish, where a reduced reproductive success was observed as a secondary trait to increased growth rate being actively selected for (Osure et al, 2006; Su et al 1996). These changes will happen many times quicker under artificial selection than they would under natural selection, as the pressures are much stronger.

An experiment was conducted on Pacific Salmon that illustrates this perfectly. Farmed Salmon are selected for enhanced growth, therefore the largest mature individuals are bred for the next generation. Multiple populations of pure-bred and hybrids were tested for their fitness in a natural environment, including farmed, native, F1 and F2 hybrids, and wild-backcrosses. It was found that individuals with all or part farmed-genome showed a reduced anti-predator response, the severity of which was dependant on the ratio of farmed genes to native genes. This showed that additive genetic effects contribute significantly to the divergence between the fast- and slow-growing strains, as phenotypic differences between strains are largely a consequence of additive gene action. This was further confirmed when the phenotypic effects largely diminished after two generations of back-crossing with native Salmon (Tymchuk et al, 2006). This faster growth rate is thought to be attributed to a higher production rate of growth hormone, subsequently increasing appetite (Huntingford, 2004; Fleming et al 2002), however we must not ignore the contribution of possible external factors such as differing nutrition and lack of parasites and disease.

Body size is one of the most important phenotypic characteristics of an animal, influencing fitness, life history and population ecology (Tymchuk et al, 2006). However, usually an animal will not reach maximum size in the wild, but the potential for enhanced growth is shown in the small number of generations needed to increase weight under selective breeding programs. For example, after only four generations of artificial selection, Coho Salmon (Oncorhynchus kisutch) demonstrated a 60% weight increase (Tymchuk et al, 2006; Iwamoto et al 1982; Myers 2001). Enhanced growth is just one of the traits artificially selected for in farmed animals that can cause secondary morphological, genetic and behavioural changes.

Another important physiological change brought about by differing environmental pressures is a decrease in brain weight comparative to body weight. It has been observed in Sheep (domestic 24% less than wild), Pigs (domestic 35% less than wild), and Fish. This is thought to represent a reduction in the functional capacity of the parts most affected, i.e. the sensory and central nervous system, attributed to the loss of 'environmental appreciation' (Arbuckle, 2002) explained earlier. The most affected areas seem to be the auditory and visual, and the limbic – associated with reactivity and aggression. The secondary changes produced by this is lower levels of neurochemicals and hormones associated with stress and aggression such as serotonin, due to a decrease in size of their associated production glands. This, in turn, produces a general decline in reactivity to the environment. The relative brain size reduction depends on the original brain size of the species' wild counterparts, how long ago they were domesticated, and the intensity of artificial selection. This is shown in an experiment involving hatchery-reared and wild Trout (Oncorhynchus mykiss). The farmed individuals had a marked decrease in the optic tectum and telencephalon (Huntingford, 2004; Marchetti and Nevitt 2003). “Behavioural responses are regulated by a fine balance between neurotransmitters and hormones. Even a slight alteration in the genes that regulate this balance can give rise to a wide network of changes in the developmental process they govern. Thus, selecting animals for behaviour may lead to other, far-reaching changes in the animals’ development. Because mammals from widely different taxonomic groups share similar regulatory mechanisms for hormones and neurochemistry, it is reasonable to believe that selecting them for similar behaviour – i.e. tameness – should alter those mechanisms, and the developmental pathways they govern, in similar ways” (Arbuckle, 2002).

A combined result of selecting for increased growth rate and reduced aggressiveness has given rise to another natural trait lost – sexual dimorphism, notably in domestic cattle. The males become less aggressive and therefore produce less testosterone (a hormone associated with growth), and there is a noticeable absence in competition and fighting for mates. A lack of resource fluctuation will also infer increased fertility in females, larger litter or clutch sizes, earlier maturation of young and reduced seasonality in reproduction.

When a species begins the process of domestication, it will experience a shift in environment. To adapt the animal will have to change certain aspects of its behaviour. As we have already covered, there will be a loss in some behaviours as the welfare becomes the keepers responsibility, such as foraging, food and shelter seeking, and predator avoidance. It may well be that the behavioural changes occur first as the animal is forced to adapt to the environment, and this consequently causes the physiological changes. However it could also be argued the changes in behaviour are a result of artificial selection altering such organs as the brain, which infer behavioural changes. This is still very much a chicken and egg debate, as nothing has been proven as yet.

One behavioural trait that is intentionally selected for is docility, and a reduced negative reaction to handling. This may seem obvious but is crucial to enable human control, and domesticated animals show a much shorter flight distance from humans than wild types. Breed comparisons in Sheep have shown greater flight distances in wild-reared Romanov type (4.0m) compared to Lacaune (2.3m) reared in intensive production systems (Mignon-Grasteau et al, 2005; Boissy et al 1996). This is linked to the aforementioned reduction in hormones, and tamer animals show a lower level of corticosterone and a lower heart rate after stressful events.

This links in to welfare, as you would expect domestic populations to have a lower ability to avoid predators, and therefore a higher death rate than wild populations when faced with predation. Shown in an experiment with Steelhead Trout, only 12% of the wild population were lost compared to 23% of the farmed population (Mignon-Grasteau et al, 2005). This is brought about by increased risk-taking in tame animals because of the reduced stress reactions and a lack of exposure, and therefore naivety, to dangerous situations. Another experiment that follows this theory is on wild and farmed families of Coho Salmon (Oncorhynchus kisutch). Individuals were ‘attacked’ with a model of a heron, then offered a food pellet every 10 seconds until they began to eat again. Farm families took significantly less time to begin eating again, and a negative correlation showed between the mean mass of the family and the time until first feed, i.e. the larger the fish the shorter the time (Tymchuk et al, 2006).

Foraging abilities are also underdeveloped, shown with Junglefowl and White Leghorns. Here the wildfowl’s ability to distinguish between nutritiously beneficial food and non-beneficial litter is much higher (67%) than the tame bird (33%). This also follows on to domesticated animals being less willing to increase their energy expenditure to gain food, for example the experiment on domesticated pig and wild boar crossbreds. The reactions of the boar to food placed out were always much quicker than the pigs, and they were more willing to overcome obstacles to obtain food (Mignon-Grasteau S et al, 2005).

“The fitness associated with an animal’s foraging behaviour has been maximised by natural selection, thereby maximising its net rate of energy intake. Wild animals will generally have to make trade-offs between the rate of energy intake and the risk of predation to maximise fitness.” (Tymchuk et al, 2006).

To summarize, the domestication of animals - namely livestock - over the past few centuries has caused accelerated and notable changes in behaviour and morphology of species through artificial selection and increased habitat pressures. Because domestication is characterised by colonising of animals in anthropogenic environments, often the selection pressures are very similar in many taxa, and as a result similar changes can be seen in a variety of species. The extent of these changes can be a measure of the conditions they have been kept in, the strategies used to exploit them for economic gain, and the amount of time they have been under domestication. Some of these traits may have connotations for welfare as a number of lost traits are those essential for survival in the wild and have caused a significant loss in fitness by decreasing the animal’s ability to cope with variations in environment. If animals are selected to accentuate certain traits which increase production, such as increased growth, resources are often diverted away from other essential systems such as reproduction, or the senses.

Up until now, humans have perceived welfare as the incidence of disease, visible discomfort, life expectancy and reproductive abilities. However, optimising these will increase productivity for humans, but they may be having evolutionary adverse effects, causing secondary changes in the animal which are decreasing fitness at a faster rate than natural selection is increasing it.

References

1. Arbuckle BS. Experimental animal domestication and its application to the study of animal exploitation in Prehistory. The First Steps of Animal Domestication – New Archaeological Approaches (edited Vigne JD, Peters J, Helmer D). Oxford Books 2002:18-33.
2. Diamond J. Evolution, consequences and future of plant and animal domestication. Nature 2002;418:700-707.
3. Helmer D, Gourichon L, Monchot H, Peters J, Sana Segui M. Identifying early domestic cattle from Pre-Pottery Neolithic sites on the Middle Euphrates using sexual dimorphism. The First Steps of Animal Domestication-New Archaeological Approaches (edited Vigne JD, Peters J, Helmer D). Oxford Books 2002:86-95.
4. Huntingford FA. Implications of domestication and rearing conditions for the behaviour of cultivated fishes. Journal of Fish Biology 2004;65:122-142.
5. Mignon-Grasteau S, Boissy A, Bouix J, Faure J, Fisher AD, Hinch GN, et al. Genetics of adaptation and domestication in livestock. Livestock Production Science 2005;93:3-14.
6. Newman S. Quantitative and Molecular-Genetic Effects on Animal Well-Being: Adaptive Mechanisms. Journal of Animal Science 1994;72:1641-1653.
7. Osure GO, Phelps RP. Evaluation of reproductive performance and early growth of four strains of Nile tilapia (Oreochromis niloticus, L) with different histories of domestication. Aquaculture 2006;253:485-494.
8. Tymchuk WE, Biagi C, Withler R, Devlin RH. Growth and Behavioural Consequences of Introgression of a Domesticated Aquaculture Genotype into a Native Strain of Coho Salmon. American Fisheries Society 2006;135:442-455.
9. Vigne JD, Helmer D, Peters J. The First Steps of Animal Domestication – New Archaeological Approaches. Oxford Books 2002:4.