# Insights from the domestication of a novel species as demonstrated in the silver fox

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## Introduction – Genetics of Domestication

Plant and animal domestication is of interest both because of its significance to human history, and because our domesticated species provide us with most of our food (1). While plant domestication is a relatively simple matter of deliberate planting, animal domestication encompasses complex behavioural changes in addition to phenotypic changes both neutral and beneficial to humans in nature. The process by which domestication occurs and what it means for a species is not well understood. Only in the relatively recent past have we begun to understand the genetic basis of the set of phenotypic and behavioural characteristics that we refer to as domestication in animals (2).

Traditionally, animal domestication has been studied using morphological analysis of domesticated animals of various breeds or landraces and their corresponding wild ancestors or relatives where possible. Various genetic analysis technologies have allowed researchers to develop a far more detailed view of the changes involved in the process of domestication and breed development (2,3). The study of domestication genetics includes multiple approaches, including locus-specific and genome-wide marker matching and analysis (2). Full genomes have been sequenced for a large and increasing number of species, allowing for genome-wide single nucleotide polymorphism panels (2). Many traits which cannot be clearly segregated or analysed using morphological data can be looked at using these genomic markers and full genome analysis.

Particular attention has been paid to the study of behavioural traits associated with domestication and the genetics underlying those traits (2). In everything from chickens (4, 5) to cavies (6), domestication has been shown to be associated with a lowered stress response or lowered fearfulness of humans. Fearfulness is linked to stress responses through adrenal activation (5,7). In rats, traits such as tameness, low aggression, and low anxiety were shown to be linked to quantitative loci related to adrenal function (7). These studies use genotyping, using microsatellite and single-nucleotide polymorphism markers, to map and compare various loci (7). A 2004 study of mRNA expression in the brains of domestic dogs, wolves, and coyotes found significant divergence in gene expression in the hypothalamus between domesticated dogs and wolves or coyotes (8). Studies such as this indicate that there is a complex genetic background for tame behaviour.

Although there are at least 148 large terrestrial herbivores and omnivores which could plausibly have been domesticated, only 14 of these species have been domesticated to date (1). The hypothesised reasons for this include a number of 'obstacles' to domestication; species displaying more than four of these traits are classed as difficult if not impossible to fully domesticate (1).

- Animals with dietary needs which are difficult to fulfill, such as hummingbirds or anteaters.
- Animals with very slow growth rates, or significant time required between births, such as tortoises or elephants.
- Animals with a particularly aggressive or vicious nature, such as rhinoceroses or eagles.
- Animals which do not breed in captivity, or do so with difficulty, such as pandas.
- Animals which lack a clear dominance hierarchy with a defined leader, such as antelope.
- Animals which respond to enclosures, capture, or the presence of predators with panic, such as most species of deer.

In 1959, a series of experiments on the genetic basis of domestication were begun in Siberia (3,9). The researchers bred populations of silver foxes (*Vulpes vulpes*), minks (*Mustela lutreola*), rats (*Rattus norvegicus*), and other animals which were selected either for tameness or for aggression (3). For each species, two populations were maintained: one selected for tameness and lack of fear, and one selected for aggression. Two colonies of rats resulting form this study are now located in Leipzig, in Germany (3), while the silver fox populations are still located in Russia. The domestication of silver foxes through this experiment has been well documented and studied, and provides insight into the process and genetic basis of domestication.

## Case Study

In 1959, Dmitri K. Belyaev started a large-scale experiment to decode the genetics of domestication (9). Two separate populations of silver foxes (*Vulpes vulpes)* were developed and maintained: one selected for tameness, defined as emotionally positive response to humans, and the other unselected (9,10). Emphasis was also placed on observing the duration of the critical socialisation period during the animals' development, the end of which is marked by the appearance of a fear response by the fox pups toward novel stimuli (9).

This study, which is ongoing (10), has found that selection for domesticated (tame) behaviour in foxes results in the decrease or elimination of defensive aggression and fear responses to humans (9). In pups from the unselected population, animals older than 40 - 45 days displayed lowered exploratory behaviour and high levels of fear responses to humans and other novel stimuli (9). Pups from the population of foxes selected for tameness did not show diminished exploratory behaviour as a result of fear responses to novel stimuli until after 65 days of age, making the duration and bounds of the critical socialisation period for these foxes similar to that of domestic dogs (9). Foxes from the tame population also display other behavioural traits more often associated with domestic dogs, including the way they position their ears, wagging their tails, willingly approaching or remaining close to a human observer, and expressing a clear willingness and desire to be touched rather than an inclination to bite or attack (10). Foxes form the tame population have also been shown to vocalise to attempt to initiate positive contact with humans or to solicit attention from humans (11).

In addition to behavioural changes, some morphological changes were also observed. Foxes from the tame population are more likely to have floppy ears and curly tails, and show a variety of colours and patterns not found in the unselected population (12). It is unclear how these morphological changes are associated with the behavioural selection for tameness. Wiener and Wilkinson (2) have suggested that a similar effect in domesticated pigs as compared to wild boar is associated with a lack of selection pressure against unusual colouration or flawed camouflage in the wild. This may be part of the answer but it is likely that there is more to it in the case of the silver fox, as the unselected population did not display any of these morphological changes in spite of being protected from the effects of natural selection against unusual colouration.

*Figure 1: Fox pups from the tame population (13)*

Sophisticated techniques were developed to score the behavioural characteristics based on multiple observations and binary evaluations of a set of behaviours (10). The actions of the investigators and the responses of the foxes were videotaped for later analysis and evaluation (10), to reduce subjective biases in observations. However, even using these techniques, there is a limit to what can be discovered regarding the nature and causes of the domesticated behaviour in the tame fox population. For that, genetic analysis was needed.

Using known cytogenetic homologies which exist between the domestic dog and the fox, and the high genomic similarity between the dog and fox, a meiotic linkage map was generated for the fox genome (14). This map was generated using 320 markers adapted from domestic dog genome microsatellites (14). Using this meiotic map and an additional 65 microsatellite markers enabled a correlation to be drawn between specific genotypes and the tame behavioural phenotype (10). A specific locus on the VVU12 fox chromosome was identified and correlated with the tame versus aggressive behavioural phenotype (10), although there was some suggestion in the results that the expression of the loci on VVU12 may be affected by genomic context (10).

Broadly, the findings of the study are that domesticated or tame behaviour is associated with a lowered fear response, and that this is a specific and highly heritable characteristic with a clear genetic basis. This matches with the study into tame versus unselected or aggressive rats (7), even though the loci identified in that study are entirely unrelated to the loci identified in the fox domestication study. That very fact demonstrates that there are multiple genetic routes to domestication (2).

## Future Directions

Only a very small number of species have been successfully domesticated, and as humans we depend on that tiny fraction for almost all of our food (1). In a world with not only a growing population, but a rising level of affluence and desire for meat within that growing population, domesticated animals are of some significance both to farmers and more broadly to our civilisation. The sole addition to the list of large, valuable domesticated mammals in the last 1000 years has been the reindeer, which is one of the least valuable of the animals on that list (1). Efforts to domesticate other large mammal species such as the zebra, eland (*Taurotragus oryx*), or musk ox have for the most part failed (1). It is possible that a clear understanding of the genetics of domestication could assist us with domesticating additional species more suited to some of the arid or marginal regions of the world – as the eland and zebra are to the dry savannahs of Africa.

An understanding of the genetics of domestication may also help us address another, perhaps more pressing issue that livestock farmers are increasingly facing. Historically, there were few breeds of livestock as we would recognise them now, although landraces did exist. That changed approximately 200 years ago (15), and with the rise of industrial farming there has been steady pressure on farmers to select for productivity or, as is more often the case, to simply use an industrial breed. Due to the efficiency of modern selection methods, the selection for productivity has led to a loss of genetic variability in many industrial breeds (15). Inbreeding and the loss of genetic diversity are a growing problem for many livestock species. In addition, the pressure on farmers to abandon their traditional breeds and landraces in favour of the more productive industrial breeds has led to the extinction of several traditional or 'heritage' breeds (15). As a result, genetic diversity in sheep, goats and cattle is very low.

One option available to breeders is to increase genetic diversity within a livestock species by backcrossing to the nearest wild relative. Traditionally this has resulted in a trade-off between increased genetic diversity and hybrid vigour, and decreases in the desirable tame behaviours (16). With an understanding of the genetics of domestication, the results of such backcrosses could be screened in utero or at birth for the genes indicating domestication and tame behaviour phenotypes. Domestication is a process, not an event, and many backcross offspring could be expected to be intermediate between the behavioural phenotypes of their wild and domesticated parent (3). However, even in this case the offspring could be screened for the presence of the domestication gene or genes for that species, and fully domesticated behaviour bred back into the line very rapidly.

Finally, it is worth noting that it not only our livestock species which have shown an adaptation which we call domestication, associated with lowered fear and aggression responses. Humans have been described as a ‘self-domesticating’ species (1) in that we appear to have self-selected against aggression in our social groups. Hare, Wobbler and Wrangham (17) described this effect in bonobos (*Pan paniscus*) as compared with chimpanzees (*Pan troglodytes*). Both bonobos and chimpanzees are, genetically, the close cousins of humans and share many behaviours and morphological traits with them. If the genetics of domestication can teach us about bonobos, they can certainly teach us something about ourselves, and perhaps some of the reasons for our evolutionary success.

## Conclusion

The genetic basis of domestication is a fascinating area of study for its own sake, but it has huge potential benefits both in terms of pure knowledge and understanding of our history as a species and a culture, and also in terms of the benefits it could have for farmers and animal breeders. While foxes may not appear to provide either of these benefits, the information that we gain from observing and studying the domestication of a new species provides a basis for further work. The genetic basis for behavioural characteristics are complex, and we are only just beginning to understand them well enough to apply that knowledge. Things that we learn in the study of domesticated foxes as compared to unselected foxes can be applied to the study of domestication in livestock species form chickens to cattle – and even to our own species.

## References:


1. Diamond J. Evolution, consequences and future of plant and animal domestication. Nature. 2002;418:700 - 7.

2. Wiener P, Wilkinson S. Deciphering the genetic basis of animal domestication. Proceedings Biological sciences / The Royal Society. 2011;278(1722):3161-70.

3. Larson G. Genetics and Domestication. Current Anthropology. 2011;52(S4):S485-S95.

4. de Haas EN, Kops MS, Bolhuis JE, Groothuis TG, Ellen ED, Rodenburg TB. The relation between fearfulness in young and stress-response in adult laying hens, on individual and group level. Physiology & behavior. 2012;107(3):433-9.

5. Campler M, Jongren M, Jensen P. Fearfulness in red junglefowl and domesticated White Leghorn chickens. Behavioural processes. 2009;81(1):39-43.

6. Künzl C, Kaiser S, Meier E, Sachser N. Is a wild mammal kept and reared in captivity still a wild animal? Hormones and Behavior. 2003;43(1):187-96.

7. Albert FW, Carlborg O, Plyusnina I, Besnier F, Hedwig D, Lautenschlager S, et al. Genetic architecture of tameness in a rat model of animal domestication. Genetics. 2009;182(2):541-54.

8. Saetre P, Lindberg J, Leonard JA, Olsson K, Pettersson U, Ellegren H, et al. From wild wolf to domestic dog: gene expression changes in the brain. Brain research Molecular brain research. 2004;126(2):198-206.

9. BELYAEV DK, PLYUSNINA IZ, TRUT LN. Domestication in the silver fox (Vulpes fulvus Desm)- Changes in physiological boundaries of the sensitive period of primary socialization. Applied Animal Behaviour Science. 1984;13:359 - 70.

10. Kukekova AV, Trut LN, Chase K, Kharlamova AV, Johnson JL, Temnykh SV, et al. Mapping Loci for fox domestication: deconstruction/reconstruction of a behavioral phenotype. Behavior genetics. 2011;41(4):593-606.

11. Gogoleva SS, Volodin IA, Volodina EV, Kharlamova AV, Trut LN. Explosive vocal activity for attracting human attention is related to domestication in silver fox. Behavioural processes. 2011;86(2):216-21.

12. Byrne RW. Animal evolution: foxy friends. Current biology : CB. 2005;15(3):R86-7.

13. Domestication of Foxes. Accessed 2014-11-10, http://domesticationoffoxes.weebly.com/.

14. Kukekova AV, Trut LN, Oskina IN, Johnson JL, Temnykh SV, Kharlamova AV, et al. A meiotic linkage map of the silver fox, aligned and compared to the canine genome. Genome research. 2007;17(3):387-99.

15. Taberlet P, Valentini A, Rezaei HR, Naderi S, Pompanon F, Negrini R, et al. Are cattle, sheep, and goats endangered species? Molecular ecology. 2008;17(1):275-84.

16. Vila C, Seddon J, Ellegren H. Genes of domestic mammals augmented by backcrossing with wild ancestors. Trends in genetics : TIG. 2005;21(4):214-8.

17. Hare B, Wobber V, Wrangham R. The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. Animal Behaviour. 2012;83(3):573-85.