The Silver Fox Domestication Experiment

How to Tame a Fox and Build a Dog*

Lee Alan Dugatkin

For the last sixty years, a team of Russian geneticists have been running one of the most important biology experiments of the 20th, and now 21st, century. Each year they have selected the calmest foxes—foxes that are most prosocial to humans—to mimic the early stages of domestication. After providing an overview of how the silver fox domestication study began, I will discuss: 1) work on social cognition in the domesticated silver foxes, 2) work on the molecular genetics of domestication in the silver foxes, including work on changes in allele frequencies and changes in gene expression patterns, 3) a new hypothesis for how selection on tameness leads to the domestication syndrome via changes in the number and migration patterns of neural crest cells very early on in development, and 4) how the silver fox domestication experiment has led to new hypotheses about self-domestication in primates, including humans.

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Domesticated animals such as dogs, cats, cows, sheep, and so on, play an important role in human life. Ever since Darwin wrote his 1868 book, *The Variation of Animals and Plants Under Domestication* [1], evolutionary biologists and animal behaviorists have been fascinated with how, starting at least fifteen thousand years ago, and perhaps longer than that, our ancestors began domesticating animals. Fossil evidence can provide some clues about when and where the domestication has occurred, as well as some information on the stages of change in animals during domestication. But it can't tell scientists how domestication got started in the first place. How had wild animals, averse to human contact, become calm enough for our ancestors to have started breeding

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them? To answer that question, the silver fox domestication experiment began in 1959 at the Institute of Cytology and Genetics in Novosibirsk, Russia, and continues to this day [2, 3]. It is widely regarded as one of the more important long-term experiments ever conducted in biology. The work began under a Russian geneticist named Dmitri Belyaev (1917–1985).

In the late 1930s, Belyaev was a student at the Ivanova Agricultural Academy in Moscow and in the 1940s, he worked as a researcher at the Institute for Fur Breeding Animals in the same city. From his reading of Darwin's *The Variation of Animals and Plants Under Domestication*, and his work with domesticated animals at the Ivanova Agricultural Academy and the Institute for Fur Breeding Animals, Belyaev was well aware that many domesticated species share a suite of traits that include juvenilized facial and body features, reduced stress hormone levels, floppy ears, mottled fur, relatively long reproductive seasons compared to their ancestors, and short, curly tails. Today, this suite of traits is known as the 'domestication syndrome'.

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Belyaev was interested in why the domestication syndrome exists. Humans have domesticated animals for many reasons, but regardless of what they are domesticated for—transportation, food, companionship or protection—domesticated animals, over time, begin to accumulate traits in the domestication syndrome. Belyaev hypothesized that selection for tameness was the key to understanding why domesticated species share so many characteristics because the one thing our ancestors always needed in a species they were domesticating was an animal that interacted relatively prosocially with them. Belyaev proposed that the early stages of all animal domestications centered on choosing the tamest, most prosocial-toward-human animals. He further hypothesized that all of the traits domesticated species share are linked to genes associated with tameness, and that is why the domestication syndrome exists.

Belyaev decided to test his hypotheses using a species he had worked with extensively at the Institute for Fur Breeding—the silver fox, a variant of the red fox (*Vulpes vulpes*). He envisioned developing a scale for scoring tameness—friendliness toward humans—and using that as the sole criteria for selecting which foxes would parent the next generation, with the top 10% of the tamest selected.

Belyaev began a pilot experiment in 1952 working with his colleague, Nina Sorokina, who was the chief breeder at a small fox farm in Kohila, outside of Tallinn, Estonia, buried deep in the Estonian forest [2]. Not so much a village as a corporate outpost, Kohila was typical of the many industrial-scale fur farms scattered across the region. Spread out over 150 acres, the farm housed about 1500 silver foxes in dozens of rows of metal-roofed long wooden sheds, each of which contained dozens of cages.

Belyaev explained the procedure he wanted Sorokina and her breeding team to follow. Every year, they were to choose a few of the calmest foxes at Kohila at the breeding time in late January and mate them with one another. From the pups that those select foxes produced, they would again choose the calmest ones and breed them. Perhaps, he suggested, this method would eventually lead to calmer and calmer foxes, the first step in domestication.

They decided they would always approach the foxes slowly—opening the cages slowly and reaching into it slowly with some food held in a gloved hand. When they did, some of the foxes lunged at them. Most of them backed away and snarled. But about a dozen out of the hundred or so they tested each year did neither. They weren't calm, but they weren't highly reactive and aggressive either. A few would even take the food offered from the workers' hands. These foxes became the next generation in the pilot work. Within three breeding seasons, Sorokina and her team were seeing some promising results. Some of the pups of the foxes they had selected were a little calmer than their parents, grandparents, and great-grandparents.

Belyaev got the chance to expand the pilot work into a large-scale experiment in 1959 when he moved to the newly established Institute of Cytology and Genetics, part of a giant new scientific complex called Akademgorodok, outside of Novosibirsk, in the

Figure 1. The first domesticated fox with floppy ears (1969). (Photo Courtesy: Institute of Cytology and Genetics, Novosibirsk.)

heart of Siberia. Quickly he became Vice Director of the Institute, and he recruited Lyudmila Trut, who had recently received her degree in biology from Moscow State University, to work with him on this experiment.

In January of 1959, a Lysenko-created committee from Moscow visited Akademgorodok. This committee had the official authority to determine what work was done at the Institute of Cytology and Genetics. Trut remembers committee members "snooping in the laboratories, questioning everyone." The word spread that the committee was clearly unhappy that genetic studies were being conducted. When the committee met with Mikhail Lavrentyev, chief of all the institutes at Akademgorodok, they informed him that "the direction of the Institute of Cytology and Genetics is methodologically wrong." Those were dangerous words from a Lysenkoist group.

Khrushchev, who was by this time Premier of the USSR, heard of the committee's report about Akademgorodok. Khrushchev had been a long-time supporter of Lysenko, and he decided to examine the situation personally in September of 1959. The staff of all the science institutes at Akademgorodok gathered in front of the Institute of Hydrodynamics for Khrushchev's visit, and Trut recalls that the Premier "walked by the assembled staff very fast, not paying any attention to them." The substance of the meeting between Khrushchev and the administrators was not recorded, but accounts from the time make clear that Khrushchev intended to immediately shut down the Institute of Cytology and Genetics. Fortunately, Khrushchev's travel partner on his visit to Akademgorodok was his daughter, Rada. A well-known journalist, Rada, who was also a trained biologist, recognized Lysenko for the fraud he was and convinced her father to keep the Institute of Cytology and Genetics, and the fox domestication experiment, open.

It is not possible here to discuss all of the results that have come out of this almost six-decade-long experiment. Briefly, starting from a population of wild foxes, within six generations[1], selection for tameness resulted in some foxes that licked the hands of experimenters, whined when humans departed and wagged their tails when humans approached. During the early years of the experiment, the tamest of the foxes made up two percent of the experimental population; today they make up more than seventy-five percent. In addition, as Belyaev predicted, selection for tameness led to the emergence of traits in the domestication syndrome. In less than ten generations, some of the domesticated foxes had floppy ears and curly tails. By generation fifteen, their stress hormone levels were about half the stress hormone levels of wild foxes. Over the course of the experiment, Trut, Belyaev, and their colleagues also found that the domesticated foxes exhibited mottled fur patterns and extended reproductive periods.

[1] Six years, as foxes reproduce annually starting at age one.

As Belyaev predicted, selection for tameness led to the emergence of traits in the domestication syndrome. In less than ten generations, some of the domesticated foxes had floppy ears and curly tails. By generation fifteen, their stress hormone levels were about half the stress hormone levels of wild foxes.

The domesticated foxes also displayed more juvenilized facial and body shapes, such as rounder and shorter snouts and shorter and thicker limbs. Gordon Lark, at the University of Utah in the United States, had discovered that in dog breeds, animals with short limbs and short snouts also had wide limbs and wide, rounded snouts. Dogs with long graceful limbs and long snouts had relatively narrow snouts. Genetic analysis performed by Lark's team found that the relationship between the length and width of dog bones was controlled by a small number of genes that affect skeletal growth. Lark then began working with Trut, Anna Kukekova, and Anastasia Kharlamova to examine similar phenomena in the silver foxes. They found that the same relationship

Figure 2. Domesticated foxes today have a rounder, shorter snout than wild foxes. (Photo Courtesy: Institute of Cytology and Genetics, Novosibirsk.)

between bone width and length they had found in dogs—short limbs and short snouts paired with wide limbs and wide, rounded snouts—was present in the domesticated foxes, and proposed an intriguing hypothesis about why these changes have emerged. In the case of foxes in the wild, as pups mature and wean off nursing, the body and face shape change in a manner that provides them with the best chance of survival. When they are pups, their faces are relatively round, and their legs are chunky. But, as they mature to adulthood, longer and more graceful legs provide more speed for chasing prey and evading predators and longer, more pointed snouts facilitate probing into the nooks and crannies of thick grasses and undergrowth while foraging for food. In wild foxes, this leads to natural selection for a change in body shape during development, producing the classic anatomy of adult wild foxes; but in the domesticated foxes, where individuals never have to forage, hunt or evade predators, that selection pressure has been eliminated. Apparently, without that pressure, the more juvenile rounded face and chunky body form continue into adulthood in the tame foxes.

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In the remainder of this article, I will discuss: (1) the effect of the process of domestication on the social cognition of the foxes, (2) recent work on the molecular genetics of domestication in the silver foxes, (3) a new hypothesis for why selection for tameness leads to the domestication syndrome, and (4) how the silver fox domestication experiment has led to new hypotheses about self-domestication in primates, including humans.

Domestication and Social Cognition

In 2002, Brian Hare was working on his PhD at Harvard, studying animal social cognition, under the supervision of Richard Wrangham. Hare's studies focused on social cognition in dogs. Work in this area had shown that on one classic social cognition test—the object-choice test—dogs performed very well. Researchers had found that if they placed two opaque containers on a table, and unknown to the animal, put food under one, and then pointed at the correct container, stared at it, touched it, or even place a marker like a wooden block on it, dogs easily solved the task.

Hare was interested in why dogs were so good at the object-choice test. Perhaps it was because dogs spend their whole lives with humans, and learn how to do this sort of thing. Or it could be that all canids are good at object-choice tests, regardless of experience with humans. Hare tested both wolves and dogs on this task. The dogs solved it, and the wolves did not. Not all canids could do this. Hare also tested dog pups of different ages, as well as dogs who had lots of interactions with humans versus few interactions, and in all the cases, the dogs solved the task: it wasn't experience with humans per se that made dogs so good at the task.

Why, Hare wondered, do dogs have this innate ability to solve hard social cognition tasks like the object-choice test, while other species do not? The answer, he thought, likely had something to do with the fact that dogs had been domesticated. "It is likely," Hare wrote in a 2002 *Science* paper, "that individual dogs that were able to use social cues more flexibly than could their last common wolf ancestor...were at a selective advantage." [4] During the process of domestication, dogs that were good at picking up on social cues emitted by their humans would get more food because they could do the things that we wanted them to do and would be rewarded.

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–Brian Hare

Hare's mentor, Wrangham, suggested an alternative explanation.

Perhaps the ability to follow human pointing was a byproduct of domestication: it had not been selected during the process of domestication but was somehow correlated with what had been, namely selection for friendliness toward humans. Hare wanted to design an experiment to distinguish between his hypothesis and Wrangham's alternative. The domesticated foxes offered a way to do that, as they were the only domesticated species where researchers knew exactly what sort of selection pressures had been in place during domestication, and that selection for social cognition, like following the pointing and gazing in the object-choice test, had **not** been selected. Hare also knew that in addition to the line of domesticated foxes, Belyaev (who died in 1985) and Trut had a control line of foxes that had been selected randomly with respect to their friendliness to humans. If Hare was correct, both the domesticated foxes and the control foxes should fare poorly on the social cognition test, because neither had been selected based on social cognition. If Wrangham was correct, and social cognition was indeed a byproduct of domestication, then the domesticated foxes should show social cognition on par with dogs, but the control foxes should not.

Hare, working with Trut and others, then ran an experiment involving pointing and gazing at one of the two objects placed in front of the foxes. Seventy-five fox pups were tested. Domesticated pups solved the problem, but control foxes did not. In fact, domesticated fox pups were just as good as dog pups on this test. The results were completely in line with Wrangham's hypothesis. Social cognition was a byproduct of domestication [5].

Molecular Genetic Studies of the Domesticated Foxes

Much of the recent work on the silver foxes has focused on identifying the molecular genetic changes that have occurred during the process of domestication.

Much of the recent work on the silver foxes has focused on identifying the molecular genetic changes that have occurred during the process of domestication. In a 2011 study that compared domesticated foxes to a separate line of foxes that had been selected for aggressive behavior to humans, Anna Kukekova, Trut, and their colleagues found that the genes associated with many of the unique behavioral and morphological changes in the tame foxes can be mapped onto a specific region of fox chromosome number 12 [6]. What made this finding particularly interesting is that just a year earlier, a paper that examined the genetics of domestication in dogs was published [7]. A comparative analysis found that some of the genes linked to domestication on chromosome 12 of the foxes were also found on the corresponding (homologous) dog chromosomes involved in their domestication.

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In a more recent study, Kukekova, Trut, and others have uncovered a hotspot for changes associated with domestication on fox chromosomes [15]. *SorCS*, one of the genes located in this hotspot, is known to be associated with synaptic plasticity, which plays a role in memory and learning. We have seen that domesticated foxes are adept at solving problems that require social cognition, [5] and together with work on *SorCS*, these studies are helping researchers understand how the process of domestication has led to crucial changes in cognitive abilities.

Right from the start of the silver fox domestication experiment, Belyaev hypothesized that the process of domestication was in part the result of changes in gene expression patterns. Gene expression is a measure of when genes 'turn on' and 'turn off' and how much protein products they produce. In a recent paper, Kukekova, Trut, and a team of researchers at Cornell examined expression patterns at the genome level, in both domesticated foxes and in a line of foxes that have been selected for aggressive behavior for more than forty years. They found that almost 150 genes in the prefrontal cortex of the brain where gene expression patterns between domesticated and aggressive foxes were different. Some of those genes are involved with serotonin receptor pathways that likely affect the behavioral temperament, including tame and aggressive dispositions. This same study uncovered differences in how common certain alleles are in the domestic versus aggressive foxes. Researchers found differences in allele frequencies at one hundred and seventy-six genes, including genes associated with what is called the 'neural crest cells'. Neural crest cells are part of the developing neural tube, which itself is a component of the very early stages of the nervous system in animals. Early on in embryonic development in mammals, neural crest cells migrate (move) to the brain, face, jaws, adrenal glands, ears, tail, fur, and other locations in a developing embryo. Because they develop into so many different types of cells after they migrate, they are referred to as 'multipotent cells'.

The Domestication Syndrome and Neural Crest Cell Migration

What makes the above finding on neural crest cells so intriguing is that neural crest cells are hypothesized to be key players in the domestication syndrome (for example, think of all the changes to the ears, tail, fur, and so on, in the domesticated foxes).

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Wilkins et al. hypothesize that when our ancestors were selecting for calm, tame behavior early in the process of domestication, they were also indirectly selecting for a reduction in the number of neural crest cells, as well as a reduction in the migratory behavior of these cells. As a result of this indirect selection, Wilkins et al. propose that "most of the modified traits, both morphological and physiological [associated with the domestication syndrome], can be readily explained as direct consequences of such deficiencies [in neural crest cells]... ." For example, fewer neural crest cells migrating to the cartilage in ears leads to 'floppy' ears, fewer neural crest cells migrating to the tail leads to a curly tail, and so on. Paired with molecular genetic work on differences in allele frequencies in genes associated with neural crest functioning in the domesticated foxes, Wilkins et al.'s unifying hypothesis for the domestication syndrome merits further investigation.

Self Domestication

By the late 1970s/early 1980s, the findings from the fox domestication experiment that he and Trut were leading led Belyaev to propose an audacious idea about how humans had become such sociable animals. He proposed that we have domesticated ourselves, by selecting tame mates and tame groupmates. Belyaev discussed this idea in two papers, the latter of which was a keynote speech at the XV International Genetics Congress in 1984 [9, 10].

Belyaev argued that “the social environment created by man himself has become for him quite a new ecological milieu.” This, of course, led to new natural selection pressures, and Belyaev proposed that “under these conditions, selection required from individuals some new properties: obedience to the requirements and traditions of the society, i.e., self-control in social behavior.” In particular, humans who were better able to cope with the stress, to stay calm rather than striking out in aggression, had the selective advantage. “One can hardly doubt,” Belyaev noted, “that the ‘word’ and its meaning has become for man an incomparably stronger stressful factor than a club blow for a Neanderthal man,” [9] favoring behaviors such as selecting calmer, ”tamer” mates and groupmates.

Much work needs to be done, but today there is a small, but growing, comparative literature on human self-domestication. There is also some evidence that self-domestication has occurred in another primate, the bonobo (*Pan paniscus*).

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Bonobos live in matriarchal fission-fusion societies in which females form alliances. Bonobos voluntarily share food, even with strangers. They play often and sexual behavior is used as a greeting, a form of play, and a means of resolving conflicts. Chimpanzees are bonobos’ closest evolutionary relatives. Chimp society is patriarchal, with males dominant to females. Males often form alliances, but unlike the female coalitions in bonobos, such alliances raid and viciously attack individuals in other groups. These differences between chimpanzees and bonobos have led Brian Hare to propose that bonobos have self-domesticated themselves.

Molecular genetic comparison of the chimpanzee and bonobo genomes suggests that they began to diverge from a common ancestor approximately two million years ago, at about the time the Congo River was forming in Africa. The Congo River split up the population of the common ancestor to bonobos and chimpanzees into two groups, with the lineage that led to bonobos living in a small area to the south of the Congo River, and the lineage that led to chimpanzees living to the north of the river in a much larger area stretching across west and central Africa. By chance, the bonobo lineage ended up in an area with higher-quality plant foods than the chimpanzee lineage. In addition, the lineage leading to bonobos faced less competition for food. There were gorillas to the north of the Congo River, but not to the south, where the bonobo lineage was.

Hare and his colleagues hypothesize that bonobos who played and cooperated with one another to obtain food, shelter, and sexual partners fared better than aggressive intolerant types, and so bonobo females may have selected the least aggressive, most friendly partners of the opposite sex as their mates. That is, they may have self-domesticated themselves, in a process similar to that outlined by Belyaev for human self-domestication [11].

Selection for tameness in bonobos, but not chimpanzees, has led to changes in their bodies and behavior that are strikingly similar to the changes seen in the domesticated foxes. Compared to chimpanzees, bonobos display many of the traits in the domestication syndrome.

This selection for tameness in bonobos, but not chimpanzees, has led to changes in their bodies and behavior that are strikingly similar to the changes seen in the domesticated foxes. Compared to chimpanzees, bonobos display many of the traits in the domestication syndrome. They have more juvenile skeletal features and lower stress hormone levels than chimps. And compared to chimpanzees, bonobos also have a longer developmental period during which they rely on their mothers, show more variation in color (e.g., white color tufts and pink lips), and have smaller skulls (but have more gray matter in their brains devoted to areas linked with empathy).

Closing Thoughts

Now in its sixtieth year, the silver fox domestication experiment continues to shed new light on the process of domestication. As they have from the initiation of the experiment, each year researchers test hundreds of foxes and preferentially breed the tamest. While much of the work today centers on the molecular genetic changes associated with domestication, changes to behavior, morphology, neurobiology and endocrinology continue to be recorded. All of this provides evolutionary biologists with a rare glimpse of continuous change is a fundamentally important experimental system.

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