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REVIEW

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The silver fox domestication experiment

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Abstract

For the last 59 years a team of Russian geneticists led by Lyudmila Trut have been running one of the most important biology experiments of the 20th, and now 21st, century. The experiment was the brainchild of Trut's mentor, Dmitri Belyaev, who, in 1959, began an experiment to study the process of domestication in real time. He was especially keen on understanding the domestication of wolves to dogs, but rather than use wolves, he used silver foxes as his subjects. Here, I provide a brief overview of how the silver fox domestication study began and what the results to date have taught us (experiments continue to this day). I then explain just how close this study came to being shut down for political reasons during its very first year.

Keywords: Domestication, Evolution, Silver foxes

Introduction, history and findings

Today the domesticated foxes at an experimental farm near the Institute of Cytology and Genetics in Novosibirsk, Siberia are inherently as calm as any lapdog. What's more, they look eerily dog-like. All of this is the result of what is known as the silver fox, or farm fox, domestication study. It began with a Russian geneticist named Dmitri Belyaev. In the late 1930s Belyaev was a student at the Ivanova Agricultural Academy in Moscow. After he graduated he fought in World War II, and subsequently landed a job at the Institute for Fur Breeding Animals in Moscow.

Both as a result of his reading of Darwin's *The Variation of Animals and Plants Under Domestication* (Darwin 1868), and his interaction with domesticated animals at the Ivanova Agricultural Academy and at the Institute for Fur Breeding Animals, Belyaev knew that many domesticated species share a suite of characteristics including floppy ears, short, curly tails, juvenilized facial and body features, reduced stress hormone levels, mottled fur, and relatively long reproductive seasons. Today this suite of traits is known as the domestication syndrome. Belyaev found this perplexing. Our ancestors had domesticated species for a plethora of reasons—including transportation (e.g., horses), food (e.g., cattle) and protection (e.g., dogs)—yet regardless of what they were selected for, domesticated species, over time, begin to display traits in the domestication syndrome. Why? Belyaev hypothesized that the one thing our ancestors always needed in a species they were domesticating was an animal that interacted prosocially with humans. We can't have our domesticates-to-be trying to bite our heads off. And so he hypothesized that the early stages of *all* animal domestication events involved choosing the calmest, most prosocial-toward-human animals: I will refer to this trait as tameness, though that term is used in many different ways in the literature. Belyaev further hypothesized that all of the traits in the domestication syndrome were somehow or another, though he didn't know how or why, genetically linked to genes associated with tameness.

Belyaev set out to test these 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*). Every generation he and his team would test hundreds of foxes, and the top 10% of the tamest would be selected to parent the next generation. They developed a scale for scoring tameness, and how a fox scored on this scale was the *sole* criteria for selecting foxes to parent the next generation. Belyaev could then test whether, over generations, foxes were getting tamer and tamer, and whether the traits in the domestication syndrome appeared if they selected strictly based on tameness.

The experiment began in 1959 at the Institute of Cytology and Genetics in Novosibirsk, Siberia, shortly after Belyaev was appointed vice director there. Belyaev

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immediately recruited 25-year-old Lyudmila Trut to his team (Fig. 1). Trut quickly became the lead researcher on the experiment, working with Belyaev on every aspect from the practical to the conceptual. Trut turned 85 years old in November of 2018 and remains the lead investigator on the work to this day (Belyaev died in 1985).

It is not possible here to do justice to all of the results this almost six-decade-long experiment has produced. Here I touch on some of the most salient (see Trut 1999, Trut et al. 2009 and Dugatkin and Trut 2017 for more). Starting from what amounted to a population of wild foxes, within six generations (6 years in these foxes, as they reproduce annually), selection for tameness, and tameness alone, produced a subset of foxes that licked the hand of experimenters, could be picked up and petted, whined when humans departed, and wagged their tails when humans approached. An astonishingly fast transformation. Early on, the tamest of the foxes made up a small proportion of the foxes in the experiment: today they make up the vast majority.

Fig. 1 Lyudmila Trut. **a** 1960 and **b** 2015

Belyaev was correct that selection on tameness alone leads to the emergence of traits in the domestication syndrome. In less than a decade, some of the domesticated foxes had floppy ears and curly tails (Fig. 2). Their stress hormone levels by generation 15 were about half the stress hormone (glucocorticoid) levels of wild foxes. Over generations, their adrenal gland became smaller and smaller. Serotonin levels also increased, producing "happier" animals. Over the course of the experiment, researchers also found the domesticated foxes displayed mottled "mutt-like" fur patterns, and they had more juvenilized facial features (shorter, rounder, more dog-like snouts) and body shapes (chunkier, rather than gracile limbs) (Fig. 3). Domesticated foxes like many domesticated animals, have longer reproductive periods than their wild progenitors. Another change associated with selection for tameness is that the domesticated foxes, unlike wild foxes, are capable of following human gaze as well as dogs do (Hare et al. 2005). In a recent paper, a "hotspot" for changes associated with domestication has been located on fox chromosome 15 (Kukekova et al. 2018). *SorCS*, one gene in this hotspot, is linked with synaptic plasticity, which itself is associated with memory and learning, and so together these studies are helping us better understand how the process of domestication has led to important changes in cognitive abilities.

Right from the start of the experiment, Belyaev hypothesized that the process of domestication was in part the result of changes in gene expression patterns—when genes "turn on" and "turn off" and how much protein product they produce. A recent study examining expression patterns at the genome level, in both domesticated foxes and a second line of foxes that has been under


Fig. 2 Mechta (Dream), the first of the domesticated foxes to have floppy ears 1969

Fig. 3 The domesticated foxes have more juvenilized facial characters, including a shorter, rounder snout, than wild foxes

long-term selection for aggressive, rather than tame, behavior, suggests Belyaev was correct (Wang et al. 2018). This study identified more than one hundred genes in the prefrontal cortex of the brain that showed different gene expression patterns between domesticated and aggressive foxes. Some of those genes are linked to serotonin receptor pathways that modulate behavioral temperament, including tame and aggressive temperaments.

When Belyaev proposed that the domestication syndrome was linked to tame behavior, he did not have a proposed mechanism, but today we are getting closer to understanding how this works. Very early on in animal development, what are known as neural crest cells migrate from the neural crest to a plethora of locations: glands in the endocrine system, bone, fur, cartilage, the brain and other spots in a developing embryo. The neural crest cell hypothesis for the domestication syndrome proposes that selection for tame behavior results in a reduction of the number of migrating neural crest cells, which subsequently leads to changes in fur coloration, facial structure, the strength of cartilage (floppy ears, curly tails and so on), hormone levels, the length of the reproductive season, and more. This hypothesis may provide the link that Belyaev was missing when he came up with the idea for the experiment (Wilkins et al. 2014).

Discussion: a cautionary tale

The silver fox domestication study is often lauded as one of the most important long-term studies ever undertaken in biology. Yet in 1959, the very year it commenced, the work came within a hair's breath of being shut down by the premier of the Soviet Union. The problem for Belyaev and Trut was that their domestication experiment, like any experiment in domestication, was an experiment in genetics. But work in Mendelian genetics was essentially illegal at the time in the Soviet Union, because of a pseudo-scientific charlatan by the name of Trofim Lysenko (Joravsky 1979; Soyfer 1994).

In the mid-1920s, the Communist Party leadership, in an attempt to glorify the average citizen, began to promote uneducated men from the proletariat into the scientific community. Lysenko was one of those men. The son of peasant farmers in the Ukraine, Lysenko didn't learn how to read until he was a teenager, and his education, as it was, amounted to a correspondence degree from gardening school. With no training, he still landed a middle-level job at the Gandzha Plant Breeding Laboratory in Azerbaijan in 1925. Lysenko convinced a *Pravda* reporter, who was writing a story about the regime's glorious peasant scientists, that the yield from his pea crop he tended was far above average, and that his technique could save a starving USSR. In the *Pravda* article the reporter wrote glowingly that "the barefoot professor Lysenko has followers… and the luminaries of agronomy visit… and gratefully shake his hand." Pure fiction, but the story propelled Lysenko to the national limelight, with Josef Stalin taking pride in what he read.

Over time Lysenko would claim to have done experiments creating grain crops, including wheat and barley, that produced high yields during cold periods of the year, if their seeds had been kept in freezing water for long stretches before planting. What's more, Lysenko claimed offspring of these plants would also produce higher yields, down through the generations. This method, he said, could quickly double the yield of farmlands in the Soviet Union in just a few years. In truth, Lysenko never undertook any legitimate experiments on increased crop yield. Any "data" he claimed to have produced he simply fabricated.

Soon Stalin was his ally, and Lysenko began a crusade to discredit work in Mendelian genetics because proof of the genetic theory of evolution would likely expose him as a fraud. He denounced geneticists, both overseas and in the Soviet Union, as subversives. His star was rising and at a conference held at the Kremlin in 1935, after Lysenko finished a speech in which he branded Western geneticists as "saboteurs," Stalin stood up to yell, "Bravo, Comrade Lysenko, bravo."

Lysenko was placed in charge of all policy regarding the biological sciences in July 1948. The next month, at a meeting of the All-Union Lenin Academy of Agricultural Sciences, he presented a talk that today is regarded as the most disingenuous, dangerous speech in the history of Soviet science. In this speech, "The Situation in the Science of Biology," Lysenko damned "modern reactionary genetics," by which he meant Mendelian genetics. At the end of his ranting, the audience cheered wildly. Geneticists present were forced to stand up and refute their scientific knowledge and practices. If they refused, they were thrown out of the Communist Party. In the aftermath of that awful speech thousands of geneticists were fired from their jobs. Dozens, perhaps hundreds, were jailed, and a few were murdered by Lysenko's henchmen.

Belyaev could not sit by idly. After reading of Lysenko's speech in the newspaper, he was furious. His wife, Svetlana, remembers it well: "Dmitri was walking toward me with tough sorrowful eyes, restlessly bending and bending the newspaper in his hands." Another colleague recalls running into him that day and how Belyaev had fumed that Lysenko was "a scientific bandit" (Dugatkin and Trut 2017). Ignoring the personal risk, Belyaev began speaking out about the dangers of Lysenkoism to all scientists, whether friend or foe.

The case of Nikolai Vavilov, one of Belyaev's intellectual idols, illustrates just how dangerous it was to speak out against Lysenko (Medvedev 1969; Pringle 2008; Soyfer 1994). Vavilov studied plant domestication and was also one of the world's leading botanical explorers, travelling to sixty-four countries collecting seeds. In his lifetime alone, three terrible famines in Russia killed millions of people and Vavilov had dedicated his life to finding ways to propagate crops for his country. His research program centered on finding crop varieties that were less susceptible to disease.

Vavilov's collecting trips are the stuff of legend. On one of three expeditions, he was arrested at the Iran-Russia border and accused of being a spy, simply because he had a few German botany books with him. On another trip, this one to the border of Afghanistan, he fell as he was stepping between two train cars, and was left dangling by his elbows as the train roared along. On yet a different a trip to Syria he contracted malaria *and* typhus.

Vavilov collected more live plant specimens than any man or woman in history, and he set up hundreds of field stations for others to continue his work.

Vavilov had actually befriended the young Lysenko in the 1920s, before it became clear that Lysenko was a malevolent charlatan. Over time, Vavilov became suspicious of Lysenko's results, and in a series of experiments trying to replicate what Lysenko said he had discovered, Vavilov proved to himself, and others that were willing to listen (though not many were), that Lysenko was a fraud. He then became Lysenko's most fearless opponent. In retaliation, Stalin forbade Vavilov from any more travels abroad and he was denounced in the government newspaper, *Pravda*. Lysenko warned Vavilov that "when such erroneous data were swept away… those who failed to understand the implications" would also be "swept away." Vavilov was undeterred, and at a meeting of the All-Union Institute of Plant Breeding declared, "We shall go into the pyre, we shall burn, but we shall not retreat from our convictions."

In 1940, Vavilov was kidnapped up by four men wearing dark suits and thrown into the KGB's dreaded Lubyanka Prison in Moscow. Next he was shipped off to an even more remote prison. There, over the course of 3 years, the man who had collected 250,000 domesticated plant samples to solve the puzzle of famine in his homeland was slowly starved to death.

Lysenko's power had its ebbs and flows. In 1959, as the fox domestication experiment was just beginning, Lysenko was getting frustrated that his hold on Soviet biology was loosening. Something needed to be done. And The Institute of Cytology and Genetics, where the fox domestication experiment had just begun, where Belyaev was vice director, and where they had the audacity to put "Genetics" in the title of the institute, seemed a good place to attack.

The Institute of Cytology and Genetics was part of a new giant scientific city called Akademgorodok. Long before this city was built, Russian writer Maxim Gorky had written of a fictional "town of science… a series of temples in which every scientist is a priest… where scientists every day fearlessly probe deeply into the baffling mysteries surrounding our planet." Here Gorky envisioned "…foundries and workshops where people forge exact knowledge, facet the entire experience of the world, transforming it into hypotheses, into instruments for the further quest of the truth." Akademgorodok was what Gorky had in mind. It was home to thousands of scientists housed at the Institute of Cytology and Genetics, the Institute of Mathematics, the Institute of Nuclear Physics, the Institute of Hydrodynamics, and a half dozen other institutes.

In January 1959, a Lysenko-created committee from Moscow was sent to Akademgorodok. This committee had been authorized to determine just what sort of work was being done at the Institute of Cytology and Genetics, and Belyaev, Trut and their colleagues understood the gravity of the situation. "Committee members were, Trut said, "snooping in the laboratories," and rumors were spreading that the committee was unhappy. When the committee met with Mikhail Lavrentyev, chief of all the institutes at Akademgorodok, they told him that "the direction of the Institute of Cytology and Genetics is methodologically wrong" (Dugatkin and Trut 2017). Ominous words from a Lysenkoist group.

Nikita Khrushchev, premier of the USSR, learned of the committee's report about Akademgorodok. Khrushchev was a supporter of Lysenko, and he decided to see for himself what was happening. In September 1959, while returning from a visit to Mao Tse-Tung in China, he stopped off in Novosibirsk and went to Akademgordok.

The staff of all the science institutes at Akademgorodok gathered for this visit, and Trut remembers that the premier "walked by the assembled staff very fast, not paying any attention to them" as he proceeded to a meeting with administrators. "Khrushchev" Trut recalls was, "very discontented, with the intention to get everyone in trouble because of the geneticists." What Khrushchev and Akademgorodok administrators said that day was not recorded, but accounts from the time make clear that the premier intended to shut down the Institute of Cytology and Genetics that day, and with it the nascent silver fox domestication experiment.

Fortunately for science, Khrushchev's daughter, Rada, was with him in Akademgorodok. Rada, a well-respected journalist, had trained as a biologist, and understood very well that Lysenko was a fraud. She somehow managed to convince her father to let the Institute of Cytology and Genetics remain open. In an ironic twist, because Khrushchev felt he had to do *something* to show his discontent, the day after his visit, he fired the head of the Institute of Cytology and Genetics. Deputy Director Belyaev was now in charge of the institute.

If Rada Khrushchev had not taken a stand for science that day the fox domestication study would likely have ended before it even got off the ground. But, it survived and thrived and continues to shed new light on the process of domestication.

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The author read and approved the final manuscript.

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