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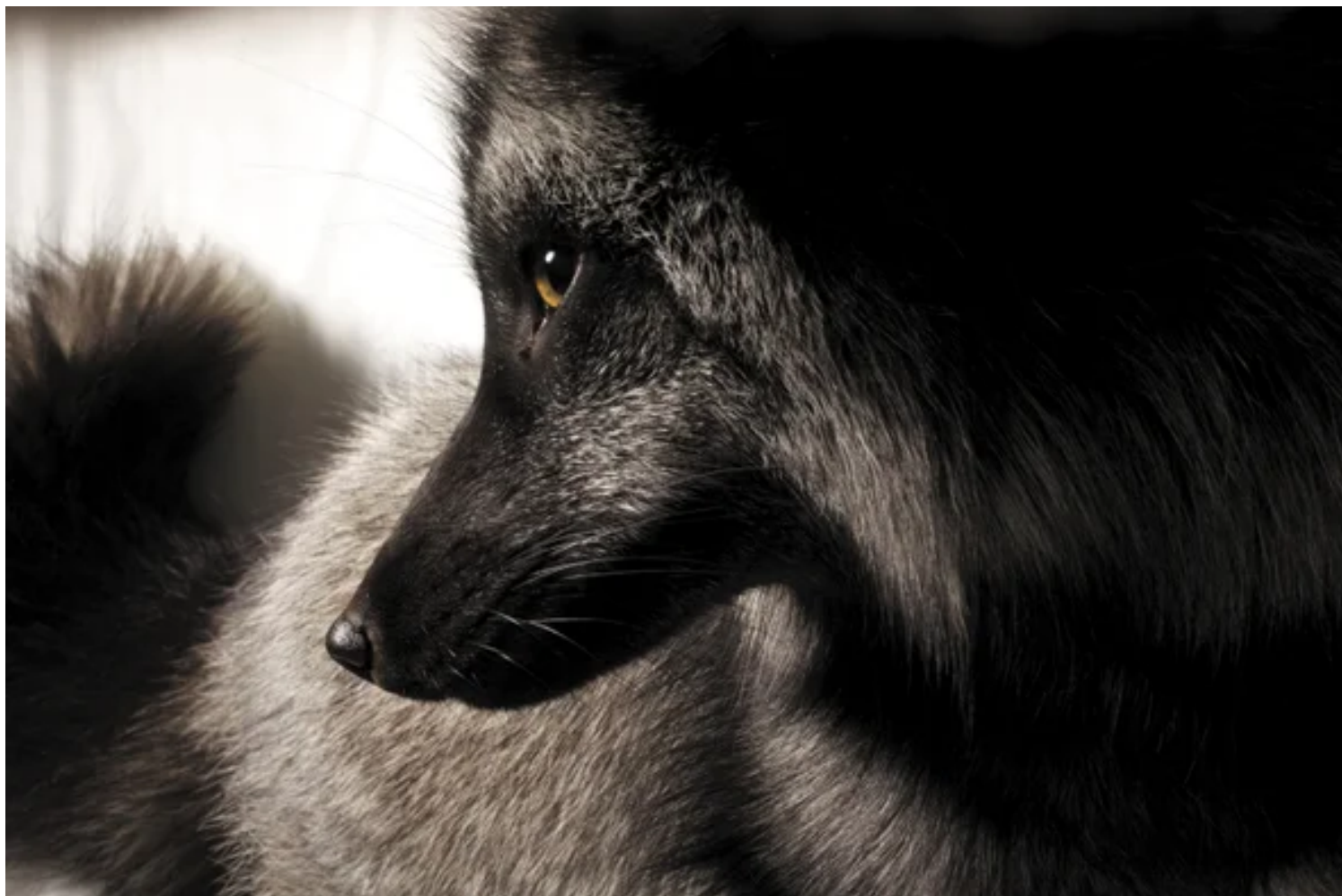
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EVOLUTION

Wild Foxes Can Be Transformed into Pets in a Few Generations

To test ideas of animal domestication, a bold experiment in Siberia put evolution on a fast track

By Lyudmila Trut, Lee Alan Dugatkin on May 1, 2017



Human life span was sufficient time to select for traits that have transformed foxes from wild to doglike. Credit: Vincent J. Musi *National Geographic*

| I N B R I E F |

Wild wolves were transformed into domesticated dogs in only the past few tens of thousands of years. Humans clearly played a role in the speciation, but the details are lost to history.

A six-decade experiment in Siberia has attempted to replay the process by which wolves evolved into dogs. In this work, another canid species—wild foxes—were selected for tameness over dozens of generations.

Within a few generations, foxes emerged that behaved like pets and that had physical characteristics associated with domestication, including mottled coats and curly tails.

The animal runs toward me, its curly tail wagging and its loving eyes full of joy. It jumps into my arms and nuzzles my face, like a dog. But it is not a dog. It is a fox—a fox that looks and behaves much like a dog. The animal and its close relatives are the result (as of early 2017) of 58 generations of selective breeding, performed in an attempt to discover in general the secrets of domestication and in particular how humans may have transformed wolves into the first dogs.



Foxes and researchers pose at their Siberian facility (1 and 2). Author Lyudmila Trut pets Pushinka's pup Penka in 1974, when all three shared a house (3). Credit: Vincent J. Musi *National Geographic* (2); Courtesy of Lyudmila Trut and Institute of Cytology and Genetics (3)

I am now 83 years old. As I look back on the experiment to which I have devoted three quarters of my life, my thoughts sometimes drift to Antoine de Saint-Exupéry's classic story *The Little Prince* and the fox's admonition to the prince that "you become responsible forever for what you have tamed."

I have thus been responsible for these foxes since shortly after I first met my mentor and friend Dmitri Belyaev in 1958. I was finishing my studies at Moscow State University when I heard that Belyaev was heading to Novosibirsk to join the new Institute of Cytology and Genetics and was looking for students to be part of a domestication experiment he was about to start.

In my first meeting with Belyaev, I was struck that he treated me, a mere undergraduate, as an equal. He explained the basic idea of the research, which was to study the process of domestication at fast-forward speed: “I want to make a dog out of a fox,” he said. Generation after generation, we would selectively breed those foxes that interacted in the most positive ways with humans. If such a process worked as we thought it would, domestication—perhaps akin to the transformation that occurred to turn wolves into dogs—would unfold before our eyes.

By the time I left Belyaev’s office, I wanted in—which meant moving to Novosibirsk, the major city in Siberia. I was excited by the prospect of becoming part of the first generation of researchers in Novosibirsk’s new “scientific city” of Akademgorodok, which housed the fledgling institute, and by the prospect of working with a man I sensed was a revolutionary thinker. Soon my husband, baby daughter and I were heading east on the long train ride from Moscow.

Belyaev’s hypothesis about the process of animal domestication was both radical and simple. He had come to think that the defining characteristic of all domesticated animals was their tameness. Therefore, from an evolutionary perspective, the process of domestication was primarily driven by our ancestors favoring animals that were the least aggressive and least fearful toward humans. Tameness was the key to working with animals to breed them for the other traits we wanted. Our dogs, cows, horses, goats, sheep, pigs and cats had to be docile, regardless of whether we were looking for protection, milk, meat, companionship, or other goods or qualities.

What is more, Belyaev thought that most, if not all, of the other characteristics that many domesticated animals possess, what we now call the domestication syndrome—curly tails, floppy ears, mottled fur pattern, the maintaining of juvenile facial characteristics (roundness and a blunted snout) into adulthood, and less reliance on strict seasonal breeding—were by-products of selecting for the tamest animals. And so, generation after generation, under Belyaev’s guidance but also with a fair share of

autonomy dealing with day-to-day experimental issues, I selectively bred the tamest foxes from animals that we initially collected from fox-fur farms around the Soviet Union.

MEET THE ELITES

Every year I made initial tests on hundreds of foxes, using a standard procedure that we developed. Wearing two-inch-thick gloves for protection, I approached each fox in its cage, stood by the closed cage, opened the cage door and placed a stick inside the cage. I scored the foxes' reactions on a scale that gave the calmest individuals the highest totals.

In the first years the vast majority of the foxes seemed less like dogs than like fire-breathing dragons: they were extremely aggressive when I approached or put the stick into the cage. I am sure these low scorers would have loved to rip my hand off. Other low-scoring foxes cowered in fear at the back of their cages. But a small number of animals remained calm throughout the test, observing but not reacting one way or the other. These animals were selected to mate and produce the next generation. I kept detailed records about every stage of development from newborn to adult. And we were especially careful to avoid inbreeding that would occur via the mating of close relatives—we hoped thus to avoid negative genetic consequences as a confounding factor in the experiment.

Even the calm foxes of the first few generations were not especially prosocial toward people—they seemed to tolerate, but not enjoy, the presence of humans. But I got a tantalizing hint of what was to come in the fourth and fifth generations: pups barely able to walk would wag their little tails in anticipation as I approached. Then came generation six.

As my colleagues and I wrote in 2009 in the journal *Bioessays*, “In the sixth generation,

there appeared pups that eagerly sought contacts with humans, not only [tail] wagging [but] also whining, whimpering, and licking in a dog-like manner.” The emergence of this constellation of behaviors was so striking we dubbed the animals the “elites.” These little foxes even looked up when they heard their names. It appeared that they “yearned for human companionship,” as we noted in our contribution to the second edition of a volume entitled *The Genetics of the Dog* in 2012. The tame pups also responded to sounds two days earlier and opened their eyes a day earlier than was typical for foxes, almost as if they were preparing to start interacting with people as soon as possible.

The elites charmed every human they met, no matter how toughened. One evening after the staff went home, Belyaev brought a famous army officer, a General Lukov, to our facility. Lukov was a formal man, hardened by the horrors of war. But when I opened a cage that housed one of the elite females and the fox scampered over and laid down next to me, the general’s dignified demeanor melted away. Apparently astonished, he approached the fox, squatted down and petted its head at length.

In that sixth generation, the elites made up but 2 percent of our domesticated foxes, but that would increase with each generation. Today the figure sits at about 70 percent.

FETAL TRANSPLANTS

Belyaev and I were geneticists by training, and any experiment on domestication is an investigation of evolutionary genetics. We needed to be certain that the changes we saw in the domesticated foxes were genetic in origin. Thus, we developed a test involving tame foxes as well as foxes from another experimental group we had developed—animals selected for their aggression toward humans. Generations of breeding had produced what we thought of as a fox equivalent of Cerberus, the multiheaded hound of Hades that guards the gates of the Underworld. These were mean foxes.



Domesticated pup enjoys human contact. Its rounded snout and mottled fur differ from those of its ancestors. Credit: Lyudmila Trut and Institute of Cytology and Genetics

Our idea was to move embryos from tame mothers into the wombs of aggressive females, and vice versa. If the newborn pups behaved like their biological, rather than their surrogate mother, we could be confident that tameness and aggression were fundamentally genetic.

Every transplant involved a pair of females, one tame and one aggressive, each about a week into pregnancy. After anesthetizing the two females, I made a surgical incision into the abdomen of one and located the uterus, with its right and left “horn,” each of which contained implanted embryos. I then removed the embryos from one horn of the donor female, gently placing them in a nutritive liquid. Then I repeated the surgical procedure, removing the embryos from one horn of the recipient female but this time replacing those with the embryos from the donor. In some of the transplants, the donor was a tame female and the recipient an aggressive female. In other transplants, the roles were reversed.

But when the pups were born seven weeks later, how would I know which litter members were the genetic offspring and which were the transplants? The foxes themselves came to the rescue here—coat color is a genetic trait in these animals, so by carefully recording the coat colors of their parents, the pups' coats would act as a marker of their lineage.

My longtime friend and colleague Tamara Kuzhutova and I recorded the pups' behavior as soon as they began interacting with humans. I particularly remember an aggressive female and her pups, only some of which were aggressive. Her foster tame offspring were barely walking, but if there was a human standing by they were already rushing to the cage doors and wagging their tails. This improper behavior appeared to vex the mother—she growled at the tame pups, grabbed their necks and threw them back in the nest.

In that same litter, the genetic offspring of the aggressive mom comported themselves in keeping with their mother's expectations: they growled aggressively and ran on their own to their nests. We saw this pattern repeatedly—pups behaved like their genetic mothers, not their surrogate mothers. Tameness and aggression toward humans thus appeared to be genetic traits.

PUSHINKA

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By 1974 we were 15 generations into the experiment. Many of the tame foxes fell into the elite category and were also showing an array of the characteristics seen in other domesticated species, as Belyaev had predicted. Their faces had become more juvenile in appearance, their tails were bushier, the levels of their stress hormones were lower and their reproductive cycles lasted longer. A few, including a favorite of mine named Mechta (“dream”), even had floppy ears.

Most domesticated species do not form close relationships with specific humans, but

dogs are different. Might this emotional affinity for people be a change that could emerge quickly, as with so many other changes we had seen in the foxes? And would living with a human come naturally to the foxes we had domesticated? To seek answers, I proposed to Belyaev that we could use our genetically tame foxes to examine deep interspecies emotional bonds akin to those that form between humans and dogs.

The fox farm at which we ran the experiment included a small house. I proposed that I move into the house with one of the elite foxes to see what bonds might develop between us. Belyaev enthusiastically agreed. And so, on March 28, 1974, Pushinka, Russian for “tiny ball of fuzz,” and I moved in together.

Pushinka had coal black eyes, silver-tipped black fur and a stripe of white on her left cheek. She had recently had her first birthday and was pregnant, just a week or two from delivering. I could therefore observe not only how Pushinka adjusted to living with me but also whether pups born in the company of humans might socialize differently than other pups, even elites, did.

Our new home had three rooms plus a kitchen and bathroom. I staked out one room to serve as bedroom and office, and I built a den in another room for Pushinka. The third room acted as a common area, with a couple of chairs and a table. Pushinka was free to roam anywhere in the house. So that I could also have some time with my human family, Kuzhutova and a few others helped out by taking over some days and nights. Whoever was on shift made detailed journal entries throughout the day and evening about all aspects of Pushinka’s behavior.

The first few days were a roller-coaster ride. When Pushinka moved in, she raced around the house, clearly agitated. She would not eat anything until I gave her a little piece of cheese and an apple that I had prepared for myself. On day two, things improved. When I returned after a short trip away from the house, Pushinka met me at the door—like a dog does. But Pushinka’s mood swings continued. She could be so

jittery that my new friend seemed at the edge of a nervous breakdown, but the next day she quietly jumped up on the bed and curled up beside me.

Although the adjustment had been rougher than I anticipated, after a week or so Pushinka settled down. She lay by my feet while I worked at my desk. She appeared to savor going out for walks with me. In one of her favorite games I would hide a treat in my pocket, and she would try to snatch it out. Sometimes she would lie on her back, inviting me to pet her exposed belly.

On April 6, Pushinka gave birth to six pups. And to my amazement, she carried one of her pups over to me and placed it at my feet. "Shame on you!" I remember saying, "Your pup's going to get cold!" But when I brought the pup back to the den, Pushinka again presented it to me. We went back and forth for a few rounds before I surrendered and did not bring the pup back to its nest.

I gave the pups names, all starting with P in Mom's honor: Prelest ("gorgeous"), Pesnya ("song"), Plaksa ("crybaby"), Palma ("palm tree"), Penka ("skin") and Pushok (the masculine version of "tiny ball of fuzz"). Within a couple of weeks the pups would come running out of their den when I entered the room.

Each had a distinctive personality: Pushok was an attention hog, Palma enjoyed jumping onto tables, Pesnya was stoic, Prelest sometimes bullied her siblings, Plaksa made mumbling sounds as she walked around, and Penka, my favorite, was a champion nap taker.

Despite Leo Tolstoy's claim that "all happy families are alike," Pushinka and her pups were a family both happy and unique. I would play ball with them all or run around to be chased by the little ones. Penka was especially fond of the latter activity, jumping on my back when she caught me. Especially rambunctious outings wore out the pups. One of my journal entries describes them as "sleeping, with no worries and with no fear."

As her offspring grew and she could spend less time watching over them, the bond between Pushinka and me deepened. She would lie by my feet and wait for me to scratch her neck. If I popped out of the house for a bit, Pushinka would sometimes sit at the window, looking out in anticipation of my return. And on seeing me approach the house, she would wait at the door, wagging her tail.

Despite all these signs of our connection, nothing could prepare me for the events of the evening of July 15, 1974. I was reading a book on the bench outside of the house, as I did often, while Pushinka rested at my feet. I heard footsteps in the distance but thought nothing of it. Pushinka, however, sensed danger. But rather than hiding or seeking my protection, she sprinted toward the perceived intruder and did something that I had never seen her do before or would see again: she barked, sounding exactly like a guard dog.

Never before had Pushinka acted in a truly aggressive, let alone fierce, manner to any human. I ran over to discover that it was just the night guard patrolling the facility who had spooked Pushinka. I began speaking to the guard in a calm voice. Pushinka, apparently sensing that all was well, stopped barking.

We had moved into the house three and a half months earlier to see whether living with a human would elicit a doglike loyalty in elite foxes that were the product of some 15 years of genetic selection. I consider that night to have provided the decisive answer.

DOWN TO THE DNA

Pushinka is long gone. But the experiment, and my involvement, continues to this day. Forty-three generations have followed Pushinka's. (Forty-three human generations ago would put us somewhere in the High Middle Ages.) The descendants of Pushinka and of her tame peers have provided insight after insight into the process of domestication, delineated in our book *How to Tame a Fox (and Build a Dog)*, but suffice it to say that

the tame foxes today are even friendlier and more affectionate toward humans. They inherently follow human gazes and gestures, and they look ever more eerily doglike—adding rounder snouts and shorter, chunkier limbs to their other characteristics.

With advances in genetics, our team has in recent years been able to probe the process of domestication at the DNA level. Many, but certainly not all, of the chromosomal regions of genetic change associated with the unique behavioral and morphological characteristics of the tame foxes have been mapped onto fox chromosome number 12. In particular, we uncovered on chromosome 12 a number of quantitative trait loci (QTLs)—stretches of DNA associated with genes underlying continuously varying traits that are linked to tame behavior. (In humans, examples of varying traits associated with QTLs include height and skin color.)

By comparing these DNA sequences with what was known about the genetics of domestication in dogs, Anna Kukekova, I and our colleagues were able to confirm that in many cases the QTLs on fox chromosome 12 were similar to QTLs involved in the domestication of dogs. We thus conclude that, through selective breeding over dozens of generations, we have loosely replayed the transformation of a wild canid to a house pet at the genetic level.

The foxes are even starting almost literally to tell us things. When Svetlana Gogoleva and I analyzed the vocalizations of tame foxes versus those of aggressive foxes, we found that the sounds made by the tame foxes are unique. The acoustic dynamics of their vocalization are remarkably similar to human laughter. We do not know how or why the tame foxes “laugh,” but a more pleasant way for one species to bond with another is hard to imagine.

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Lyudmila Trut is an evolutionary geneticist and a professor at the Institute of Cytology and Genetics in Novosibirsk, Russia, where the fox-domestication experiment takes place. She has lived this story, told in her voice, since 1959. *Credit: Nick Higgins*



Lee Alan Dugatkin is a professor of biology at the University of Louisville. His newest book is *Power in the Wild: The Subtle and Not-So-Subtle Ways Animals Strive for Control over Others* (University of Chicago Press, 2022). Twitter: @Leedugatkin; Facebook: [facebook.com/lee.dugatkin/](https://www.facebook.com/lee.dugatkin/) *Credit: Nick Higgins*

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