

CHAPTER ONE

The Wolf that Rolled Over



Please don't judge me. I am about to tell you something you may find shocking, and I am concerned you may think badly of me. When I've told people before, it has divided opinion. Some have been curious, others downright disgusted. They've told me it's unnatural and asked me how I could do such a thing. I've no idea how you'll react, so I'll just come straight out and say it.

I own a genetically modified wolf.

I really do. My husband and I got him from a breeder that we found on the Internet. We exchanged a couple of emails, transferred a hefty wedge of cash then collected him from a pre-arranged location in southern England. The little animal howled all the way home.

Five years later, we now trust him so much that he lives in our house, sleeps on our bed and plays with our kids. If we were to set him free, I'm almost certain he wouldn't survive. He's never hunted fresh meat or brought down a caribou. He'd probably hang around by our back door, sulk and wait to be let back in again.

Higgs, as we call him, is a weird-looking wolf. His DNA has been altered so he is less than half the size of his free-roaming ancestors. His skull is smaller, his snout less pointy and his ears flop down rather than standing

erect. The classic sleek pelt has been replaced with what can only be described as an embarrassment of soft, messy curls. He is black all over, except for his nose, belly, tail and feet, which are white ... or brown when he's been digging in the garden. His tail wags rhythmically when he hears the word 'cheese'. Behaviourally, all trace of wolf cunning has been obliterated. The result is an animal so far removed from its original wild form that he barks at bin bags and often refuses to go out in the rain.

Before you pass judgement on this apparent lupine freak, let me tell you I am not the only one to own a genetically modified wolf. Millions of people, all over the world, keep similar animals but know them by a different name. They call them dogs. For dogs *are* genetically modified wolves.

When people think about genetic modification (GM), they tend to think about animals and plants whose DNA has been sculpted using the modern tools of genetics, but domesticated species have been genetically manipulated too. From the diminutive dachshund to the massive Saint Bernard, all dogs are descended from the European grey wolf. At some point in the past, humans and wolves crossed paths, and then somehow, somewhere, the wolf began to change. Its appearance altered. The wolf began to shrink. Its coat changed colour and its face changed shape. Physiological differences emerged, like the ability to digest starch and give birth more often. Its behaviour changed. The fearsome apex predator morphed from an animal that actively shuns human company into one, like Higgs, that demands it. All of these differences are underpinned by changes to the

wolf's genetic code. Now, although wolves and dogs still share around 99.5 per cent of their DNA, the tiny fraction that is different is enough to imbue them with their vastly different features.

Today, dogs have become such a normal part of our lives that it's easy to take them for granted, but their emergence marks a defining moment in the natural history of our world. Dogs were the first domesticated animals. It was the first time humans took a species and then fashioned it to become something more preferable. It was the first time we wrestled control of evolution and began to steer the biology of living things in a different, post-natural direction. The emergence of dogs paved the way for other domesticated species to follow, triggering a chain of cause and effect that would change our world for ever.

According to the most recent estimates, modern humans evolved in Africa sometime between 350,000 and 260,000 years ago, and for the vast majority of the time that followed, we simply lived off the land. We existed as hunter-gatherers, and were entirely dependent on wild animals and plants for our survival. Domestication changed all that. Around 10,000 years ago, after we had domesticated dogs, we began to strike up alliances with other wild organisms. The repeated harvesting and sowing of wild cereals led to the creation of domestic crop strains that were more bountiful and easier to grow. We domesticated other animals, like sheep, cows and goats, and as we began to corral and keep them, and tend to our crops, we found ourselves increasingly tied to the land. The nomadic hunter-gatherer way of life gave way to a more settled existence, leading to the formation of

villages. Because they could be bred, domestic animals provided a renewable source of meat and milk for food, and wool and leather for clothing. Food became more plentiful and the population began to grow. In time, because they could be owned and were easily transportable, domestic animals and plants went on to become a source of capital and wealth, so domestication fuelled the rise of trade. It drove the development of new technology, like ploughs, which further accelerated the rise of agriculture and in time led to the development of urban communities. When we think about key innovations, it's all too easy to dwell on recent inventions like the Internet and antibiotics, but it's no understatement to say that domestication helped to fuel the rise of civilisation, and changed the course of human history.

Looking around me now, I see a world full of domesticated species. My genetically modified hound, Higgs, slumbers peacefully at my feet. In the garden outside, our five chickens peck at corn, while our two rabbits nibble on a carrot. There are ponies in the field next door, and sitting on the fence post, a wayward tabby cat eyes me with disdain. Sitting at my desk sipping milky tea, * it's hard to imagine a time when the world was not full of domesticated animals, plants and the products derived from them. Yet, for the vast majority of time that there has been life on Earth, there have been no domesticated animals or plants. So when and where did this momentous change take place?

* Dogs, chickens, rabbits, ponies, cats, corn, carrots and tea are all species that have been domesticated.

What Was the Time Mr Wolf?

Until quite recently, scientists thought dogs were domesticated around 15,000 years ago, towards the end of the last Ice Age. It was a time when the ice sheets were retreating, when the landscape was newly green, and when humans and other animals began to colonise the northerly regions of Europe and Asia. There are plenty of dog fossils from this time, found in archaeological sites across Europe, Asia and North America, and the scientists who have studied them all agree: these remains belong to dogs, not wolves. The proportions of their skulls and the shapes of their teeth are all quite different. But then came a fossil that left people scratching their heads.

The skull was discovered in the Goyet Cave in Belgium. It's a remarkable archaeological site jam-packed with the bones of ancient humans, Ice Age animals and other captivating relics. 'The skull is quite small,' says Mietje Germonpré from the Royal Belgian Institute of Natural Sciences in Brussels, who studied the fossil. 'It is about the same size as a modern German Shepherd skull.' Wolves have long, slender snouts, but this animal had a shorter, wider muzzle and a broader braincase. It also had large, primitive-looking teeth. Collectively the features suggested that this animal was more dog than wolf. 'So we decided it was a primitive dog,' she says.

Then came the bombshell. Radiocarbon dating revealed that the skull was actually much older than previously thought. The creature was 36,000 years old, potentially pushing back the origins of domestication by a staggering 21,000 years. 'We were very surprised when we found out,' says Mietje. The skull divided opinion.

Some people agreed with Mietje. Others did not. ‘They said it’s too old and they don’t consider it to be a dog,’ she says. Critics pointed out that wolf skulls from this time vary enormously in size and shape and suggested that the Goyet skull belonged to an odd-looking wolf rather than an early dog. Then a different group of researchers made a computer-generated 3D reconstruction of the skull and concluded that certain features, like the way the snout protruded from the skull, were also wolf-like. It could have been an end to the debate, but then other fossils cropped up. Mietje has studied dog-like skulls from the Czech Republic and Russia that are over 25,000 years old, while a separate research group has described the 33,000-year-old skull of a presumed dog found in Siberia’s Altai mountains. What to think?

It’s bound to be tricky. If these animals really are early dogs, then they’re ‘only just’ dogs so they’re bound to have dog- and wolf-like features. So it’s here that scientists are turning to another form of historical evidence to help resolve the conundrum: ancient DNA.

Although DNA breaks down after death, sometimes the molecule can be preserved inside fossils, and extracted and studied. This gives scientists another way of studying the transition from wolf to dog. In the early days, genetic analyses painted a confusing picture. One study, for example, compared the full genetic sequences, or genomes, of modern dogs and wolves, to determine that dogs were domesticated between 11,000 and 16,000 years ago. Another study of ancient canids, which focused on a subtype of DNA hidden in the cells’ energy-generating mitochondria, suggests a date between 19,000

and 32,000 years ago. The results present a massive discrepancy. On the one hand, they suggest dogs were domesticated around the end of the last Ice Age at a time when agriculture was emerging. On the other, it seems they were established on the other side of the Last Glacial Maximum, the time when the ice sheets were at their greatest reach.

The debate moved on in 2015 after Swedish researchers discovered a fragment of rib protruding from a Siberian riverbank. They originally thought the bone belonged to a reindeer, but DNA analysis later confirmed that it came from a wolf. Radiocarbon dating suggested that the animal died around 35,000 years ago, long before dogs were thought to be domesticated, but then further genetic tests muddied the waters. The ancient wolf seemed to be equally related to both modern domestic dogs and modern wolves, but how could this be if dogs had yet to evolve? The team concluded that the ancient wolf must have lived just after the split between the ancestors of today's dogs and the ancestors of modern wolves. This means an earlier date of domestication, around 35,000 years ago, looks increasingly likely. Then in 2017, a different group of researchers arrived at a similar conclusion, this time using Neolithic dog fossils.

As more studies are added, an early date for the metamorphosis of wolves into dogs looks increasingly likely. Genetic analyses and fossil evidence hint at a deep connection between humans and dogs that stretches back much further than was initially assumed. It predates the rise of agriculture and settled societies, and now researchers find themselves arguing over when and where the transition occurred.

Today, the grey wolf is the only member of the canid family to have paws in both the Old and New Worlds. Its current range encompasses much of Europe, Asia and North America, but in the past, its territory was even greater. This makes it hard to know where to start. We know that dogs cannot have been domesticated in North America, because humans didn't arrive there until well after the Last Glacial Maximum when domestication was already well under way elsewhere, but that still leaves much of the globe to consider. Fossil finds point to Europe and further east to Siberia where the earliest, most primitive dog skulls have been found, but ancient DNA studies throw up alternative scenarios. Some suggest dogs became man's best friend in East Asia, while others hint at origins in Central Asia or the Middle East. Meanwhile, a recent study that compared genetic material from modern and ancient specimens revealed an old, deep split between East Asian and Western Eurasian dogs. The most obvious explanation, according to the study's author, Greger Larson from the University of Oxford, is that domestication occurred in at least two different places. The story of dogs may have no single origin. Dogs could have been domesticated multiple times in multiple places.

What intrigues me most, however, is *how* this relationship began. We can be pretty certain that our ancestors didn't just wake up one day and declare they wanted something that would fetch a stick, yet the process of domestication had to begin somewhere.

Hounds of Love

The winter had been cold and long, but now the sun climbed higher in the sky and leaves were beginning to

unfurl. The youngster sat on his haunches, staring into the embers of a fire that was dying down. He felt resentful. Not quite a boy, but not yet a man, he had been left behind in camp while the adults went out to search for food. Now he found himself alone, contemplating mischief.

A few days earlier he had followed his father out of the camp and into the woods. His father showed him a place where a large tree had fallen, wrenching deep-seated roots out of the rust-coloured earth, and the resultant hole that had been exposed in the hillside. Sharp-clawed paw prints framed the entrance to a dark tunnel: the unmistakable signature of a she-wolf's den. 'Be careful,' his father had warned him. 'These animals are dangerous.'

Back in camp, the boy knew he had hours before the hunting party would return, so he picked up a spear and slipped out of camp. He returned to the den to find fresh scats on the ground outside. The mother wolf had been there but when she heard his clumsy footsteps, she had beaten a swift retreat. Now she hovered in the background, watching as the human dropped to his knees and plunged his arm deep into the lair. When he stood back up, he was holding a small, wriggling wolf cub. It squirmed and whined, making the boy tighten his grip. Then he swaddled his find in a reindeer hide and carried it back to camp.

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Although humans and wolves have shared the same landscape for many tens of thousands of years, they interacted little. Both would have been wary of the other and kept their distance, but then something must have

changed. Academics argue over the nature of this initial interaction, but one scenario is that humans actively decided to invite the wolf into their world. Someone, like our Palaeolithic boy, went out and collected a cub. Skilled hunter-gatherers with an in-depth knowledge of their local environment, they would have known where the wolf dens were. It wouldn't have been difficult to scoop one up and bring it back to camp. Then, having done it once, it would be all too easy to repeat the process. The cubs that were kept would inevitably have been the ones that were easiest to catch, so over time, as the genes for their more relaxed nature were passed through the generations, domestication got under way.

Back in camp, the animals would have been kept for pragmatic purposes. As cubs, they could have entertained the children. As adults, they could have acted as sentries, and if they ever got too boisterous or aggressive to look after, they could have been set free or killed for their meat and fur.

We certainly know that Palaeolithic people wore specialised cold-weather clothing, including a variety of fitted garments made from well-tanned pliable hides. A 24,000-year-old ivory figurine from southern Siberia, for example, depicts what seems to be an individual wearing a carefully tailored all-in-one fur suit. Evidence for a wolf-fur onesie? It's a possibility. Similarly ancient wolf bones have been found with distinctive cut marks, indicating that the animals were probably skinned for their fur. They may also have held symbolic significance. One skull, studied by Mietje, is interesting because it has a bit of mammoth bone wedged between its front teeth. The fragment must have been inserted into the animal's

mouth after it died, suggesting human intervention, while other skulls sport conker-sized holes where their brains were removed. There were easier meals to be had than brain, so Mietje thinks these unusual relics are evidence that dogs held special significance. 'I'm in favour of the active involvement of the Palaeolithic people,' she says. 'I think they actively started to collect these animals and then kept them, not just for their fur, but for rituals too.'

It is, perhaps, easiest to imagine that humans chose the wolf, and that the wolf had no option but to go along with our plans. As a species, we like to think we are superior and separate from the animal kingdom, when really we're just animals too. Today, if we want a dog, we can just go out and get one, but it would be naive to presume that our ancestors followed the same thought process.

So an alternative theory proposes, not that humans chose wolves, but that wolves chose humans. Leftovers discarded by humans lured the wolves out of the shadows. The animals that were least afraid of us were the ones most likely to enter our campsites. As a result, they were better fed, healthier, and more likely to reproduce than warier pack members. The genes underpinning their more relaxed nature were passed between generations, and over time, the animals became progressively tamer. In this 'self-domestication' scenario, humans were stooges. We didn't invite wolves in, but by being messy, we created an ecological niche they were only too happy to fill.

It's a possibility. Modern wolves are adaptable animals. In Canada, there are two types of wolf: 'nomadic' wolves

that follow the caribou around and ‘sedentary’ wolves that tend to stay in one place. From time to time, their paths cross, but they don’t really get on. They’re like the Starks and the Lannisters, and will fight each other to protect what they consider to be *their* caribou. So maybe, 35,000 years ago there were one or more groups of migratory wolves that considered us to be their property. Instead of tracking caribou or reindeer, they followed us around, not because they wanted to eat us but because they benefited from the shared association.

So which was it? Did humans choose wolves or did wolves choose humans? We’ll probably never know but the upshot was the same. After contact was made, humans and wolves began to interact and over time, the relationship strengthened. Primitive dogs probably accompanied humans on their hunts and so tipped the odds in favour of a kill – a reciprocal arrangement that benefited both parties. At some point, when we started to physically keep them with us, we would have started engineering which animals got to reproduce. In the early days, it would have been the calmer animals that would have tolerated living in captivity, but in later times we would have selected for other characteristics, like being a good sentry or scaring the neighbours. It was the beginning of a long and beautiful friendship, and a defining moment in the story of evolution. Of course, dogs were only the beginning ...

Pigeon Parade

If Charles Darwin is to be remembered for only one book, it has to be the now classic *On the Origin of Species by Means of Natural Selection*. Published in 1859, this

highly readable doorstep outlines the great man's theory of evolution by natural selection. According to the theory, individual members of the same species are similar but slightly different. These variations make the individual more or less suited to the surrounding environment. The best adapted or 'fittest' individuals are more likely to reproduce and pass their winning characteristics on to future generations, while those less suited are more likely to die out without any such legacy. Selection – where certain characteristics are favoured over others – is driven by natural forces, like the availability of food, enabling species to change and evolve over time. Darwin cited evidence gathered from his time on HMS *Beagle*, including, most famously, his work on the Galápagos finches, but does *Origins* start with the story of Darwin's finches? No, it does not. Instead, Darwin focused on a different passion: his beloved pigeons.

At the time, pigeon-fancying was all the rage in Victorian England, and Darwin kept a loft-full in his garden at Down House. He wrote that spending time with them was 'the greatest treat which can be offered to a human being', and loved them so much that when his daughter's cat did what cats do, and killed a couple, he had the miscreant moggy shot. So much for survival of the fittest; if only the cat had had time to evolve a Kevlar coat! It's said that his daughter, Henrietta, never forgave him, but Darwin was blinkered. He bought as many different varieties as he could. There was the 'Pouter' with its balloon-like crop, the 'Jacobin' with its luxurious 'feather boa' collar, and the short-faced tumbler, which flies to great heights then somersaults out of the sky, to

name but a few. Darwin realised that although the birds were incredibly different, they must all have descended from the same common ancestor, the rock pigeon. Instead of being sculpted by natural forces, Darwin thought that the birds' idiosyncrasies must have been shaped by artificial means, namely the whim of the pigeon-fanciers who bred them.

Then in 1868, he published a lesser-known tome, *The Variation of Animals and Plants under Domestication*, which explored domestication more deeply. One of the things he noticed is that domesticated animals share a suite of characteristics not seen in their wild forebears. They tend to be smaller, with patchy markings, curly tails and floppy ears. Think about it for a moment ... can you name a wild animal that is piebald? I know we have zebras and pandas and skunks and orcas and magpies, but their markings are more ordered than the irregular patches of a Holstein cow or a collie dog. How about ears? Can you name a wild species that has droopy, spaniel-like ears? Elephant ears don't count. They're flappy rather than floppy. I'm struggling. Darwin concluded, 'Not a single domestic animal can be named which has not in some country drooping ears.*' Sometimes, the proportions of body parts are altered. Compared with a wolf, for example, the English bulldog has a short skull and muzzle with a pronounced underbite – the bottom jaw sticks out further than the top one, giving the breed its iconic

* There are, of course, exceptions. I've yet to meet a goldfish with spaniel ears, but the colourful creatures can differ greatly in size from their wild ancestor, the carp, and do sometimes have piebald markings, both tell-tale signs of domestication.

grimace. Pigs have extra bones in their spine and longer bodies than their wild boar ancestors. The reproductive habits of domesticated animals are also often changed, with many species able to breed all year round.

Darwin recognised this hodgepodge of shared features – the so-called Domestication Syndrome – but couldn't fathom how it came about. Indeed it's been called one of the oldest conundrums in genetics. Darwin wasn't sure if these features had been deliberately selected for – if our distant ancestors deliberately chose floppy-eared animals and bred them together, for example – or whether they came about by chance. And although he could experiment with species that were already domesticated, like his beloved pigeons, he thought that domestication happened so slowly it would be impossible to study directly. If only there was a way to study domestication in real time.

The Silver Fox

Autumn. A gentle breeze caressed the golden leaves as blackbirds plundered the last of the berries from tangled brambles. The fox was trying to ignore me. An inquisitive blur of perpetual motion, the delicate animal scoured the hedgerow, then headed into the open field. I was just a dead weight on the other end of an extendable lead. The fox kept a respectful distance: close enough so he didn't overstretch the cord that connected us, but far enough away that I wouldn't impede his explorations. He wheeled around me, tracing a series of never-ending circles.

'You'll have to spin round with him so you don't get tangled up,' Emma advised. 'I'd rather you didn't switch

hands, because there's always the chance you might drop the lead.'

'What would happen if I did?' I asked.

'Oh, he probably wouldn't go anywhere,' she answered, 'not while I've got the treats.' She held up a pouch full of chicken pieces.

It's not every day you are given the opportunity to take a silver fox for a walk, so when the owners of Heythrop Zoo offered, I jumped at the chance. Silver foxes are a melanistic version of the red fox. This means that although they share many of the red fox's features, including the pinched muzzle and long, bushy tail, their colouring is different. Silver foxes are, as the name suggests, varying shades of grey and not red at all.

My fox,* Glacier, is particularly beautiful. Olive eyes peer quizzically from a face framed in silver-flecked fur. Dainty black legs support a compact body draped in a dense, luxurious coat that is dark at the base and silver at the tip. His thick, bushy tail is silver too, but it looks like the end has been dipped in a pot of white emulsion paint.

'You can touch him if you like,' says Emma.

To attempt this with a silver fox straight out of the wild would be nothing short of disaster. The animals have speedy reactions and very sharp teeth, but Glacier is different. Heythrop Zoo, one of the largest private animal collections in Europe, provides trained animals to the media, for use in films, commercials, music videos and the like. Glacier is one of them. He was donated to the

* I say 'my fox', although sadly Heythrop would not let me take him home.

zoo by private owners, who reared him from a cub, then took him into schools for educational purposes. Things went well until, at around a year of age, Glacier's hormones kicked in and the adolescent fox cub became harder to manage. Kids became nervous, bookings dropped off, and the couple found Glacier increasingly difficult to manage. So Heythrop took him in.

He now lives in the Cotswolds in a large, outdoor enclosure that he shares with a handful of other regular foxes. He's built up a trusting relationship with Emma Hills, one of the zoo's specialist animal trainers, who has spent hundreds of hours working with him. She applies the principles of American psychologist B. F. Skinner, where positive behaviours are rewarded, and negative behaviours are ignored. So Glacier has learned that putting his head in a collar or sitting on command earns him a piece of chicken. Everybody's happy.

'He always has the choice whether or not to interact with us,' Emma explains. 'When I present him with the collar and lead, he decides whether he wants to come for a walk or not. If he backs away, we leave it for another day. If he puts his head into the collar, he gets a reward and then we go and explore. If you raise your finger in the air, he knows to sit and if you say the word "touching", he gets to choose whether or not you touch him. If he stays sitting, you can stroke him. If he backs away then you leave him alone.'

Watching the busy creature whirling on the end of the lead, I found it hard to imagine Glacier paying any attention to me at all, but I gave it a go.

'Glacier,' I called in a sing-song voice. The little fox stopped immediately and eyed me inquisitively. Then I

raised my index finger and he sat. 'Touching,' I said, then when Glacier showed no signs of moving away, I bent down and ran my hand down his silver-grey back. It is the smoothest, glossiest, thickest fur coat that I have ever felt. I offered him a piece of chicken and our moment was concluded. He returned to his explorations, and we continued on our way.

Glacier is clearly not a domesticated animal, yet somehow he's not quite wild either. He lives in captivity and goes for walks on a lead, yet I certainly wouldn't trust him not to snaffle the chickens from my garden. He's trained but he's not exactly what you'd call tame. He interacts with humans but you get the feeling that he'd much rather be with foxes. Glacier is an enigma wrapped up in a conundrum bundled up in the world's most beautiful fur coat. Yet the silver fox has taught us more about the transition from wolf to dog, and indeed about the process of domestication, than any other animal.

The Fox that Rolled Over

It was a dangerous time to be a geneticist. Although the Soviet dictator Joseph Stalin was dead, his legacy cast a long shadow. In the Great Purge of 1936 to 1938, Stalin had tried to stamp out the corruption he thought pervaded Soviet society. Under his orders, 1.3 million 'saboteurs' and 'counter-revolutionaries' were arrested, of whom half were killed. Paranoia and mass murder ruled. Then, when the Second World War ended and the Cold War began, relationships between the Soviet Union and the 'capitalist' West disintegrated. Stalin denounced Western ideals. Genetics was banned and research

laboratories were shut down. Practising scientists and open supporters of Darwin were declared enemies of the state. If you were lucky, this meant losing your job. If you were unlucky, it meant losing your life.

It was against this backdrop of repression, violence and fear that a Russian scientist decided to set up one of the greatest genetics experiments of all time. That scientist was Dmitri Belyaev.* Like Darwin, Belyaev was fascinated by evolution and the process that carved wild animals into their myriad domestic forms. Unlike Darwin, however, he didn't think that domestication had to be so painfully slow. Breeding experiments with mink had led him to believe that features of the domestication syndrome could occur relatively quickly. So he decided to try to domesticate an animal from scratch so he could study how the process occurred.

The silver fox was an obvious choice. A member of the canid family – the group of carnivorous mammals that includes dogs and wolves – it's an intelligent, social animal that lives in small family groups. Unlike the dog, however, it had never been domesticated. When he began his experiment in 1959, the fur trade was big business. Silver foxes were farmed on an industrial scale and widely exported. This provided him with a ready supply of test subjects, and a smokescreen for his controversial genetic research. He told the Russian authorities that his breeding experiments were to improve the quality of the animals' pelts.

* Belyaev was a remarkable man, not least because when he started his experiments, his geneticist brother, Nikolai, had already been executed by the secret police.

He set up his experiment in the wilds of Siberia in a place called Novosibirsk. It was about as far away from prying eyes as was physically possible. He sourced his foxes from fur farms where the animals had been bred for around 50 years, but the animals were by no means domesticated. Most of the initial batch of 130 foxes would bare their teeth and lunge at him, but a small subset – around 10 per cent – were marginally less aggressive, so he chose these as the founders for his breeding experiment. The foxes were never fussed or petted. The idea was not to tame or train them, as Glacier has been trained, but to select the animals that were least fearful and allow them to breed. Then, when those animals grew up, the process was repeated. The least aggressive foxes became parents, while the more aggressive foxes became fur coats. Like any good scientist, Belyaev also set up a control group; a second skulk* of foxes that were allowed to breed at random. This gave Belyaev a yardstick against which to measure change. His idea was that when our ancestors started domesticating dogs and other animals, they too must have begun by selecting the tamest individuals. And if tameness had a genetic component, which Belyaev felt sure was the case, then over time he expected tameness to become more pronounced.

Change came thick and fast. By the fourth generation, foxes from the experimental group had started to wag their tails. By the sixth generation, they were licking the scientists' faces. The proportion of amicable foxes in each

* 'Skulk' is the collective noun for foxes. Other favourites include a bloot of hippos and a smack of jellyfish.

litter grew, until by generation 45, virtually all of the foxes were behaving like friendly dogs. Physical changes began to happen too. After just 10 generations, some of the foxes were starting to develop floppy ears, curly tails and piebald coats. Their classic argentine fur became peppered with white patches. They began to breed more often and their skeletons began to change. Their legs were shorter, their snouts became smaller and their skulls became broader, giving them a less vulpine, more dog-like appearance.

Today, a visit to the fox farm is a joyful encounter. Now *all* of the foxes in the experimental group are super-friendly. Geneticist Anna Kukekova from the University of Illinois visits the Novosibirsk farm at least once a year as part of her research. 'It's really fascinating to see these animals,' she says. 'They live in rows of cages in a big shed, and when you walk in, they're just so friendly. You read that they are tame, but you do not realise how happy they are to see people. These are grown-up animals but they act like little puppies.' There's even evidence to suggest that the foxes have started to *think* more like dogs too. Dogs are well known for their ability to interpret human gestures. Hide a treat under one of two upturned cups and a dog can infer where it is by watching as a person points or gazes at the correct location. Remarkably, the tame fox kits can do this too. They are every bit as good at deciphering human gestures as regular dog puppies and run rings around kits from the control group.

To make sure his results weren't just some quirk of fox biology, Belyaev tried using the same approach to tame other species. Starting in the seventies, he repeated the

experiment with Siberian grey rats, mink and river otters, all with broadly parallel results. As the proportion of tame animals grew across generations, changes in colour, anatomy and physiology followed.

The experiments all point towards the same broad conclusion. Domestication doesn't have to take the achingly long time periods that Darwin envisaged. It can be replicated quite quickly in laboratory settings, by doing just one thing: selecting for tameness. Consistently breeding the friendliest animals, year in, year out, is all it takes to produce the seemingly unrelated mishmash of features seen in the domestication syndrome. Our distant ancestors didn't necessarily select dogs on the basis of their floppy ears or ability to read our body language; instead, these skills could have occurred as a by-product of selecting for their friendly nature. We didn't deliberately engineer the domestication syndrome. If you like dogs with floppy ears, which I do, you can consider it a happy accident.

Panimals

In 2004, scientists put forward a theory to explain *why* repeatedly breeding friendly animals together leads to the features of the domestication syndrome. Tecumseh Fitch from the University of Vienna and his colleagues believe the answer lies in a group of cells called the neural crest. Early in life, when vertebrate embryos are developing, cells from the neural crest migrate away to different parts of the body where they go on to form various different cells and tissue types. They help to form ears, teeth and pigment-producing cells. They also contribute to the adrenal gland, which helps prepare the

body for ‘fight or flight’. And in dogs, they travel all the way down the length of the body to the tail, where they help give the appendage its characteristic size and structure.

The idea is that, as tameness is selected for over generations, something happens to the neural crest. Neural crest cells start migrating but many of them never make it to their final destination. The ears don’t get to form properly, so they tend to flop rather than stand proud. The snout doesn’t fully extend, resulting in a shorter dog-like muzzle. There are changes to the tail, making it curly rather than straight, and pigment-producing cells don’t mature properly, creating patchy coloured splotches of fur. Critically, the adrenal gland never gets to fully mature, so the fear response is dampened. The end result is an animal that never quite matures properly, physically or mentally.

This seems to fit. It’s as if domestication derails normal development and suspends animals in a state of frozen youthfulness. Belyaev’s tame adult foxes behave like wild fox kits. Dogs are essentially wolf puppies that never really got the chance to grow up. Domesticated animals are the Peter Pan of the animal kingdom or, as I prefer to call them, ‘Panimals’.

When Darwin put forward his theory of evolution, he realised that certain characteristics were inherited, but he didn’t know how. Today, we know it’s DNA that is passed between generations. Random changes to the molecule – mutations – provide the source material for natural selection to act on. Advantageous mutations are favoured, while unfavourable ones are weeded out. When our ancestors began interbreeding the least wary

animals, and kick-started the process of domestication, they were unwittingly selecting for the genetic mutations that underpin a docile temperament. Somewhere along the way, it's likely that one or more neural crest-related genes acquired a mutation and were also inadvertently selected, leading to the features of the domestication syndrome.

Anna Kukekova has been searching for the relevant mutations by studying DNA from Belyaev's foxes and so far has highlighted more than 100 relevant genes. This is to be expected. Domestication, with its varied physical, behavioural and biological components, is likely to have a complex genetic basis. As predicted, some of the genes relate to the neural crest, but others are involved in brain function and potentially behaviour. This is important. 'When you visit the animals, it's not the physical changes, but the behavioural changes that stand out,' says Anna. One of the genes – called *SorCS1* – is known to influence the way that neurons communicate with one another inside the brain. Here then, at last, is a suite of genetic changes that could help to explain the behavioural transition from wild to tame.

The Novosibirsk fox-breeding experiment continues to this day. When Belyaev died in 1985, his long-time assistant Lyudmila Trut took over. Times became hard after the fall of the Soviet Union, so many of the experiments were scaled down and the Institute for Cytology and Genetics began selling the tame foxes as pets. According to Trut, a number of the animals now live happily with families in Russia, Western Europe and North America. From time to time, the owners write to Trut to tell her how the foxes are doing. She gets letters

from their owners, who tell her how sociable and affectionate their pets are, but these are not easy animals to keep.

Owing to vaccination regulations, the foxes can only be exported to the US or Europe when they are over six months old. This means that the early, formative parts of their life are unavoidably spent behind bars in the Novosibirsk sheds. As a result, the kits become adapted to their cages and enclosures, then struggle to adapt to life 'on the outside'. Like so many of my former boyfriends, they also have a strong odour, are annoyingly overactive at night, and can be difficult to houstrain. Often, they don't take well to apartment-style living and have to be kept caged, or under close supervision on the end of a lead. 'They were selected to be friendly to humans but they were not selected to fit the human lifestyle,' says Anna. Although you can take the fox out of the wild, it seems difficult to fully take the wild out of the fox. Although these animals have changed immensely over the course of the breeding experiment, whether or not they are fully domesticated is an issue that remains contentious.

Are We Nearly There Yet?

By selecting for tameness over generations, Belyaev pressed the fast-forward button on domestication, but it would be unrealistic to expect that our ancestors did the same thing. In laboratory conditions, domestication *can* happen relatively quickly, but Darwin was right when he surmised that the process usually takes much longer. Just as we can't see one species evolve into another, so too we are unable to witness the moment

when wild becomes domestic. There was no instant in time when the wolf suddenly stopped being a wolf and started being a dog; instead the changes would have occurred so slowly it's unlikely our ancestors realised what was happening.

When I first started researching domestication, I thought that defining it would be as simple as pointing at some animals and saying 'chicken, cow, sheep', yet it's now obvious to me that the boundary between wild and tame is blurry and indistinct. Belyaev's foxes illustrate this beautifully, as does the so-called 'domestic' cat. It's thought the famously independent creature began to domesticate itself after agriculture took off in the Middle East around 9,500 years ago. When vermin started ransacking grain stores, wild cats reinvented themselves as pest control. Compared to dogs, however, cats have changed little on their journey from the wild. They still look and act similarly to their wild ancestors. They hunt wild food and they have wild sex. In Scotland, domestic cats are interbreeding with the endangered Scottish wildcat, an act that is diluting the wildcat's gene pool and nudging it towards extinction. The domestic cat's infamous sangfroid nature arguably suggests another species whose domestication is a work in progress.

In Mongolia, native domestic horses roam free and are only caught when needed. Descended from the war steeds of the legendary Genghis Khan, the horses graze the vast grasslands of the Eurasian Steppe, followed at a distance by the nomadic Mongols who own them. Sometimes, the domestic horses interbreed with wild horses, and sometimes feral horses are caught and added to the herd. The domestic Mongol horses are among the

most genetically diverse of all horses, meaning that across all individuals there is a healthy smattering of genetic variation, and that humans have interfered little in the breeding process. Their journey through the generations has been dominated by natural rather than artificial selection, yet we arrive at a species that is still considered domestic. A nomadic Mongol herder wouldn't consider his horses to be wild. They are his property. He milks them. He rides them. He races them. Sometimes, he even boils them up in a stew. But a junior member of the British Riding Club, who has grown up plaiting the mane of her infinitely more domesticated steed, would run screaming if asked to mount the same saddle-free spirit.

Textbook definitions suggest that, alongside certain other features, domesticated animals should have an inherited tameness. By this yardstick, Glacier, the silver fox I met at Heythrop Zoo, is not domesticated because although he is relatively manageable, he did not acquire his disposition from his parents. Although his provenance is uncertain, it's thought Glacier is descended from fur-farm stock rather than Belyaev's epic experiment. So his amenable manner is not down to his DNA; it's down to his trainer, Emma. My dog, on the other hand, was born sappy. But what of the millions of stray dogs that live wild? They may well be genetically distinct from wolves, have curly tails and piebald markings, but they're certainly not pets. They don't live with us or depend on us directly for food, but they're not exactly wild either.

With their unique DNA, unusual looks and inherited bonhomie, Belyaev's silver foxes must, at the very least, be well on the way to becoming domesticated. The

Russian's experiment has shown us that domestication can occur relatively quickly and that tameness goes hand in hand with other, more visible changes, but it also teaches us that domestication itself is frustratingly hard to pin down. This should not come as a surprise. There is no 'moment' when a wild animal becomes domesticated; rather, the animals exist on a never-ending continuum. Domestication is a process rather than an event, or, if you prefer hackneyed self-help rhetoric, it's a journey, not a destination. Every generation is subtly different from the one that precedes it, and it's only with the benefit of palaeontological and genetic hindsight that we see grand changes in operation. It's easy to imagine that the dogs and cows and chickens we see around us today are the zenith of domestication, when in reality, they are still in transition. Living things don't stop responding to their environment and evolution never stands still. Domestication is just a human-influenced form of evolution.

In addition, our conceptions of the past are tainted by cultural bias. We imagine that early dogs looked 'dog-like' but our conception of what 'dog-like' means is tainted by the cultural space that we occupy. Let me give you an example. The British Museum hosts an etching by William Hogarth entitled *Gulielmus Hogarth*. This exquisite self-portrait, created in 1749, shows the English painter – a dead ringer for John Malkovich – posing with his beloved pet pug, Trump. But this is not the bug-eyed, scrotum-faced lapdog of your twenty-first-century preconception. It's an altogether different dog, muscly and wizened with a wrinkle-free face that protrudes in three rather than two dimensions, and eyes

that sit comfortably in its skull. Back then, the breed was celebrated, not as a family pet, but for its feisty ‘pugnacious’ spirit, so it held symbolic importance for Hogarth, who used the dog as an emblem in his career. To Hogarth, Trump must have seemed the absolute pinnacle of domestication, the very epitome of ‘pugness’, yet to us this dog looks somehow primitive and unworthy of the pug moniker. So is it a pug or not? I would argue that it is a pug, but add we must remember that over time, the animals we gave this arbitrary label to have sported a whole range of different features. ‘We constantly map onto the past what we think about the present,’ says Greger Larson from Oxford University, who studies domestication, ‘but we’re always wrong because things are always changing through time.’

All this makes it difficult for those who seek to define domestication or pinpoint its inception. For most of its history, domestication was actually a very loose arrangement. ‘What we’re talking about here is a long-term process by which people, plants and animals become acclimated to one another,’ says Greger. Animals got used to people, and people got used to animals. We just hung out. Then, as we started to influence their environment by feeding them, keeping them and moving them around, the animals began to change. Domestication got under way. It wasn’t intentional. ‘Nobody set out to domesticate a cow,’ he says. ‘Nobody set out to domesticate a sheep or a pig or a dog or anything else. Instead, domestication was a side effect of the tightening relationship between humans and animals.’

As new forms of animals and plants began to emerge, domestication changed our world. It led to the

emergence of agriculture, trade and settled urban living. The process steered animals and plants away from one evolutionary trajectory, towards another. Domestication has had a huge influence on the course of human history, and yet it's intriguing to think that the process was never actually planned or premeditated.