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Opinion

The History of Farm Foxes Undermines the Animal Domestication Syndrome

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The Russian Farm-Fox Experiment is the best known experimental study in animal domestication. By subjecting a population of foxes to selection for tameness alone, Dimitry Belyaev generated foxes that possessed a suite of characteristics that mimicked those found across domesticated species. This 'domestication syndrome' has been a central focus of research into the biological pathways modified during domestication. Here, we chart the origins of Belyaev's foxes in eastern Canada and critically assess the appearance of domestication syndrome traits across animal domesticates. Our results suggest that both the conclusions of the Farm-Fox Experiment and the ubiquity of domestication syndrome have been overstated. To understand the process of domestication requires a more comprehensive approach focused on essential adaptations to human-modified environments.

Highlights

The 'domestication syndrome' has been a central focus of research into the biological processes underlying domestication. The Russian Farm-Fox Experiment was the first to test whether there is a causal relationship between selection for tameness and the domestication syndrome.

Historical records and genetic analysis show that the foxes used in the Farm-Fox Experiment originated from fur farms in eastern Canada and that most traits attributed to the behavioral selection for tameness predated the experiment, undermining a central pillar of support for the domestication syndrome.

The overall weight of evidence, including data from other species, does not unambiguously support the existence of the domestication syndrome in animals. Competing theories to explain domestication syndrome should be reconsidered after the traits themselves are more clearly connected to the early stages of domestication.

The Origins of Domestication Syndrome

The domestication syndrome describes a suite of behavioral and morphological characteristics consistently observed in domesticated populations. It was first described in animals (although not named as such) by Charles Darwin [1]. The term itself, coined by botanists in the early 1900s [2,3], was applied to animals in the 1980s [3]. Usage has risen dramatically since the mid-1990s, by more than 20-fold (see the supplemental information online) [4].

The concept of a domestication syndrome is appealing. The grouping of a collection of traits allows easier identification and facilitates the definition of domesticated taxa. It also inspires a search for causal mechanisms, whether genetic or environmental, responsible for their collective appearance. Characteristics attributed to domestication syndrome vary, but include **tamability** (see Glossary), loss of **reproductive seasonality**, and changes in coat color, ear form, tail form, and craniofacial morphology (Figure 1) [1,5–13].

Testing the Domestication Syndrome in the Silver Fox

The Russian Farm-Fox Experiment is widely cited as a demonstration that the domestication syndrome exists and that domestication results from selection on tameness, with clear changes in behavior and morphology appearing rapidly. Its founder, Dr Dimitry Belyaev, designed the project to test whether the suite of characteristics that Darwin associated with domestication were linked to selection on tameness [14,15]. Starting with 30 male and 100 female silver foxes (*Vulpes vulpes*) from Soviet fur farms, he selectively bred foxes who responded less fearfully when a hand was inserted into their cage [15]. The oft-repeated narrative is that with just ten generations of selection on wild foxes, he produced foxes who craved human attention and exhibited a range of unconnected phenotypes including floppy ears, turned-up tails, piebald coats, di-estrous reproductive cycles, and later, shorter and wider faces. Belyaev proposed that selection on behavior altered the regulation of multiple interconnected systems that produced the traits Darwin described [1,14,15].

Belyaev's observations, which seemed to prove a causal relationship between selection on tameness and other syndrome traits, led to the acceptance of the domestication syndrome across diverse fields [16–21]. It has even been used to define which populations are domesticated [8,22]. Scientists investigating the biology of domestication developed hypotheses to explain the suite of traits and many invoked either **linkage** or **pleiotropy**. The neural crest hypothesis proposes that domestication is driven by pleiotropic changes to neural crest cells – developmental precursors for nearly all domestication syndrome traits [12]. The pedomorphosis hypothesis (sometimes termed neoteny) proposes

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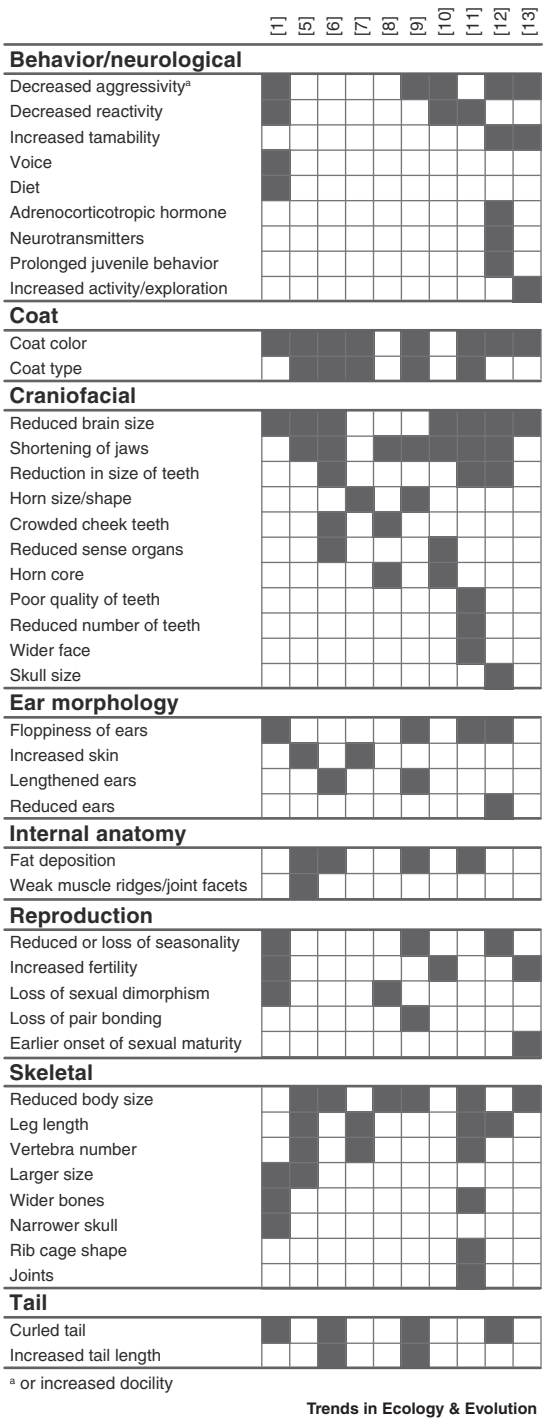

Figure 1. No Consistent Set of Traits Defines Domestication Syndrome.

In ten publications on domestication syndrome in animals, no single trait is included in every one. The most commonly included traits are coat color (80%), brain size (70%), jaw length (70%), and diverse characteristics related to ear and skeletal morphology. See [1,5–13].

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that domestication alters developmental timing, such that adults retain a suite of juvenile characteristics [23]. The thyroid rhythm hypothesis proposes that domestication is driven by changes in thyroid hormone release, which alters growth, maturation, and environmental response [24].

These hypotheses assume that the domestication syndrome exists, but with little supporting data. The defining characteristics vary widely (Figure 1) and have not been observed in most domesticated species [25]. Many studies fail to distinguish traits that accompanied domestication from those only in modern breeds (Box 1), and some traits are reported anecdotally without any accompanying frequencies or measurements.

In the context of this general paucity of empirical data, it is difficult to overstate the importance of the Farm-Fox Experiment for our understanding of animal domestication [16]. It alone claims a causal relationship between selection for tameness and phenotypic changes consistent with the domestication syndrome. Here, we investigate the historical background of the Farm-Fox Experiment and critically evaluate its use as a foundation for the existence of the domestication syndrome.

The Canadian Origins of the Russian Farm-Fox Experiment

A widespread misconception maintains that the Farm-Fox Experiment started with wild foxes and recapitulated the entire process of domestication [16,20]. Belyaev himself accurately described the founders as fur-farm foxes, but by referring to the unselected population as 'wild controls', contributed to this misconception [14]. In reality, the experiment started with a fox population from eastern Canada that had been captive and purpose-bred since the late 1800s, something Belyaev and his colleagues may have been initially unaware of [26,27] (Box 2).

The history of the Farm-Fox population undermines the commonly repeated narrative that a suite of domestication syndrome traits emerged solely as a result of selecting on tameness [15,28]. There is no temporal link between most of the syndrome traits, which first appeared in Prince Edward Island (PEI) fur farms, and the later behavioral selection in Russia. The rate of behavioral change is consistent with selection on standing variation in the population (Box 2). Finally, the small **effective population size** makes the experimental fox populations highly susceptible to large shifts in allele frequencies due to chance alone [29,30].

Today, the behaviorally distinct Farm-Fox Experiment populations offer a resource for investigation of the genomics and biology of behavior [31]. The selected foxes carry heritable differences in social development, including changes in the timing of the critical period of socialization in juveniles relative to the unselected population [32], and transcriptomic analysis of their brains suggests changes in key signaling pathways [33,34].

The Farm-Fox Experiment does not, however, validate the domestication syndrome.

Box 1. Population Types

We distinguished between three types of populations in evaluating the evidence for domestication syndrome.

i. Wild: A wild population is a population that is noncommensal with humans.

ii. Domesticated (non-breed): A domesticated population is one that is commensal with humans or otherwise generally reliant on a human-modified environment for survival. A non-breed domesticated population is any population of domesticated individuals that is not part of a breed.

iii. Breed: A genetically isolated subpopulation of the domesticated population, usually less than 50–100 generations old, with markedly reduced genetic diversity due to human action. Breeds may be subject to intentional selection for phenotypic extremes. This includes: pedigreed populations selected to a particular standard (e.g., dog breeds); laboratory colonies (e.g., laboratory rats), and populations resulting from human transplantation (e.g., rabbits in Australia).

Glossary

Admixture: mixing of genetic ancestry that occurs when genetically separated populations interbreed.
Affective state: the underlying emotional attitude of an animal; incorporates both arousal and whether the emotion is aggressive or affiliative.
Affiliative behavior: an action that reinforces social bonds.
Aroused: a physical and psychological state of increased activity and alertness.
Commensal: a relationship in which one species benefits and the other species (in this case, humans) neither benefits nor is harmed.
Effective population size: size of the idealized population that would lose genetic diversity through genetic drift at the same rate as the real population.
Fecundity: number of offspring an animal is capable of producing over a lifetime.
Free-living: not selectively bred, such that reproductive success and survival are not strictly determined by humans.
Genetic drift: the change in frequency of an existing genetic variant due to random sampling rather than selection.
Linkage: the tendency of genetic changes close together on a chromosome, and the phenotypes they produce, to be inherited together.
Monestrous seasonal: one estrus period per year during occurring during a seasonally defined, discrete window of time.
Pleiotropy: the production, from a single genetic change, of two or more apparently unrelated phenotypic effects.
Reproductive seasonality: synchronization of reproduction with seasonal variation in food availability or climate.
Standing genetic variation: genetic variation that already exists in a population rather than resulting from new mutational events.
Tamability: the ease with which an animal can form social bonds with species other than its own.

Reevaluating the Evidence for Domestication Syndrome

Given this history, we reconsidered the evidence supporting each of the domestication syndrome traits reported in the Farm-Fox Experiment in both foxes and seven other well-studied mammalian species (Figure 2; see the supplemental information online for details). Here, the domestication syndrome is defined as a suite of traits that rises in frequency as a direct consequence of selection on tameness due to linkage or pleiotropy. For a characteristic to be included in domestication syndrome, it should fulfill three essential criteria:

(i) Onset: A trait must appear (or, at a minimum, rise rapidly in prevalence) in conjunction with the onset of selection for tameness.

(ii) Frequency: A trait must be significantly more common in the selected population.

(iii) Association: A trait must be associated with tameness in individuals, not just at the population level (i.e., within the selected population, the tamer the animal the more likely it is to exhibit characteristics of domestication syndrome).

We note that, when considering other domesticated species, a domestication-related trait should be seen in non-breed domesticated populations (Box 1) and not exclusively in modern breeds. If there are no non-breed populations, traits seen across all breeds may be cautiously inferred to predate the breeds and potentially be domestication related.

When we applied these criteria to domestication syndrome traits reported in the Farm-Fox population, we were unable to identify a single species for which all three criteria were met.

Box 2. The 'Domesticated' Foxes of Prince Edward Island

The Canadian farm-fox population dates to the mid-19th century, when the fur industry was confronting a supply crisis. Fur traders were anxious to overcome their reliance on wild-caught animals, but repeated attempts to breed foxes in captivity had failed [26,81]. Wild foxes are generally monogamous, monestrous, seasonal breeders and notorious escape artists [58,82]. Whether wild or captive born, most foxes would not breed in captivity, and females often ate their young [26].

The first Canadian fox farm was established in 1887 by Charles Dalton, after he was convinced by Robert Oulton to make the foxes' environment more natural [26]. Their farm, in the province of PEI in eastern Canada, had large enclosures furnished with hollow logs as dens. By 1883, they had their first breeding pair, and 4 years later they started the first fox farm with two breeding pairs [26,82]. They monopolized the market for the next three decades.

From the start, the foxes were selected for both appearance and behavior. Dalton bred jet-black foxes, while Oulton favored white barring on guard hairs [26]. While we found no reports of intentional selection for **affiliative behavior**, contemporary experts linked docility to improved fecundity [83] and the PEI farm foxes were unusually friendly (Figure 3). By 1913, breeding pairs sold for CA$30 000, equivalent to US$500 000 today (https://www.bankofcanada.ca/rates/related/inflation-calculator/) [82].

In 1928, Leo Frank, a promoter of the fur industry, supplied 65 fox pairs from Rosebank farm to establish a Russian fur-farm industry (Figure I) [26]. Thus, the Russian Farm-Fox Experiment started with foxes descended from a population of unusually friendly Canadian foxes – a phenomenon Belyaev accentuated by preferentially including exceptionally calm foxes [62,84,85]. Mitochondrial DNA analyses of 24 Farm-Fox Experiment foxes showed 100% of haplotypes derived from Canadian foxes, predominantly from the east [85].

This history reframes the behavioral selection in the Farm-Fox Experiment as selection on **standing genetic variation** and explains the rapid behavioral change (within ten generations). A study in dogs saw change within just three generations after starting with founders exhibiting the trait of interest (nervousness) [75]. When Belyaev started a rat experiment with commensal rats living close to humans (P. Borodin, personal communication), significant behavioral changes occurred within 13 generations [86]. When he started with a wild population of river otters (*Lutra lutra*) unaccustomed to people, few bred successfully in captivity and the experiment was discontinued [87,88].

This history also makes it difficult to validate domestication syndrome. The Farm-Fox Experiment population experienced at least three major founder events at the founding of PEI fox farms, the importation to Russia, and the inclusion in Belyaev's experiment. Like dog breeds, both the selected and unselected fox populations have small effective population sizes, making them susceptible to **genetic drift** [29,89]. Thus, even large allele-frequency differences between the two populations can be explained by chance alone.

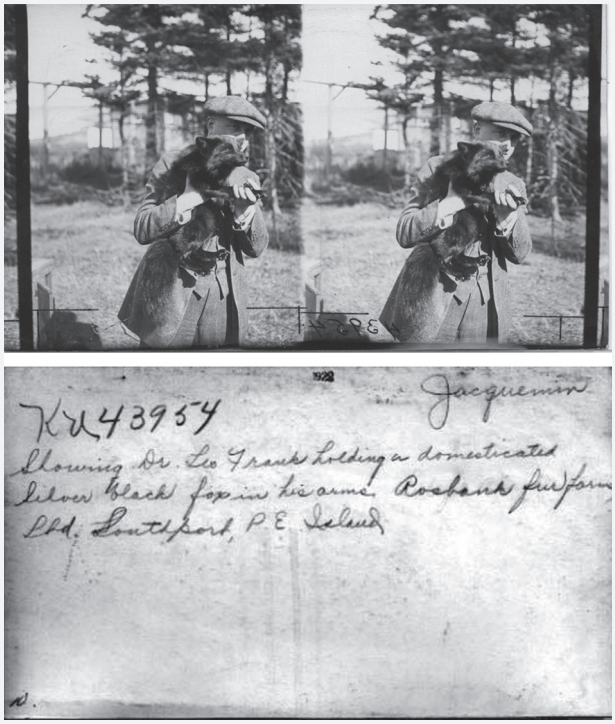

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Figure I. Leo Frank and one of his farm foxes at Rosebank Farm

The caption on this stereoscopic photo from 1922 reads 'Showing Dr. Leo Frank holding a domesticated Silver black fox in his arms. Rosbank fur farm Ltd. Southport, P. E. Island'. Image from Keystone-Mast Collection, California Museum of Photography, University of California, Riverside.

Tooth Size and Craniofacial Morphology

Changes in head and face shape are included in virtually every description of domestication syndrome, but we found few primary data supporting this (Figure 2A). For example, domesticated dogs, cats, pigs, and goats are described as having shorter muzzles [12], yet the skull shape of domesticated cats is indistinguishable from that of their closest wild relative, the African wild cat (*Felis silvestris lybica*) [35,36]. Some dog breeds have extreme morphologies, but when a spectrum of breeds is considered, any difference from other *Canis* species disappears [37]. We found no data comparing muzzle length in non-breed goats and pigs to wild populations, and ongoing **admixture** with wild ancestors would complicate such comparisons [38,39].

In the selected Farm-Fox population (Figure 2C,D), foxes with shortened snouts, underbites, and widened and elongated skulls are anecdotally described without prevalence data [15,28], but cranial morphology did not distinguish selected foxes [40].

Tail Form

Change in tail form is a complicated phenomenon to assess since it conflates two distinct phenotypes: (i) skeletal changes; and (ii) changes in tail carriage (due to either emotional state or soft-tissue

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(A)	Dog *Canis lupus*	Cat *Felis catus*	Goat *Capra aegagrus*	Pig *Sus scrofa*	Rabbit *Oryctolagus cuniculus*	Rat *Rattus norvegicus*[b]	Mouse *Mus musculus*	(B) Fox *Vulpes vulpes*	(C) Russian Farm-Fox Experiment
Skeletal changes (relative to body size)									
Shortened jaws	Breeds only	Breeds only	Breeds	Breeds	Unclear	No data	Unclear	No data	Anecdotal
Wider face	Breeds only	No	No data	No data	No data	No data	Unclear	No data	No
Smaller teeth	Unclear	No data	No data	No	Unclear	No data	No	No data	No data
More crowded teeth	No	Breeds	No	No data	No data	No data	No data	No data	No data
Change in leg length	Breeds only	Breeds only	Unclear	No	Breeds	No data	Unclear	No data	Anecdotal
Curled tail									
Skeletal (change in vertebrae)	Breeds	Breeds	No data	No data	No data	Breeds	Breeds only	No data	No data
Tail carriage	Unclear	Unclear	No	Unclear	No data	No data	No data	No data	Yes
Coat color									
Depigmentation	Yes	Yes	No	Breeds	Breeds only	Unclear	Breeds only	Yes	Yes
Increased variation	Yes	Yes	Yes	Breeds	Breeds	Unclear	Breeds	Yes	Yes
Ear morphology									
Larger ears, causing drooping	Breeds	No data	Breeds	Breeds	Breeds	No data	No	No data	No data
Increased skin, causing drooping	Breeds	No data	Breeds	Breeds	No data	No data	No data	No data	No data
Distal portion of ears folded	Yes	Breeds	Breeds	Breeds	No data	No data	No data	Yes	Yes
Ears droop where attached	Breeds	Breeds only	No data	No data	Breeds	Anecdotal	No data	No data	No data
Change in seasonality									
Loss of seasonality	Yes (all)	No	No	No	No	No data	No	No	No
Shift to >1 viable litter per year	Yes	No	Yes	Yes	No	No data	No	No	No
Reduced seasonality[a]	NA	No	Yes	Yes	Unclear	No data	No	Yes	Yes
Other									
Reduced brain size	Unclear	Unclear	No data	Yes	Breeds	No data	No data	No data	No
Earlier sexual maturation	Yes (all)	No data	Unclear	No	No	No data	No data	No	Yes

[a] longer breeding season [b] no data found for noncommensal rat populations for any trait

(D) **Farm-fox experiment: association with selection on tameness**

	Onset	Population frequency	Association
Craniofacial morphology	Unknown	Some variation reported. Not sufficient to distinguish selected foxes [40]	No data
Curled tail	Unknown	9% in selected; 1% in unselected [90][c]	No data
Depigmentation	PEI	12% in selected; 1% in unselected [90][c]	No data
Increased variation (brown mottling)	PEI	0.45% in selected; 0.09% in unselected [90][c]	No data
Delayed ear raising	PEI	0.23% in selected; 0.17% in unselected [90][c]	No data
Change in seasonality	PEI	Longer breeding season in 16% of selected[c]; no pups survive out-of-season matings [61]	No data
Early sexual maturation	Farm-Fox Experiment	1 month earlier in selected population (compared with unselected)[c] [52]	No data

[c] statistical significance not reported

Yes (all)	In all domesticated animals; not in wild population
Yes	In some domesticated animals; not in wild population
Unclear	Conflicting reports
Breeds	In some breeds; no data for non-breed populations
Breeds only	In some breeds; no difference between wild and non-breed domesticated
No	No difference between wild and domesticated
Anecdotal	Described in 1 or a few individuals; no prevalence data
No data	No data found

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Figure 2. Many of the Traits Associated with Domestication Syndrome Are Not Supported with Published Data.

We attempted to apply consistent criteria across a diverse field of literature. We describe our reasoning in detail, and list all references, in the supplemental information online. 'No data' denotes an absence of evidence, not evidence of absence. (A) The published literature for seven well-studied domesticated species shows that most of the domestication syndrome traits are either reported only in breed populations or not supported by published data. If we found no data for non-breed domesticated populations, we considered traits occurring in unquestionably domestic ancient populations, or universally across a wide spectrum of breeds, to be sufficient evidence that the trait would be likely to be seen in non-breed domesticated populations. (B) Comparison of Canadian farm foxes from Prince Edward Island (PEI) fox farms and wild red foxes (*Vulpes vulpes*) shows that many proposed domestication syndrome

(Figure legend continued at the bottom of the next page.)

changes). Skeletal changes have been described only in breeds (e.g., bulldogs [41], laboratory mice [42]). Changed (upraised) tail carriage is anecdotally described in **free-living** non-breed dogs, but we found no studies that compared them with wolves. In rabbits, a prey species, an upraised tail is a signal to pursuing predators, potentially changing the evolutionary forces shaping tail carriage compared with predator species like cats and dogs.

Foxes, like wolves, carry their tails hanging relaxed but bring them up when **aroused** (see the supplemental information online). In the Farm-Fox Experiment, about 10% of individuals in the selected population carried their tails in a curved, upright state [15], but tail carriage has not been associated with tameness in individuals (Figure 2D).

Coat Color

Coat color changes are included in nearly all definitions of domestication syndrome (Figure 1). Of the seven species we investigated in detail, however, we found only two (cats and dogs) where both depigmentation (white spotting) and coat color variation is demonstratively more common in the domesticated population than the wild population (Figure 2A). In free-living cats and dogs, the frequency of the white spotting can exceed 50% [43,44]. Both wild and domesticated goats have white spotting, but free-living domesticated goats in India have a wide range of additional coat color variation [45]. **Commensal** rats are agouti, black, albino, yellow, and even piebald, but without data for a noncommensal population we could not confirm any change. In rabbits, coat color variation is rare in wild populations and common in some breeds, but we found no data for non-breed domesticated populations [46].

The farm-fox breeders of PEI intentionally selected for white spotting and other unusual coat patterns (Figure 3) [47]. They noticed that crossing two white-marked foxes occasionally resulted in animals that held their heads askew, a phenomenon Belyaev would later describe in his population [48], suggesting shared genetic etiology. White spotting was more common in Belyaev's selected than unselected populations, but has not been associated with less fearful behavior in individuals (Figure 2D) [15]. Quantitative trait locus (QTL) mapping shows that white spotting does not cosegregate with less fearful behavior in rats selected for tameness [49], a question not addressed in QTL mapping studies of the Farm-Fox Experiment foxes [50].

Ear Form

Changes in ear morphology (e.g., floppy ears) are included in most descriptions of the domestication syndrome and encompass a wide range of traits (Figure 1). While common in some breeds of dogs, cats, goats, pigs, and rabbits, changes in ear morphology are rare in non-breed domesticated populations (except dogs [51]) and are almost never seen in wild populations (Figure 2A).

The farm foxes of PEI occasionally had floppy ears, even as adults (Figure 3C). In the Farm-Fox Experiment, 'delayed ear raising' was noted (ears floppy past 3 weeks of age, but not necessarily into adulthood) [52]. While slightly more common in the selected population, the trait is extremely rare [15], and no association between delayed ear raising and less fearful behavior in individuals has been described (Figure 2D).

Change in Seasonality

Reproductive traits, while inconsistently defined, are included in most descriptions of the domestication syndrome (Figure 1). In wild animals, reproduction is often seasonal. In domesticated animals, human control of resources can temper seasonality and increased **fecundity**. In some species, this change is primarily genetic. Wolves are strictly **monestrous seasonal**, with an annual breeding season

traits were described in the Canadian farm foxes before Belyaev started his experiment. (C) Comparison of selected and unselected populations from the Russian Farm-Fox Experiment highlights two (tail carriage and earlier sexual maturation) that were first described in the selected fox population. (D) Domestication syndrome traits described in the Farm-Fox Experiment do not meet three essential criteria that would support a direct connection to the selection on tameness. See [40,52,61,90].

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Figure 3. Affiliative Behaviors Towards Humans, and White Spotting, Predate the Russian Farm-Fox Experiment.

(A) Prince Edward Island farm foxes in 1922, being fed by Leo Frank [90]. (B) In the late 1950s, Dr Dmitry K. Belyaev started his decades-long experiment to breed tame foxes in Siberia using foxes from the Russian fur industry, which was started with farm foxes from Canada [19]. (C) An adult Canadian fox with depigmentation (white spotting), one floppy ear, and reduced fear towards human handlers. Credit: Bruno Delsman, Hartland, Wisconsin [47]. (D) An adult fox with a similar white-spotting phenotype in the Russian experimental population [48].

lasting a few days, even in captivity [53]. Male dogs are constantly receptive and female dogs come into estrus on average every 8 months [53]. In others, the change is environmental, with feral populations reverting to wild-type seasonality. For example, wild boar, while seasonal, will breed year round when resources are available [54] and domesticated pigs, while they can reproduce year round, have reduced fertility outside the ancestral season [55]. In some species with reduced seasonality, this does not constitute a change from their wild ancestors. While domesticated cats can breed out of season, most breeding still follows ancestral patterns of seasonality, much like African wild cats, who will reproduce out of season when sufficient food is available [56,57]. Both free-living cats and African wild cats can have multiple litters per year.

Like wolves, wild foxes are monestrous seasonal, with an annual breeding season of about 1 week between December and March (varies with latitude) [58]. The natural breeding season is hard to measure in modern fox farms, as males and females are housed separately and farmers determine the start of breeding season. However, in the early fox farms on PEI, mated pairs were housed together and contemporary documents suggest an extended breeding season. In 1913, breeding at one farm began on 12 March and finished on 4 June, and a 1922 report described a female breeding twice in one season after her first litter did not survive [59,60].

In the Farm-Fox Experiment (which follows the modern practice of single housing), there is an extended breeding season in the selected foxes but no increase in fecundity [61]. No vixens produced two viable litters in 1 year [14] and no pups survived from matings outside the normal breeding season [14,15,62]. The shift in seasonality may be a direct consequence of the selected foxes being less fearful, rather than a distinct domestication syndrome trait. Chronic stress limits reproduction in captivity, and the unselected foxes had higher corticosteroid levels [61]. Consistent with this, an early study from the Farm-Fox Experiment reported that less fearful animals bred earlier and that if a fox became more fearful with age, it would no longer breed early [27].

Decreased Brain Size

Decreased brain size is included in most definitions of the domestication syndrome and may reflect adaptation to environments where survival is less cognitively demanding [63]. We were able to find only one species – pigs – where a decrease in brain size relative to body size in the domesticated population was well supported [63]. In dogs, data for many breeds (and sizes) of dogs show that relative brain size is smaller than in modern wolves [63]. Modern dogs, however, are not descended from the same *Canis* lineage as modern wolves [64] and instead may be descended from a Pleistocene wolf closer in size to a village dog [65]. As relative brain size decreases with body size in the *Canis* lineage [63], modern dogs may not be that different from their wild ancestors. In rabbits, comparing eight wild and eight purebred domesticated rabbits found smaller relative brain size, but the domesticated rabbits were fourfold heavier than their wild counterparts [66]. As in dogs, giant breeds may not reflect changes that occurred during domestication.

Reduced brain size was not observed in Belyaev's selected fox population [67], perhaps unsurprisingly, since the cognitive demands for survival did not differ between the selected and unselected fox populations.

The Limitations of the Farm-Fox Experiment as a Model for Domestication

The Farm-Fox Experiment is a powerful study of behavioral genetics. Belyaev and his successors established a model system ideal for mapping genetic loci that shape complex behavioral traits [31,33,34,68]. Its utility as a model for domestication, however, is unclear. Moreover, it does not provide support for a domestication syndrome in animals.

While the Farm-Fox Experiment is often described as having domesticated foxes, this depends on the definition of domestication. To argue that the foxes were domesticated because they exhibit domestication syndrome traits is insufficient and circular, as the project is often cited as a validation of domestication syndrome. Any behavior-defined transition to domestication was arguably completed in PEI fox farms. Even that transition may have been minimal. While many canids (e.g., wolves) actively avoid human contact [69], wild foxes regularly live commensally with humans and have been known to use cat doors to access dens under homes [70,71], can be tamed [71], and may have been exploited in the earliest human settlements [72].

Having selected only for behavior, the Farm-Fox Experiment is at best an incomplete model for the complex process of domestication. Comparing dogs and wolves, for example, reveals that some of the strongest signatures of selection are not associated with behavioral genes but with genes involved in starch digestion, presumably reflecting adaptation to anthropogenic diets [73]. Changes in brain size and structure have been hypothesized to reflect adaptation to anthropogenic environments where survival (through foraging, hazard avoidance, and reproduction) is less cognitively demanding [63]. In the Farm-Fox Experiment, both selected and unselected populations were raised and fed in captivity, with the selection focused only on the fear response phenotype.

The rapidity of behavioral change (within approximately ten generations [15]) in the Farm-Fox Experiment can also be explained by the population's history. Like dog breeds, the Farm-Fox population was initially established in the late 1800s with a small number of individuals (introducing a strong founder effect) and was subsequently subjected to strong selection for behavioral and morphological characteristics [30,74].

The Farm-Fox Experiment selected for a behavioral trait that already existed in the population (Figure 3), essentially recapitulating a selection experiment performed on numerous occasions with dog breeds. For instance, working lines of dogs are created by starting with dogs who exhibit desirable behavioral characteristics (e.g., herding or not killing livestock) and then selectively breeding those that best exemplify the characteristic [19], yielding behavioral change in as few as three generations [75]. The change in the critical period of socialization in the selected foxes is more like the

difference between more and less easily socialized dog breeds [76,77] than between dogs and wolves [78].

Taken together, the results from the Farm-Fox Experiment offer little support for the existence of the domestication syndrome in animals. In addition to the uncertainty about whether the population can be referred to as domesticated, many of the purported domestication syndrome traits predate the experiment, making it impossible to infer a causal relationship with behavioral selection. Other traits reflect **affective state** and may directly result from the selection for tameness. Finally, Belyaev designed his experiment to test whether Darwin's catalog of domestication traits co-occurred with increasing tameness [14]. These traits would be apparent to the researchers, potentially leading to unconscious bias in behavioral evaluations and breeding decisions that would be difficult to control for [79].

Concluding Remarks

Domestication is an evolutionary process of adaptation, special only in that the major selective pressure is imposed (however intentionally) through association with the anthropogenic niche. Understanding the mechanisms responsible for its appearance, and identifying changes associated with its origins, is crucial given domestication's role in human societies over the past 10 000 years.

While the Fox-Farm Experiment is fundamentally important in many regards, its ramifications for understanding domestication have been overstated. When its full history is considered, the weight of evidence (including sparse data from other species) does not unambiguously support the existence of domestication syndrome in animals. Competing theories to explain the emergence of traits associated with domestication syndrome may merit reconsideration after the traits themselves are studied for connection to the early stages of the process.

We propose that understanding the process of domestication requires an approach focused on essential adaptations to human-modified environments, such as reduced flight distance, breeding in proximity to humans, and utilizing altered food resources associated with a human niche. The specific adaptations may vary between species, but these selective pressures are common for all species.

Rather than focus on the domestication syndrome, we should instead consider how domesticated species have changed, and are still changing, in response to human-modified environments (see Outstanding Questions) [80]. This effort will provide a robust framework to investigate the cultural and biological processes that underlie one of the most important evolutionary transitions.

Acknowledgments

We thank the many people who contributed comments, suggestions, and photographs to this opinion article and especially Lorna Coppinger, Jean MacKay, Joseph Glass, Isaac Knoflicek, Patrick Litza, Nicole Miller, Millard Susman, Jessica Hekman, Diane Genereux, Marjie Alonso, and Ilya Shlyakhter. K.A.L. and E.K.K. were supported by a BroadIgnite award from the Broad Institute of Harvard and MIT. G.L. was supported by the European Research Council (ERC) (Grant ERC-2013-StG-337574-UNDEAD).

Supplemental Information

Supplemental information associated with this article can be found online at https://doi.org/10.1016/j.tree.2019.10.011.

Outstanding Questions

Domesticated species offer a unique perspective on human history and how species adapt to anthropized ecosystems. Our review shows that key questions still need to be addressed:

- What is domestication? For each species, the changes associated with domestication will depend on how humans have altered their specific ecological niche. Increased tameness, a characteristic of domesticated dogs and cats and the focus of selection in the Russian Farm-Fox experiment, may not be advantageous for all species. Are there common features that can define domestication?
- When is a species 'domesticated'? Should farm foxes, either in Canada or in Russia, be considered domesticated? If so, how is that distinction made, and can the same criteria be applied consistently in other species? Existing definitions vary widely and often rely on inferences of human intent or comparisons with wild populations that are poorly studied, admixed, or no longer exist. The lack of a uniform standard is particularly problematic when comparing domesticated species.
- Is there an animal domestication syndrome? Is it reasonable to expect that all domesticated animals will share common traits or does this simplification limit our understanding of a complex evolutionary process? Do some domesticated species – particularly phylogenetically distant ones – share common adaptations (convergent evolution) and can this give us insight into the underlying biological processes?

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