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#### References

1. Lord, K.A. *et al.* (2019) The history of farm foxes undermines the animal domestication syndrome. *Trends Ecol. Evol.* 35, 125–136
2. Vahrameyev, K.A. and Belyaev, D.K. (1948) *Guide for Fox Breeding*, International Book (in Russian)
3. Rayner, B.I. and Jones, J.W. (1912) Domestication of the fox. *J. Hered.* 3, 37–45
4. Belyaev, D.K. (1969) Domestication of animals. *Sci. J.* 5, 47–52
5. Trut, L.N. *et al.* (2004) An experiment on fox domestication and debatable issues of evolution of the dog. *Genetika* 40, 794–807 (in Russian)
6. Keeler, C.E. (1964) Coat colour gene synthesis of tame behaviour in the rat, mink and fox. *Mind Over Matter* 9, 16–30
7. Robinson, R. (1975) The red fox, *Vulpes vulpes*. In *Handbook of Genetics* (King, R.C., ed.), pp. 399–419, Springer
8. Cole, L.J. and Shackelford, R.M. (1943) White spotting in the fox. *Am. Nat.* 77, 289–321
9. Belyaev, D.K. *et al.* (1981) Inherited activation–inactivation of the star gene in foxes: its bearing on the problem of domestication. *J. Hered.* 72, 267–274
10. Trut, L.N. *et al.* (1991) Intracranial allometry and craniologic changes during domestication of silver foxes. *Genetika* 27, 1605–1611 (in Russian)
11. Petryaev, P.A. (1934) *The Biology of Reproduction, Heredity and Variability of Silver-Black Foxes*, All-Union Scientific Research Institute of Fur and Game Industry Management (in Russian)
12. Johnson, J.L. *et al.* (2015) Genotyping-by-sequencing (GBS) detects genetic structure and confirms behavioral QTL in tame and aggressive foxes (*Vulpes vulpes*). *PLoS One* 10, e0127013

## Letter

### Reply to Zeder and Trut *et al.*: An Attractive Hypothesis in Need of Evidence

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Recently, two letters published in *TREE* raised questions about our opinion article [1]. In it, we critically assessed the domestication syndrome: the hypothesis that a suite of behavioral and morphological characteristics is consistently observed in

domesticated populations. As with any scientific hypothesis, the burden of proof is clear. To be broadly accepted, the domestication syndrome must be affirmatively supported through rigorous research. We concluded that such research does not yet exist.

Zeder argues that, if traits and species with no data are ignored, there is compelling evidence for domestication syndrome [2]. Yet, it is precisely this lack of data that led us to question domestication syndrome. We found no evidence that a set of shared characteristics is consistently observed in domesticated animal populations. Zeder's Table 1 masks the missing data, and merely shows what we intended: a lack of ubiquity of domestication traits in any domesticate or population. There is no connection between the status of the animal and the presence of a trait. Our conclusions are supported by new work showing that the domestication syndrome traits (both morphological and behavioral) do not covary among 78 dog breeds [3], further undermining the assumed link between domestication syndrome traits and early domestication. We whole-heartedly agree with Zeder that the evidence for domestication syndrome is anecdotal, and that rigorous studies comparing wild and domesticated, nonbreed populations are needed.

Zeder cites the documentation of both tame behavior and other domestication syndrome traits in the Canadian farm foxes, the founder population for the Russian Farm-Fox Experiment, as support for the domestication syndrome. Historical records show that the Canadian fox farmers were breeding for both behavioral and morphological traits, precluding any inference of a causal link between selection on tameness and other traits. The simplest explanation for the co-occurrence of these traits in the Canadian farm foxes is artificial selection on each individual trait, not the domestication syndrome.

By contrast, in a second letter, Trut *et al.* argue that the behavioral changes and other syndrome traits observed in the Farm-Fox Experiment did not predate the project [4]. Instead, Trut *et al.* ascribe the behavioral changes we describe in the Canadian farm foxes to nonheritable taming. This is implausible. If the behavior described in the Canadian farm foxes had been purely environmental, breeders would have started new populations from wild foxes, rather than paying the equivalent of US \$500 000 for a single pair of farm foxes [1].

Tame behavior is the result of both genetics and environment, and particularly early socialization. A dog raised without human contact will be fearful of humans [5], but is still genetically domesticated. The results from the Farm-Fox Experiment itself suggest the farm foxes were genetically primed to be easily tamed. The experiment entailed a substantial change in environment for the foxes, moved from fox farms that housed thousands of foxes, to a research facility where hundreds of foxes were closely observed by human caretakers. While it may be true that not a single tame animal was found in their starting population, by the third generation, nearly all the foxes crossed that threshold [6], suggesting the change was in large part environmental.

We do not argue that Prince Edward Island fox tameness and Belyaev's fox tameness are identical. Instead, we contend that the quick selection for extreme tameness in the Farm-Fox Experiment is more easily explained as selection on variants that already existed in the population. This is akin to dog breeders repeatedly selecting on, for example, the most extreme manifestations of herding behavior in order to create a working border collie line.

Trut *et al.* also argued that the morphological variants seen in the Farm-Fox Experiment, and specifically the mutation they called S,

have distinct etiology from those described in Canada. However, we found no conclusive evidence that these are novel mutations. The Canadian fox population exhibited a diverse range of depigmentation phenotypes referred to as white-faced, white-spotted, or white collared interchangeably [7], and included a mutation linked to a movement disorder, similar to S, and a mutation that was homozygous lethal, similar to W. White-spotting phenotypes were also documented in Russian commercial fox farms [8]. The S white-spotting phenotype is highly variable [‘ranging from 3–5 unpigmented hairs gathered in a cluster to a spot (2–3 cm<sup>2</sup>) and sometimes significantly more’] and has incomplete penetrance, varying depending on the genetic background of the population [8]. It is more likely that the population of ‘standard silver blacks’ used to start the experiment carried unexpressed white-spotting alleles, including S, rather than the alternative scenario in which multiple independent *de novo* mutations – causing phenotypes strikingly similar to traits documented in the parent population – occurred within the first 10 years of the project.

We thank Trut *et al.* for clarifying that the Canadian origins of the foxes were known to the researchers in Russia. The literature they cite is not easily accessible outside Russia. We wanted to allow for the possibility that the early Farm-Fox Experiment researchers may not have considered the population history of the Canadian farm foxes because they were not aware of the full details. Regardless of the number of foxes brought from Canada to Russia, the diversity of the population is shaped by the small number of foxes used to start the farm fox population in Canada. The effective population sizes and inbreeding coefficients reported for the Farm-Fox Experiment populations are equivalent to those for a dog breed [9–11].

The concept of the domestication syndrome is certainly compelling, as are the hypotheses that have been promoted to explain it. It may be a genuine biological phenomenon. Our contention is that anecdotal observations have often taken the place of the robust, experimental evidence required to definitively establish its existence. Along with Zeder and Trut *et al.*, we look forward to the rigorous scientific approaches that may well confirm both its existence, and the mechanisms responsible for its appearance.

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#### References

1. Lord, K.A. *et al.* (2020) The history of farm foxes undermines the animal domestication syndrome. *Trends Ecol. Evol.* 35, 125–136
2. Zeder, M.A. (2020) Straw foxes: domestication syndrome evaluation comes up short. *Trends Ecol. Evol.* 35 (8), 647–649
3. Wheat, C.H. *et al.* (2020) Morphology does not covary with predicted behavioral correlations of the domestication syndrome in dogs. *Evol. Lett.* Published online April 10, 2020. <https://doi.org/10.1002/evl3.168>
4. Trut, L.N. *et al.* (2020) Belyaev’s and PEI’s foxes: a far cry. *Trends Ecol. Evol.* 35 (8), 649–651
5. Freedman, D.G. *et al.* (1961) Critical period in the social development of dogs. *Science* 133, 1016–1017
6. Belyaev, D.K. (1979) Destabilizing selection as a factor in domestication. *J. Hered.* 70, 301–308
7. Cole, L.J. and Shackelford, R.M. (1943) White spotting in the fox. *Am. Nat.* 77, 289–321
8. Belyaev, D.K. *et al.* (1981) Inherited activation-inactivation of the star gene in foxes: its bearing on the problem of domestication. *J. Hered.* 72, 267–274
9. Dreger, D.L. *et al.* (2016) Whole-genome sequence, SNP chips and pedigree structure: building demographic profiles in domestic dog breeds to optimize genetic-trait mapping. *Dis. Model. Mech.* 9, 1445–1460
10. Kukekova, A.V. (2004) A marker set for construction of a genetic map of the silver fox (*Vulpes vulpes*). *J. Hered.* 95, 185–194
11. Johnson, J.L. *et al.* (2015) Genotyping-by-sequencing (GBS) detects genetic structure and confirms behavioral QTL in tame and aggressive foxes (*Vulpes vulpes*). *PLoS One* 10, e0127013

## Forum

### Photic Barriers to Poleward Range-shifts

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**With climate warming, organisms are shifting their ranges towards the poles, tracking their optimal thermal environments. Day-length, the driver of daily and annual timing, is, however, fixed by latitude and date. Timing and photoreception mechanisms adapted to ancestral photic environments may restrict range-shift capacity, resulting in photic barriers to range-shifts.**

#### A Thermal–photic Mismatch

Organisms are shifting their ranges polewards at a median rate of 16.9 km decade<sup>-1</sup> as they track their optimal thermal environment under climate warming [1]. Predictions of species’ abilities to establish and persist in these new ranges, however, rarely take into account that latitudinal **range-shifts** (see **Glossary**) result in exposure to novel photic environments. Many organisms have physiology and behavior (e.g., vision, **circadian rhythms**, and **phenology**) that optimize fitness under the photic environment of their ancestral latitude [2–4]. These adaptations integrate **photic cues** to allow for the successful anticipation of, and response during, the diel and annual cycles, and may, thereby, restrict range-shift capacity via a thermal–photic mismatch. A photic barrier would effectively cap the poleward range-shift of species that are unable to adapt to extremes in duration and annual transition in **photoperiod**. This mismatch may be especially problematic for species predicted to move into high-latitude photic environments [3], which have phases of continuous light and dark near and above the polar circles (66.6°N and 66.6°S).