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Letter

Brain Size Does Not Rescue Domestication Syndrome

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In a recent letter, Wright *et al.* question the conclusions of our opinion article 'The history of farm foxes undermines the animal domestication syndrome' [1,2]. We argue that, while the hypothesis that a universal set of traits accompanies domestication in animal species is intriguing, there is, thus far, insufficient supporting data to meet the burden of proof required to conclude the domestication syndrome exists. Wright *et al.* propose that by applying a less-restrictive definition of the domestication syndrome, an alternative conclusion can be reached.

We define a domestication syndrome trait as one causally linked to the process of domestication. In populations experiencing selective pressure that favors tameness, as in the Russian Farm Fox project, domestication syndrome traits would rise in prevalence as a consequence. Wright *et al.* propose that domestication syndrome should be defined purely phenotypically, and if one does so, abundant evidence exists for shared changes in behavior, body size, brain size, and color across almost all domesticated animals when compared with their wild relatives.

Even if a purely phenotypic definition is used, however, we find little support for the domestication syndrome. We restricted our analysis to mammals because of the difficulty of defining traits consistently across orders, yet still found wide variation in how traits were measured, and in how the wild and domesticated populations were defined, making cross-species comparisons challenging. Many studies used modern breeds as the representatives of domesticated populations, but trait differences in breed subpopulations are not related to domestication, but instead to the later improvement process to which existing domesticates have been subjected.

To demonstrate that a trait is universal among almost all domestic animals, we would ideally compare modern domesticates with their pre-domestic wild ancestors, but this is not possible in any species. Most domestication syndrome traits cannot be measured in ancient remains. Modern wild populations are not representatives of the ancestral pre-domesticated population, as is sometimes implied, but are instead sister taxa with their own evolutionary history. They are not even necessarily descendants of the lineage from which the species was domesticated (e.g., dogs, the wild Eurasian wolf ancestor of which is extinct [3]), and thus observed phenotypic differences may predate domestication by hundreds of thousands of years. In some cases, populations thought to represent the wild lineage are instead feralized domestic populations.

The work on reduced brain size, described by Wright *et al.* in Table 1 in that article, perfectly illustrates these difficulties [2,4]. The comparison populations used to assess brain size reduction vary widely, and a critical assessment reveals that many are invalid. For example, domestic horses were compared with modern Przewalski horses [5]; a severely bottlenecked and heavily managed lineage that has recently been shown to be the feral descendants of the first domestic horses, and thus not wild in any sense [6]. In dogs, while early work from Coppinger described a decrease in the ratio of brain volume to skull area in dogs, these findings were amended in a later rewrite [7]. Breeds selected for giant size do possess a smaller ratio, but average sized dogs show no significant difference relative to modern wolves.

The comparison of alpacas and llamas with guanacos (*Lama guanicoe*) suggests a change in the ratio of brain weight to body weight, but the choice of wild population is suspect because alpacas are descended from vicunas (*Vicugna vicugna*) [8]. In sheep, two modern breeds (North German moorland sheep and blackhead sheep) were compared with European wild sheep (*Ovis ammon musimon*), a species that diverged from the closest modern relative of domesticated sheep, Asiatic Mouflon (*Ovis orientalis*), more than a million years ago [9]. Wild mink were compared with ranch mink [10,11], an artificially selected wild population rather than a true domesticate. Similarly, wild gerbils were compared with a bottlenecked laboratory population established using wild gerbils [12].

In pigs, a comparison of breeds of varying sizes with wild boar suggested a decrease in the ratio of brain weight to body weight [13]. Yet even here, the choice of an appropriate comparison wild population is confounded firstly by ancestry, since pigs were domesticated independently from two geographically distinct subspecies [14]. Secondly, a strict dichotomy between wild and domestic populations is undermined by long-term gene flow within and between both domestic pigs and wild boar [15].

One trait, increased tameness, is shared across domesticated animals, because it is inherent in how we define a species as domesticated. For other traits, the evidence is weak. Even when differences between populations are found, varying definitions of 'wild' and 'domestic' make it impossible to conclude that the process of domestication is the critical feature explaining the differentiation between those populations. The null hypothesis – the degree of phenotypic change expected between similarly genetically differentiated populations in the absence of domestication – has rarely if ever been defined. A recent large-scale study failed to find the covariation between morphology and behavior expected if the domestication syndrome were real [16]. Although it is a long-standing hypothesis, the domestication syndrome has not yet been rigorously tested, as any scientific hypothesis must be, and cannot be assumed to be true.

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