Preprint

Addendum to "The parasite-mediated domestication hypothesis"

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Abstract

The parasite-mediated domestication hypothesis (PMD) assumes an important role of endoparasites in the process of domestication, primarily in the initial phase, i.e. proto-domestication. It predicts that the frequency of domestication syndrome traits in the wild population increases i) with decreasing genetic resistance to parasites and/or ii) with increasing parasite load. This addendum expands on the aspect of genetic resistance/tolerance to parasites, explains the limitations associated with artificial and relaxed selection, and suggests a possible experimental approach to testing PMD.

Keywords: parasite-mediated domestication, endoparasites, domestication syndrome

Interpretative limitations of genetic resistance/tolerance

As for genetic resistance to parasites, the PMD (Skok, 2023) points out that "*special caution must be taken with domesticated animals that may have been artificially selected for parasite resistance, because in this case the results are inevitably misleading and the conclusions biased*". Here, the concept of artificial selection and genetic resistance/tolerance to parasites in domestic animals should be considered in a broader context, as it can be problematic when testing PMD.

The first aspect concerns the possible artificial selection of resistant/tolerant animals, which aims to increase the frequency of parasite resistance alleles in the population (McManus et al., 2014). Therefore, domestic animals artificially selected in this way may have a deceptively high resistance/tolerance to parasites, perhaps even higher than their wild counterparts.

The second aspect concerns relaxed selection, in which the source of selection that used to be important for the maintenance of a particular trait is weakened or even eliminated (Lahti et al., 2009). Since domestication, animals have been confined, at least to some degree, and thus prevented from being exposed to the full range of parasites that could infect/infest them in their natural environment. The selection pressure from parasites during the domestication process could therefore have been reduced, which could influence the evolution of genetic resistance in domestic (parasite-naïve) animals.

For instance, the major histocompatibility complex (MHC) is a large locus of genes responsible for the adaptive immune system, helping to activate not only appropriate T cells that help the organism to eliminate intracellular pathogens (e.g. viruses), but also B cells involved in the elimination or neutralisation of extracellular pathogens, including parasites (Janeway et al., 2001; McManus et al., 2014). It is assumed that animals with limited MHC gene diversity also have low resistance to parasites.

Indeed, constant selection pressure by various parasites leads to rapid adaptive evolutionary changes that result in an adaptive shift in allele frequency, implying that parasite-mediated selection directly contributes to the maintenance of MHC polymorphism (Eizaguirre et al., 2012). Accordingly, Smallbone et al. (2021) found a significantly lower number of MHC alleles and MHC supertypes per individual in domesticated guppies compared to the wild type. They pointed out that artificial selection for desirable, economically important traits may lead to the loss of key immune functional alleles and thus reduce the immunogenetic diversity that protect populations from the risk of parasite infection/infestation, which could significantly impair host resistance

to parasites. Similar results have been shown for the red junglefowl compared to the domestic chicken (Nguyen-Phuc et al., 2016). In contrast, studies on the pig and zebra finch did not follow the same premise and showed that domestication does not appear to act as a bottleneck limiting MHC diversity (Moutou et al., 2013; Newhouse and Balakrishnan, 2015). However, MHC diversity does not necessarily imply higher functional resistance, but may simply be the signature of the pathogens and parasites that the animal has been confronted with in the course of evolution (Mikko et al., 1999; see also Portanier et al., 2019, showing that MHC diversity in mouflons is associated with resistance to nematodes but not to coccidia). In addition to MHC, there are other quantitative trait loci for parasite resistance (McManus et al., 2014), which makes this aspect of PMD testing even more challenging.

Testing PMD on the basis of parasite load/resistance/tolerance in existing populations of wild or domestic animals and simply comparing them is therefore interpretatively quite complex, although relatively easily feasible.

Possible experimental approach

The most reliable way to test PMD would therefore be to examine the frequency of domestication syndrome traits in the wild population in relation to its parasite resistance/load, or to examine the parasite resistance/load of wild individuals showing signs of domestication syndrome (e.g. tameness) in comparison to fully wild individuals of the same population, as originally proposed (Skok, 2013). The other option would be the experimental approach, i.e. experimental proto-domestication, similar to the Belyaev fox experiment (Belyaev, 1979). However, instead of selecting animals for tameness, an experimental population of wild animals (preferably the wild counterpart of domestic animals) would be experimentally exposed to parasites, selected against parasite resistance (whereby more infected/infested, less resistant individuals would be selected) and the frequency of domestication syndrome traits in the population would be recorded over generations. It is predicted that the frequency of typical domestication syndrome traits (tameness, depigmentation, floppy ears, etc.) would increase in a parasite-susceptible population.

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