Dogs defy the domestication syndrome: morphology does not covary with predicted behavioural correlations within breeds

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Abstract

Domesticated animals display suites of morphological, behavioural and physiological differences compared to their wild ancestors, a phenomenon known as the domestication syndrome (DS). Domestication experiments, and the convergent patterns seen across domesticated species, have been adduced to support a singular developmental source for the DS. Specifically, the suite of DS traits are hypothesized to arise via selection solely upon tameness [1] resulting in neural crest deficit, which as a developmental by-product gives rise to morphological changes such as white pigmentation and floppy ears [2]. Consistent with this, genomic studies highlight evidence of selection upon genes associated with neural crest development, in e.g. domesticated foxes [3], horses [4] and dogs [5]. However, genes associated with neural crest development were only a subset of many showing selective signatures, complicating assessment of the single developmental source hypothesis for DS phenotypes. If components of the DS syndromes originate from a single underlying source, they should be evolutionary stable and difficult to decouple (*sensu* [6]), which is a testable hypotheses at the phenotypic level. Here we focus upon the classic morphological phenotypes associated with domesticated animals (floppy ears, white pigmentation, curly tails [1]), and quantify how these covary with the strength of behavioural correlations expected in the DS among 78 dog breeds. Contrary to the expectations embedded in the hypothesis of a singular developmental source of the DS, we found that these morphological traits and behavioural correlations vary independently among dog breeds. These findings suggest that morphological and behavioural traits within the DS are decoupled, allowing for the wide range of breed-specific trait combinations.

Methods and Results

Floppy ears, white pigmentation and curly tails have been referred to as morphological markers of domestication [1] (Figure 1a). We assessed the presence or absence of these traits in 78 registered dog breeds by consulting defined breed standards by the Fédèration Cynologique Internationale, the worlds largest federation of kennel clubs [7]. We used both a relaxed and conservative definition to assess our morphological traits (Supplemental Methods, Supplemental Figure 1). The results for relaxed and conservative measures produced similar conclusions (Supplemental Results) and we present the results for the relaxed assessments below. For the behavioural components of the DS, domesticated animals show reduced expression of fear and aggression along with increased expression of sociability and playfulness compared to their wild counterparts [1,8]. We used estimates of effect sizes for these behavioural correlations among these four traits, derived from data extracted from the Swedish Kennel Club's database on 76,158 dogs completing a highly standardized behavioural test battery (see Hansen Wheat et al. 2019 for in depth description of methods and data analyses). We then matched these effect sizes of behavioural correlations with our estimates of morphological traits from the 78 breeds.

We placed the morphological traits and average effect sizes for behavioural correlations onto the latest dog phylogeny [9], revealing large variation among breeds in both our morphological and behavioural traits (Figure 1b, full phylogeny in Supplemental Figure 1). First, we used three different methods to test whether the presence of morphological DS traits covary amongst themselves. None of these analyses produced even marginally significant results (Supplemental Methods and Results). Then, to test for a moderating effect of breed morphology on behaviour, we designed a Bayesian phylogenetic multilevel meta-analytic model. This model uses the estimated effect sizes from the correlations as its response variable and compares the average effect size between morphological categories. The level of support and effect of morphology were allowed to vary between the different predicted associations through the inclusion of group level effects. We also accounted for repeated measures from the same breeds, as well as the non-independence of breeds due to shared ancestry. We performed two versions of this nested meta-analysis. To test whether the presence of floppy ears, curly tails or white pigmentation predicts the strength of any of the behavioural correlations, we evaluated these traits as binary predictors of DS support. We found that there was no difference between presence or absence of any of the three morphological traits in predicting the strength of the behavioural correlations (Figure 1c, see Supplemental Figure 2 and Supplemental Results for results on specific behavioural correlations). Secondly, we assigned a linear "morphology score" to each breed, which ranged from 0 - 3 depending on how many, if any, of the three morphological traits is present in a breed (Figure 1b). We found that the number of morphological traits present in a breed did not predict the strength of behavioural correlations (Figure 1d). In sum, our results document that the hypothesized morphological traits do not predict the strength in effect sizes of behavioural correlations in dogs.

Discussion

The DS concept embodies the diverse observations that specific traits vary in a correlated fashion between wild species and their domesticated counterparts. However, whether these traits arise from a singular developmental source [2], or simply appear to covary when comparing domesticates and their wild progenitors, is not well resolved. While functional studies of diverse domesticated species find evidence of shared mechanisms that are associated with neural crest functioning, whether DS phenotypes covary as predicted has rarely been tested. A high covariance among DS phenotypes suggests a strong, central role for their shared origin in single developmental source (e.g. white pigmentation arising as a by-product of increased tameness [2]), while a lack of covariance suggests a more complex genotype to phenotype relationship. Here we quantitatively demonstrate that within dog breeds the DS suite of morphological traits do neither covary, nor covary with behavioural correlations. Whether behavioural traits of the DS are correlated has only recently been formally tested [10], revealing that over the course of domestication, behavioural correlations have been decoupled in dogs. Together, these results document a lack of covariance between and within categories of traits in the DS, suggesting a more complex developmental relationship among DS traits than a single shared source. Thus, whether the lack of covariance between morphology and behaviour in dogs is due to novel variation, decoupling possibly caused by altered selection regimes during breed formation, or these traits never having developmentally covaried, remains an open question.

Supplemental information

Supplemental information including methods, statistical analyses, two figures and supplemental results can be found with this article online at [link]

Acknowledgements

We thank Rasmus Erlandsson for designing the dog illustrations in Figure 1a.

Author contributions

CHW and CWW conceived the study. CHW prepared the data and all authors discussed how to analyse it. WvdB analysed the data. CHW prepared the manuscript draft and WvdB and CWW provided comments to produce the final version.

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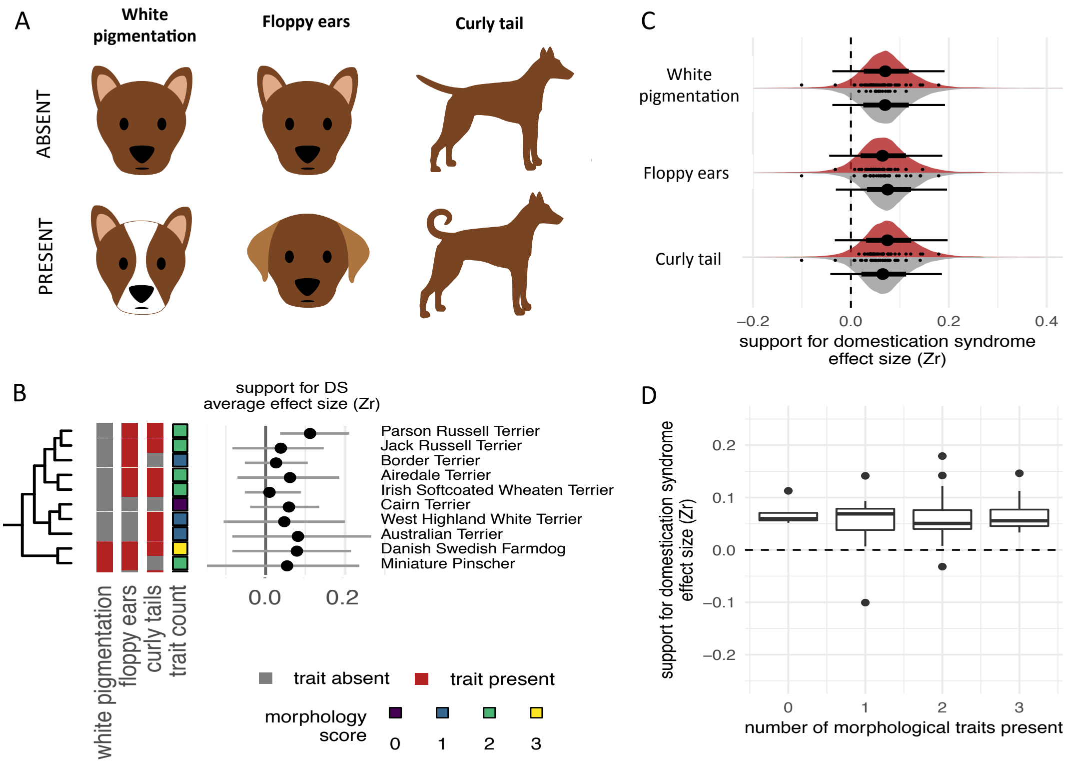

Figure 1. Predictive value of morphological traits on the strength of behavioural correlations. A) Examples of presence and absence of the three morphological markers of domestication: white pigmentation, floppy ears and curly tails. B) The predictive value of the presence or absence of morphological traits on the support for the DS, quantified as the strength of behavioural correlations (Z_r). Effect of white pigmentation: Posterior mean = 0.000, posterior sd = 0.013, 95CI = [-0.025, 0.026], Effect of floppy ears: Posterior mean = -0.011, posterior sd = 0.016, 95CI = [-0.041, 0.020], Effect of curly tails: Posterior mean = 0.010, posterior sd = 0.012, 95CI = [-0.012, 0.033]. C) A subset of morphological scores based on the presence or absence of white pigmentation, floppy ears and curly tail, and average effect sizes for behavioural correlations placed onto the latest dog phylogeny, please see Supplementary Figure 1 for the full figure. D) The predictive value of the number a morphological traits present, i.e. morphological score, on the strength of behavioural correlations within the DS: Posterior mean of the slope = 0.001, posterior sd = 0.009, 95CI = [-0.015, 0.018].