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

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Supplemental methods

We based our study on the 78 dog breeds used in a recent study to test behavioural correlations within the domestication syndrome [1]. We carefully inspected the breed standards for those 78 breeds by consulting the Fédèration Cynologique Internationale [2], the world's largest federation of kennel clubs, to assess our the presence or absence of our three chosen morphological traits; white pigmentation, floppy ears and curly tails. We used both relaxed and conservative assessments of the three morphological traits (Supplemental Figure 1). We defined white pigmentation as any form of depigmentation in the breed, regardless of its placement, shape or size. We also classified dogs with a white base colour, such as Dalmatians and West Highland Terriers, to express white pigmentation. For our conservative assessment of white pigmentation, only breeds that are described to have a white base colour or breeds with characteristic white patches were included. For the relaxed assessment, we also included breeds in which white pigmentation is not allowed, but a few white hairs, for instance on the chest, are accepted. Floppy ears were assessed based on whether a breed has ears that are either erect or to some degree floppy (i.e. from just the tip to hanging straight down). Thereby the presence or absence of floppy ears was assessed as a completely binary trait, and did not differ between the relaxed and conservative assessments. For our conservative assessment of curly tails, only breeds described to specifically have their tail in a curl were included. For the relaxed assessment breeds that carry their tail in a curl, but can let it down straight, and breeds that can carry their tail even in a slight curve were assessed as having curly tails.

For the behavioural component of our study, we used the dataset presented in Hansen Wheat et al. 2019, in which the strength and direction of behavioural correlations between aggression, fearfulness, sociability and playfulness across the 78 dog breeds were investigated. Behavioural data were provided by the Swedish kennel Club for dog completing the Dog Mentality Assessment, a highly standardized behavioural test for dogs in Sweden. We refer to this paper for full disclosure of the methods used to extract the effect sizes for these behavioural correlations.

Statistical analyses

To evaluate the relationship between breed morphology and agreement with the domestication syndrome hypothesis, we assessed the correlation between our morphology scores, treated as dichotomous variables. First, we estimated the phi coefficient (ϕ) for presence/absence of each of each trait in pairwise combinations with significance determined using Fisher's Exact Test, as implemented in the xtab_statistics function of the sjstats package v. 0.17.5 [3]. Second, we

repeated this analysis on the pairwise contingency tables using a chi-squared test with similar results. Third, we assess whether the presence/absence of traits were correlated while taking into account phylogenetic correction, using a pairwise bionomial phylogenetic glm.

To evaluate the relationship between breed morphology and agreement with the domestication syndrome hypothesis, as quantified by the strength and direction of behavioural correlations, we used two meta-analytic models. The models are identical, except for how the morphological traits are implemented. Both are multi-level models that use 1326 observed correlation coefficients [1], and their associated uncertainty, as the dependent variable. These correlations test multiple predictions by the DS, such as a positive association between sociability and playfulness, or a negative association between sociability and aggression [4-5]. The correlations test six such DS predictions. For some predictions multiple correlations per breed were measured, since the Dog Mental Asssesment test provided multiple measurements for aggression and fearfulness. 17 correlations were obtained per breed. Therefore, we treat the DS as a nested compound hypothesis, with six predicted associations and 17 correlations. We aligned the sign of the correlations with the predicted directions, i.e. we flipped the sign of correlations expected to be negative, so that positive effect sizes represent support in favour of the DS.

To account for this nested structured, we included group level effects that allow the support for the DS to vary between the different predicted associations and the measured correlations. We additionally included group level effects of morphology for the associations and correlations, so that the moderating effect of morphological traits could be stronger or weaker depending on what behavioural correlations were measured. Since each breed was represented by multiple correlations, we included a group level intercept for breed. And because breeds are non-independent due to shared ancestry [6], an additional group level effect was added with the expected covariance matrix of the phylogeny.

In the first model, morphology was modelled as three additive binary effects, one each for the presence or absence of floppy ears, curly tails and white pigmentation. In the second model, we modelled the morphically traits as a linear morphology score counting the number of traits presents, ranging from 0 to 3.

We implemented the models in the probabilistic programming language Stan [7], using the interfacing R [8] package brms [9-10]. In brms syntax, the models were of the form: *Zr | se(vi, sigma = TRUE) ~ morphology + (1 + morphology || prediction/correlation) + (1 | breed) + (1 | phylogeny)*, where Zr is the z-transformed correlations coefficients, vi is the measurement error and sigma = TRUE allows for the estimation of the residual standard deviation. The morphology terms differed between the two models as described above. Posterior distributions for the parameters were obtained through MCMC sampling, using eight chains of 2000 iterations each, of which 500 were warmup. We adjusted the adapt delta to 0.995 and the maximum tree depth to 20 to eliminate any divergent transitions. For population level effects, we used the default weak student-t prior with a mean of 0, scale parameter of 10 and 3 degrees of freedom. The same prior was used for standard deviations of group-level effects and the residual standard deviation, but there it was restricted to be non-negative. Trace plots indicated that the chains were well mixed, and we obtained an effective sample size of more than 1500. The largest $\hat{r}$ was 1.01, indicating convergence.

Supplemental results
Neithe phi coefficients (ϕ), chi-squared values or phylogenetically corrected correlations for the three morphological traits produced significant results: white pigmentation vs. floppy ears ($\phi = 0.026$, $\chi^2 = 0$, p = 1), white pigmentation vs. curly tail ($\phi = 0.06$, $\chi^2 = 0.06$, p = 0.78), floppy ears vs. curly tail ($\phi = 0.05$, $\chi^2 = 0.4$, p = 0.84), Statistical outputs for Supplemental Figure 2 and analyses using conservative morphological assessments are available at [Dryad link]

Supplemental Figure 1
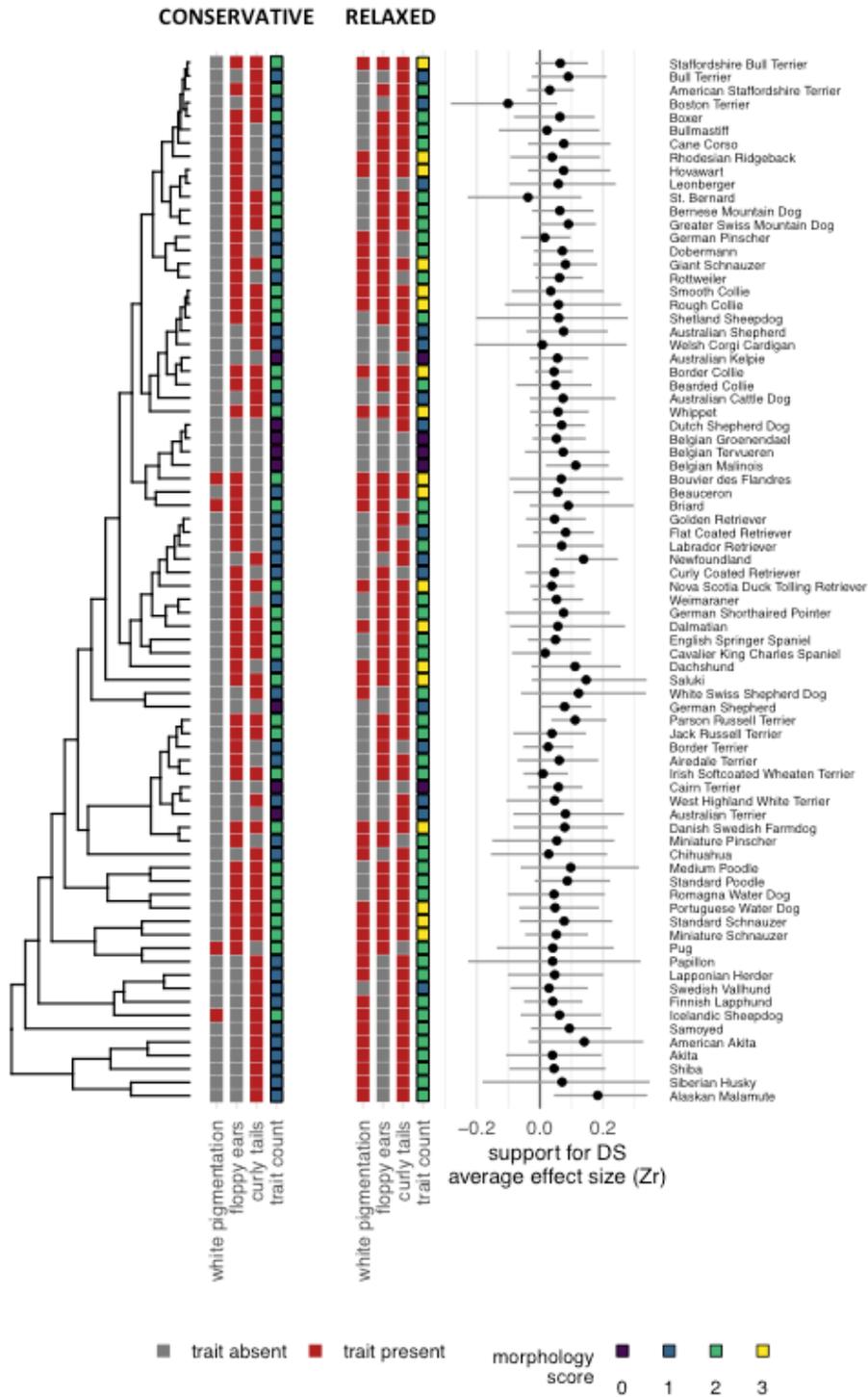
Supplemental Figure 1. Morphological scores and behavioural correlations fitted onto a phylogeny. Conservative and relaxed morphological assessments of 78 dog breeds, each followed by a morphological scores based on the number of traits present in each breed. Support for the domestication syndrome is assessed as the strength and direction for posterior distributions of within breed behavioural correlations between aggression, fear, sociability and playfulness. These assessments have been fitted onto the latest available dog phylogeny [11].

Supplemental Figure 2
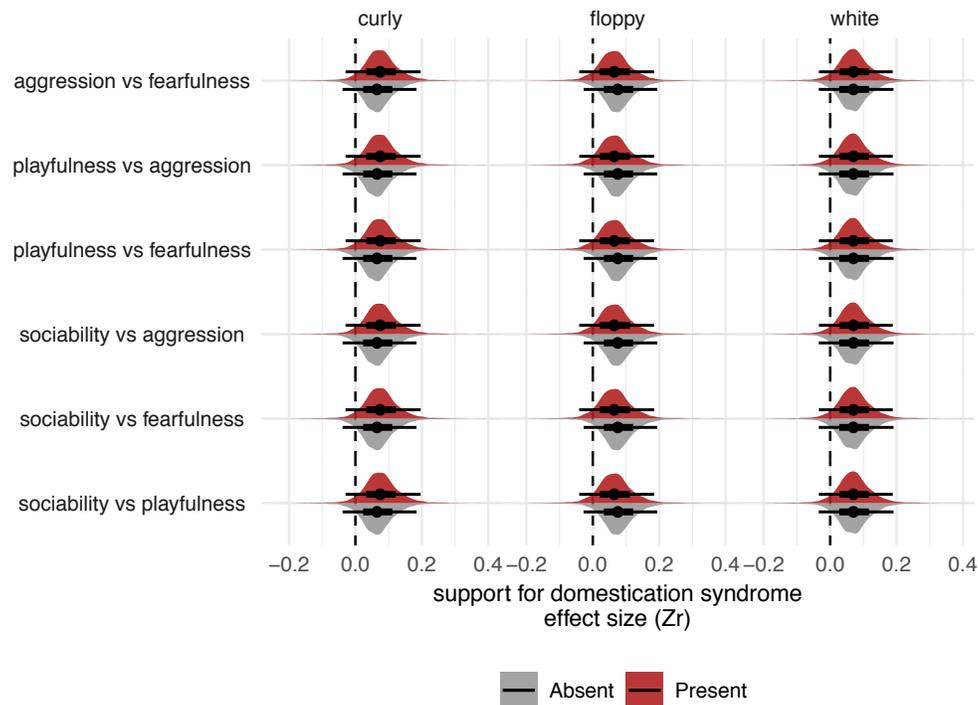
Supplemental Figure 2. Predictive value of morphological traits on the strength of separate behavioural correlations. The predictive value of the presence or absence of white pigmentation, floppy ears and curly tail on the support for the DS, quantified as the posterior distribution of the strength of the six individual behavioural correlations (Z_r) aggression vs fearfulness, playfulness vs aggression, playfulness vs fearfulness, sociability vs aggression, sociability vs fearfulness and sociability vs playfulness. None of the distributions are significant.

Supplemental references

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