

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

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11 **Abstract**

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

## 35 **Methods and Results**

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

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53 We placed the morphological traits and average effect sizes for behavioural  
54 correlations onto the latest dog phylogeny [9], revealing large variation among breeds  
55 in both our morphological and behavioural traits (Figure 1b, full phylogeny in  
56 Supplemental Figure 1). First, we used three different methods to test whether the  
57 presence of morphological DS traits covary amongst themselves. None of these  
58 analyses produced even marginally significant results (Supplemental Methods and  
59 Results). Then, to test for a moderating effect of breed morphology on behaviour, we  
60 designed a Bayesian phylogenetic multilevel meta-analytic model. This model uses  
61 the estimated effect sizes from the correlations as its response variable and compares  
62 the average effect size between morphological categories. The level of support and  
63 effect of morphology were allowed to vary between the different predicted  
64 associations through the inclusion of group level effects. We also accounted for  
65 repeated measures from the same breeds, as well as the non-independence of breeds  
66 due to shared ancestry. We performed two versions of this nested meta-analysis. To  
67 test whether the presence of floppy ears, curly tails or white pigmentation predicts the  
68 strength of any of the behavioural correlations, we evaluated these traits as binary

69 predictors of DS support. We found that there was no difference between presence or  
70 absence of any of the three morphological traits in predicting the strength of the  
71 behavioural correlations (Figure 1c, see Supplemental Figure 2 and Supplemental  
72 Results for results on specific behavioural correlations). Secondly, we assigned a  
73 linear “morphology score” to each breed, which ranged from 0 - 3 depending on how  
74 many, if any, of the three morphological traits is present in a breed (Figure 1b). We  
75 found that the number of morphological traits present in a breed did not predict the  
76 strength of behavioural correlations (Figure 1d). In sum, our results document that the  
77 hypothesized morphological traits do not predict the strength in effect sizes of  
78 behavioural correlations in dogs.

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## 80 **Discussion**

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

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103 **Supplemental information**

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

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109

110 **Author contributions**

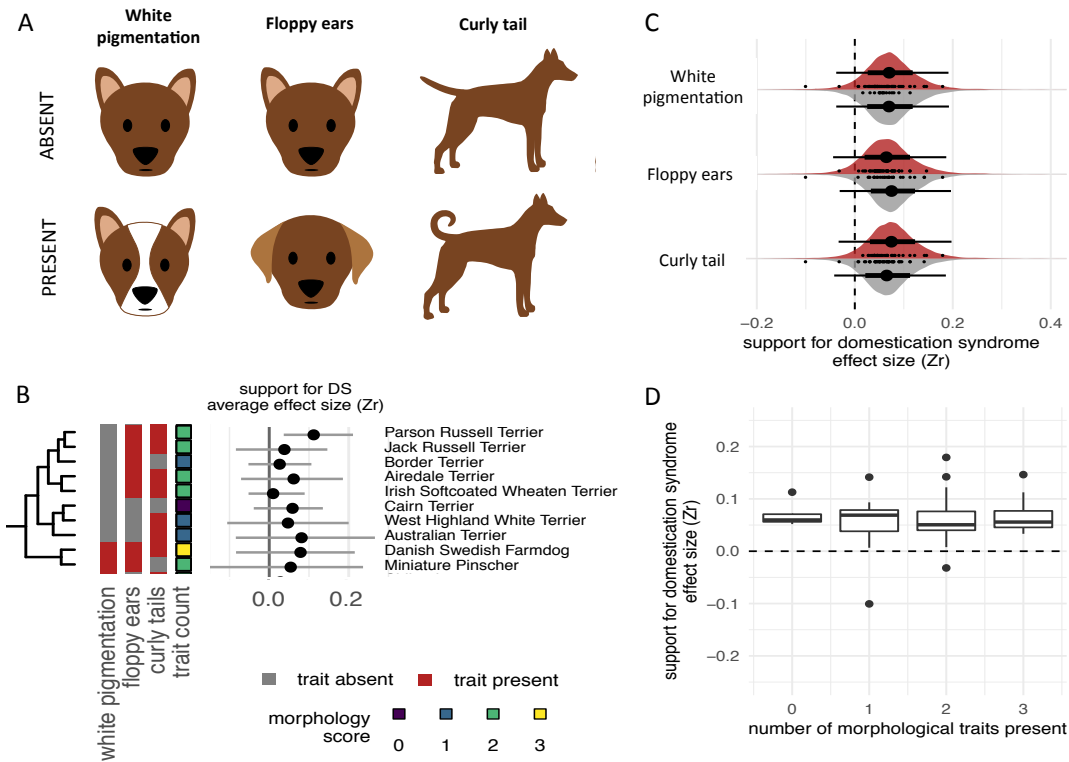
111 CHW and CWW conceived the study. CHW prepared the data and all authors  
112 discussed how to analyse it. WvdB analysed the data. CHW prepared the manuscript  
113 draft and WvdB and CWW provided comments to produce the final version.

114

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142 **Figure 1. Predictive value of morphological traits on the strength of behavioural correlations.** A)

143 Examples of presence and absence of the three morphological markers of domestication: white

144 pigmentation, floppy ears and curly tails. B) The predictive value of the presence or absence of

145 morphological traits on the support for the DS, quantified as the strength of behavioural correlations

146 ( $Z_r$ ). Effect of white pigmentation: Posterior mean = 0.000, posterior sd = 0.013, 95CI = [-0.025,

147 0.026], Effect of floppy ears: Posterior mean = -0.011, posterior sd = 0.016, 95CI = [-0.041, 0.020],

148 Effect of curly tails: Posterior mean = 0.010, posterior sd = 0.012, 95CI = [-0.012, 0.033]. C) A subset

149 of morphological scores based on the presence or absence of white pigmentation, floppy ears and curly

150 tail, and average effect sizes for behavioural correlations placed onto the latest dog phylogeny, please

151 see Supplementary Figure 1 for the full figure. D) The predictive value of the number a morphological

152 traits present, i.e. morphological score, on the strength of behavioural correlations within the DS:

153 Posterior mean of the slope = 0.001, posterior sd = 0.009, 95CI = [-0.015, 0.018].