1　　　　　　　　**Absolute Brain Size Predicts Dog Breed Differences**
2　　　　　　　　　　　　　**in Executive Function**

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Abstract

5

6   Large-scale phylogenetic studies of animal cognition have revealed robust links between

7   absolute brain volume and species differences in executive function. However, past comparative

8   samples have been composed largely of primates, which are characterized by derived neural

9   scaling rules. Therefore, it is currently unknown whether positive associations between brain

10   volume and executive function reflect a broad-scale evolutionary phenomenon, or alternatively, a

11   unique consequence of primate brain evolution. Domestic dogs provide a powerful opportunity for

12   investigating this question due to their close genetic relatedness, but vast intraspecific variation.

13   Using citizen science data on more than 7,000 purebred dogs from 74 breeds, and controlling for

14   genetic relatedness between breeds, we identify strong relationships between estimated absolute

15   brain weight and breed differences in cognition. Specifically, larger-brained breeds performed

16   significantly better on measures of short-term memory and self-control. However, the relationships

17   between estimated brain weight and other cognitive measures varied widely, supporting domain-

18   specific accounts of cognitive evolution. Our results suggest that evolutionary increases in brain

19   size are positively associated with taxonomic differences in executive function, even in the absence

20   of primate-like neuroanatomy. These findings also suggest that variation between dog breeds may

21   present a powerful model for investigating correlated changes in neuroanatomy and cognition

22   among closely related taxa.

23   **Keywords:** cognitive evolution, brain evolution, brain size, executive function, breed differences,

24   citizen science

1. Background

Comparative studies suggest that variance in brain size is linked to species differences in some aspects of cognition (Benson-Amram, Dantzer, Stricker, Swanson, & Holekamp, 2016; Deaner, Isler, Burkart, & Van Schaik, 2007; Garamszegi & Eens, 2004; Kotrschal et al., 2013; Kotrschal, Corral-Lopez, Amcoff, & Kolm, 2015; MacLean et al., 2014; Madden, 2001; Overington, Morand-Ferron, Boogert, & Lefebvre, 2009; Reader & Laland, 2002; Shultz & Dunbar, 2010; Sol, Bacher, Reader, & Lefebvre, 2008; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005). Studies of relative brain size have revealed interspecific links with problem solving in carnivores (Benson-Amram et al., 2016) and innovativeness in birds (Overington et al., 2009), while intraspecific examinations have linked relative brain size to numerical learning, spatial learning, and reversal learning in guppies (Buechel, Boussard, Kotrschal, van der Bijl, & Kolm, 2017; Kotrschal et al., 2013, 2015). Phylogenetic studies of absolute brain size have demonstrated a strong relationship between absolute brain volume and components of executive function (a suite of cognitive abilities involved in behavioral control, including working memory and inhibition) (Deaner et al., 2007; MacLean et al., 2014; Shultz & Dunbar, 2010). However, much of the work linking absolute brain size to executive function has been conducted with primates, and recent advances in comparative neuroanatomy reveal that primates are characterized by unique neural scaling properties, which contrast with those of other orders (Herculano-Houzel, 2012, 2017; Herculano-Houzel, Collins, Wong, & Kaas, 2007). Specifically, in most mammals, as brain volume increases, average neuron size tends to increase as well, and neurons become less densely populated in the brain (Herculano-Houzel, 2014, 2017; Herculano-Houzel, Mota, & Lent, 2006). In contrast, as primate brains increase in volume, both neuron size and density remain constant, resulting in isometric (i.e. 1:1) scaling between these variables (Herculano-Houzel et al.,

48 2007). As a result, for a given primate and non-primate mammal of equivalent brain size, the

49 primate's brain is expected to contain more neurons and to have greater neuron density. Similarly,

50 in primates, a two-fold change in brain volume is expected to lead to a two-fold increase in the

51 number of neurons in the larger brain, whereas a two-fold change in volume leads to the addition

52 of many fewer neurons in non-primate mammals. This phenomenon has been proposed to account

53 for the uniqueness of the human brain (but see [Mortensen et al., 2014] for evidence that long-

54 finned pilot whales have more neocortical neurons that humans, but lower neuron density), the

55 'primate advantage' of increases in brain volume, and previously observed associations between

56 brain volume and species differences in executive function (Deaner et al., 2007; Herculano-

57 Houzel, 2012; MacLean et al., 2014). Consequently, it remains unknown whether the relationship

58 between brain volume and executive function reflects a broad-scale evolutionary phenomenon, or

59 alternatively, a unique consequence of primate brain evolution.

60   Therefore, an important test of the association between brain volume and executive

61 function requires analysis with a large sample of taxa that do not adhere to primate-like neural

62 scaling rules. Domesticated dogs, with their extraordinary degree of intraspecific morphological

63 variation (including variation in brain size [Kruska, 1988; Wosinski, Schleicher, & Zilles, 1996]),

64 offer a unique opportunity for such a study. New evidence shows that dogs adhere to the same

65 cortical scaling rules as other non-primate mammals, and that domestication appears to have had

66 no effect on allometric brain scaling in dogs (or other domesticated carnivores examined) (Jardim-

67 Messeder et al., 2017). Additionally, previous phylogenetic studies of links between brain size and

68 cognition have been critiqued for ignoring heterogeneity resulting from variation in evolutionary

69 trajectories or different selection pressures on neuroanatomy across taxa (Logan et al., 2018). As

70 the relative sizes of different brain structures are likely to be less variable within, than across

71 species (Finlay & Darlington, 1995; Gould et al., 2013; Healy & Krebs, 1992; Lucas, Brodin, de

72 Kort, & Clayton, 2004) dogs allow us to assess the cognitive correlates of changes in absolute

73 brain size while better controlling for changes in the relative sizes of specific brain regions, or

74 other factors that vary considerably across diverse taxonomic groups (Barton & Harvey, 2000;

75 Barton & Venditti, 2014; Gould et al., 2013). Although breed-level variation in neuroanatomy

76 remains largely unexplored, preliminary data suggest that the relative sizes of neural structures do

77 not vary significantly across dog breeds with large degrees of variation in brain volume and skull

78 shape (Roberts, McGreevy, & Valenzuela, 2010; Thames et al., 2009).

79   Here we report the results of analyses investigating the association between estimated brain

80 weight and breed differences in dog cognition, measured in a sample of more than 7,000

81 individuals from 74 breeds, on a battery of cognitive tests designed to probe diverse aspects of

82 cognition (broadly defined as the processes through which animals acquire, store, and act on

83 information from the environment [Shettleworth, 2009]).

84 **2. Methods**

85   Cognitive data were collected through *Dognition.com*, a citizen science website that

86 provides dog owners with instructions for completing cognitive experiments with pet dogs in their

87 homes (Bonney et al., 2009; Cooper, 2016). Analyses of these data replicate findings from similar

88 tests conducted in laboratory settings (Stewart et al., 2015), and psychometric analyses of citizen

89 science data yield underlying factors consistent with those obtained from conventional approaches

90 (MacLean, Herrmann, Suchindran, & Hare, 2017). We included data from all ten of Dognition's

91 primary cognitive tasks in our analyses, measuring a wide range of cognitive skills including

92 components of executive function, inferential and causal reasoning, and communicative processes

93 (Table 1, Online Resource 1). We analyzed data from 7,397 purebred adult dogs representing 74

94 breeds (Online Resource 1: Tables 1-3). Breed-average body weights were compiled from the

95 Canine Behavioral Assessment and Research Questionnaire (C-BARQ) (Hsu & Serpell, 2003;

96 McGreevy et al., 2013), and breed-average brain weights were estimated from a scaling function

97 described by Bronson (1979) and validated using C-BARQ body weights for a sample of 24 breeds

98 with known brain weights (Online Resource 1: Figure 1). To control for genetic relatedness

99 between breeds, the associations between estimated brain weight and cognitive measures were

100 tested using Efficient Mixed Modeling for Association studies (EMMA) (Kang et al., 2008; Zhou

101 & Stephens, 2012). Genetic covariance between breeds was incorporated using a breed-average

102 identity-by-state (IBS) matrix (Boyko et al., 2010), using molecular data from Hayward and

103 colleagues (2016). For analyses including individual level data across breeds, breed-level IBS

104 matrices were multiplied by an individual-level incidence matrix to generate an individual-level

105 IBS matrix. To avoid the assumption that members of the same breed were clonal, pairwise within-

106 breed IBS values were set to the average IBS value between members of that breed. Tests were

107 conducted using the 'EMMREML' package (Akdemir & Godfrey, 2015) in the R environment

108 (v.3.3.1) (R Core Team, 2016). Associations were considered significant at an alpha level of 0.05.

109 Data are available as electronic supplementary material (Online Resource 2).

110 **Table 1**

Task	Description	Total dogs	Total breeds	β	χ^2	p
Yawning	While sitting on the floor, the owner yawns audibly every 5 seconds for 30 seconds total. The dependent measure is the difference between whether or not the dog yawns during the 30 second trial and a control condition. Two trials are conducted.	7344	74	-0.00053	1.19	0.27
Eye Contact	The owner stands holding a treat directly below his or her eye and makes eye contact with the dog. The dependent measure is how long it takes the dog to break eye contact for longer than two seconds. Three trials are conducted.	6413	69	-0.018	0.12	0.73
Arm Pointing	The owner places two treats at arm's length on his or her right and left. The owner then points to one of these locations. The dependent measure is which location the dog approaches first as the owner sustains pointing. Six trials are conducted.	4342	59	0.00068	4.18	**0.041***
Foot Pointing	Same as Arm Pointing, but rather than pointing, the owner extends his or her foot toward one of the locations. The dependent measure is which location the dog approaches first as the owner keeps his or her foot extended. Six trials are conducted.	4044	58	-0.00013	0.15	0.70
Cunning	The owner places a treat in front of the dog while verbally forbidding the dog from taking it. The dependent measure is the difference between the time it takes for the dog to take the treat while the owner is watching and while the owner is not watching. Six trials are conducted.	2710	44	-0.10	13.15	**<0.001***
Watching Condition		2711	44	0.33	9.98	**0.002***
Not Watching Condition		2753	44	0.43	17.94	**<0.001***
Memory vs. Pointing	The owner places a treat under one of two cups in full view of the dog, and then points to the other cup. The dependent measure is which cup the dog approaches first as the owner sustains pointing. Six trials are conducted.	2123	36	-0.0013	3.99	**0.046***
Memory vs. Smell	The owner places a treat under one of two cups in full view of the dog, and then blocks the dog's view while switching the treat to the other cup. The dependent measure is which cup the dog approaches first. Four trials are conducted.	1949	34	-0.00023	0.15	0.70
Delayed Memory	The owner places a treat under one of two cups in full view of the dog. The owner then waits 60, 90, 120, and 150 seconds across four trials before releasing the dog. The dependent measure is which cup the dog approaches first.	1888	34	0.0021	14.18	**<0.001***
Inferential Reasoning	The owner hides a treat under one of two cups and sham baits the other. The owner then lifts the incorrect cup to show that it is empty. The dependent measure is which cup the dog approaches first. Four trials are conducted.	1432	26	0.00011	0.03	0.87
Physical Reasoning	The owner places two sheets of folded paper flat on the ground, and hides a treat under one of them while the dog's view is blocked. The result is that the paper in the correct hiding location is propped up by the treat, while the other is not. The dependent measure is which hiding location the dog approaches first. Four trials are conducted.	1322	23	0.00042	0.30	0.59

111 **Table 1.** Descriptions of each cognitive task presented in the order in which they were conducted, the number of
112 individual dogs contributing data per task, the number of breeds represented in each task's analysis, and results from
113 mixed linear models (controlling for genetic relatedness) predicting cognitive performance from estimated brain weight
114 for each task. Significant p-values are denoted in bold.

115

116   **Figure 1**

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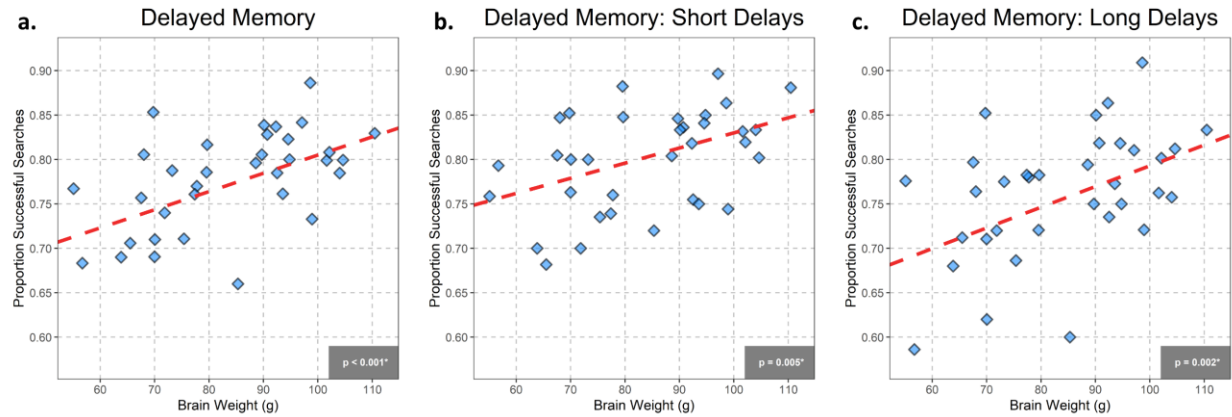
118   **Figure 1.** Scores on a measure of short-term memory (Delayed Memory) as a function of estimated absolute brain
119   weight across dog breeds. The dashed lines shows the regression slopes from statistical models controlling for genetic
120   relatedness between breeds **(a)** across all trials, **(b)** across short delays of 60 and 90 seconds, and **(c)** across long delays
121   of 120 and 150 seconds. Each breed included in the analyses had at least 20 individuals complete this task, and is
122   represented by one diamond.

123   **3. Results**

124   **(a) Absolute brain size predicts breed differences in executive function.** Based on previous

125   studies linking absolute brain size to executive function, we hypothesized that larger-brained

126   breeds would score higher on cognitive measures related to executive function. To test this

127   hypothesis, we fit mixed-models predicting breed-average scores on two tasks indexing

128   components of working memory (short-term memory) and of inhibitory control (self-control) as a

129   function of estimated absolute brain weight. These models revealed significant associations

130   between estimated brain weight and performance on both tasks (Table 1, Figure 1, Figure 2).

131   In the Delayed Memory task, larger-brained breeds correctly remembered the location of

132   hidden food at significantly higher levels than smaller-brained breeds when examining

133   performance after all delays lengths combined ($\beta = 0.0021$, $\chi^2(1) = 14.18$, $p < 0.001$; Figure 1a),

134   as well as after short (60s and 90s) and long (120s and 150s) delays (Short delays: $\beta = 0.0017$,

135    $\chi^2(1) = 7.91$, $p = 0.005$, Figure 1b; Long delays: $\beta = 0.0023$, $\chi^2(1) = 9.70$, $p = 0.001$, Figure 1c).

136   The slope of the association between estimated brain weight and performance was greater at long

137   delays than short delays, suggesting that the gap in performance between breeds of varying brain

138   size generally widens as a function of increased cognitive demands. The effect was weakest at 60

139   seconds ($\beta = 0.0014$, $\chi^2(1) = 2.84$, $p = 0.09$), but became significant as delay length increased (90s:

140    $\beta = 0.0020$, $\chi^2(1) = 6.99$, $p = 0.01$; 120s: $\beta = 0.0027$, $\chi^2(1) = 5.78$, $p = 0.02$; 150s: $\beta = 0.0020$, $\chi^2(1)$

141    $= 5.18$, $p = 0.02$).

142   In the Cunning task, dogs were prohibited from eating a visible food reward, and whether

143   the experimenter watched the dog varied across conditions. Although designed as a measure of

144   sensitivity to human perception, all conditions in this task pose demands on self-control, as dogs

145   were required to inhibit a desire to consume the visible food (see Müller and colleagues [2016] for

146   a similar measure assessing self-control in dogs). In this task, larger-brained breeds were

147   significantly slower to pilfer prohibited food placed directly in front of them than smaller-brained

148   breeds in a condition where a human's eyes were closed or back was turned (Not Watching),

149   compared to a condition where a human actively watched the subject (Watching; $\beta = -0.10$, $\chi^2(1)$

150    $= 13.15$, $p < 0.001$; Figure 2). Although greater self-control is likely required to inhibit the desire

151   to steal food when not being actively monitored, variation in perspective-taking ability may also

152   contribute to this effect, or smaller-brained breeds may simply be more likely to restrain their

153   actions while being monitored. Thus, we conducted separate analyses of the Watching and Not

154   Watching conditions for this task. In both conditions, larger-brained breeds exhibited greater self-

155   control by waiting significantly longer to eat the forbidden food ([Cunning] Watching: $\beta = 0.33$,

156    $\chi^2(1) = 9.98$, $p = 0.002$; [Cunning] Not Watching: $\beta = 0.43$, $\chi^2(1) = 17.94$, $p < 0.001$). Additionally,

157   the slope of the association between estimated brain weight and time to pilfer food was greater in

158   the Not Watching condition than in the Watching condition, supporting the idea that greater self-

159   control is required to resist temptation when not being actively monitored. Therefore, with

160   increased task difficulty in both the Cunning and Delayed Memory tasks, the slopes of the

161   associations between cognitive performance and brain size generally become more pronounced.

162   **Figure 2**

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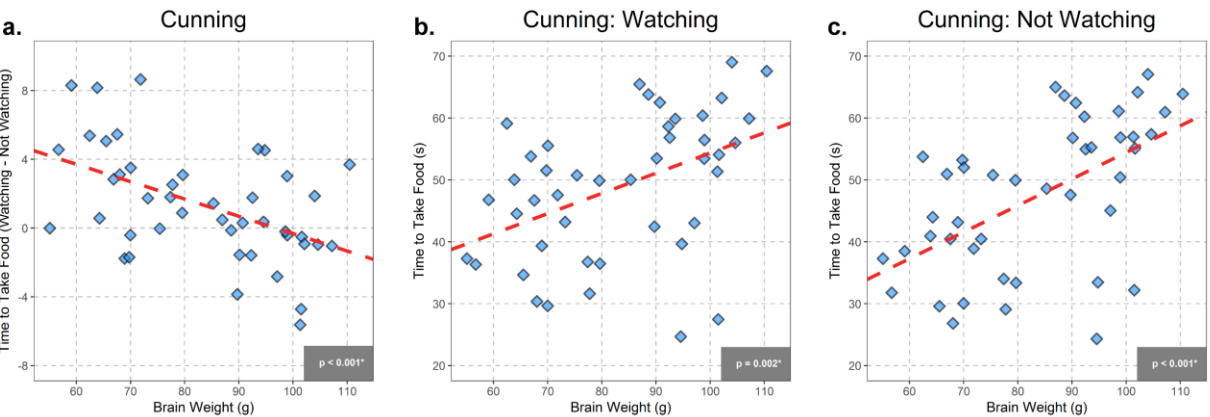
164   **Figure 2.** Difference scores between the Watching and Not Watching conditions in the Cunning task **(a)** and scores
165   on measures of self-control (**[b]** Cunning: Watching condition; **[c]** Cunning: Not Watching condition) as a function of
166   estimated brain weight across dog breeds. The dashed lines show the regression slopes from statistical models
167   controlling for genetic relatedness between breeds. Each breed included in the analyses had at least 20 individuals
168   complete this task, and is represented by one diamond.

169   **(b) Associations between brain size and cognition vary across cognitive domains.** A

170   fundamental question in the cognitive sciences is whether skills for solving diverse problems are

171   subserved by a common set of cognitive processes that are flexibly applied across contexts

172   (domain generality), or alternatively, by specialized processes that are differentially applied in

173   specific contexts (domain specificity). Due to the practical challenges of conducting cognitive

174   experiments with large samples of species, most previous studies investigating links between brain

175   volume and cognition used a small number of cognitive tasks, precluding assessment of the

176   specificity of associations between brain size and measures of cognition. To test the predictions of

177   the domain-general and domain-specific hypotheses, we investigated whether estimated brain

178   weight broadly predicts breed differences across diverse cognitive measures, or alternatively, if

179   these associations are limited to executive function.

180   Consistent with domain-specific hypotheses (Amici, Barney, Johnson, Call, & Aureli,

181   2012; MacLean et al., 2017), the relationship between estimated brain weight and breed

182   differences in cognition was highly variable across the ten cognitive measures (Table 1, Figure 3).

183   For 6 of the 10 tasks, there was no association between estimated brain weight and breed-average

184   performance ([contagious] Yawning: β = -0.00053, $\chi^2(1)$ = 1.19, p = 0.27; Eye Contact: β = -0.018,

185    $\chi^2(1)$ = 0.12, p = 0.73; Foot Pointing: β = -0.00013, $\chi^2(1)$ = 0.15, p = 0.70; Memory vs. Smell: β =

186   -0.00023, $\chi^2(1)$ = 0.15, p = 0.70; Inferential Reasoning: β = 0.00011, $\chi^2(1)$ = 0.03, p = 0.87;

187   Physical Reasoning [visual causality]: β = 0.00042, $\chi^2(1)$ = 0.30, p = 0.59). In addition to

188   significant associations between estimated brain weight and components of executive function,

189   larger-brained breeds were also significantly more likely to search for food in a location indicated

190   by an arm-pointing gesture (Arm Pointing: β = 0.00068, $\chi^2(1)$ = 4.18, p = 0.041), and were

191   significantly more likely to rely on this pointing gesture when it was pitted against their own

192   memory of where food had been hidden (Memory vs. Pointing: β = -0.0013, $\chi^2(1)$ = 3.99, p =

193   0.046).

194   To explore whether behavioral data were stable across trials within tasks significantly

195   associated with estimated brain weight, and whether any variation across time differed as a

196   function of estimated brain weight, we fit mixed-models predicting task performance from trial

197   number alone, as well as from a trial number by estimated brain weight interaction term. To

198   account for repeated measures, all models included a random intercept for breed. Trial number

199   alone was significant predictor of task performance in Cunning due to dogs pilfering forbidden

200   food significantly faster over the course of the trials in the Watching condition but not in the Not

201   Watching condition, as well as in Memory vs. Pointing such that dogs became less likely to follow

202   the pointing gesture over time (Online Resource 1). However, in no cases were there any

203   significant trial number by estimated brain weight interactions (Online Resource 1). The lack of

204   significant interactions between trial number and brain weight demonstrates that while

205   performance varied across trials in some measures, it did not vary differentially across breeds as a

206   function of brain weight. Therefore, the significant associations identified between estimated brain

207   weight and cognitive performance in our main analyses are unlikely to be due to differential

208   learning between small and large-brained breeds over the course of each task.

209   **Figure 3**

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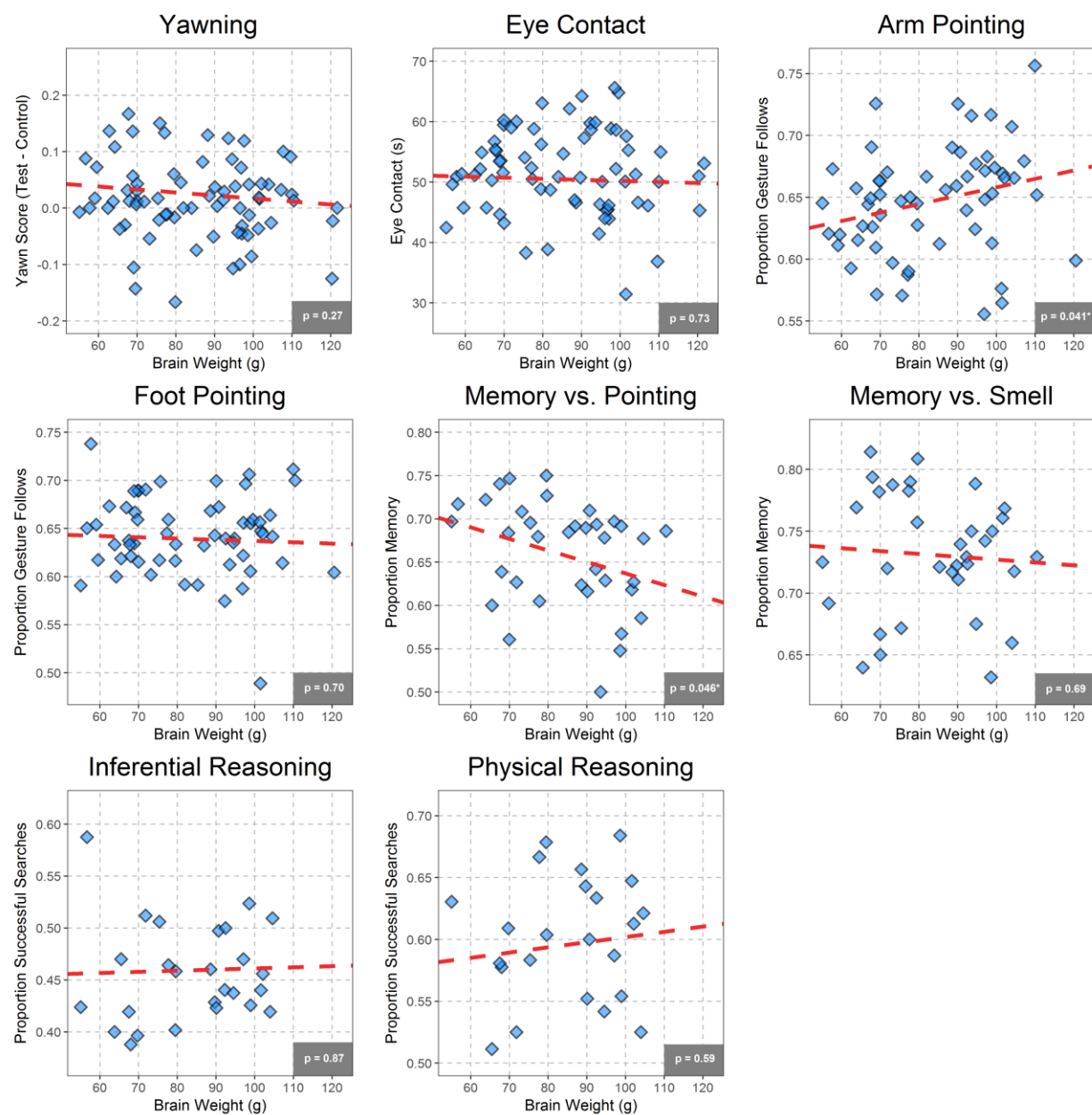
Figure 3. Scores on all cognitive tasks except Delayed Memory and Cunning (see Figure 1 and Figure 2) as a function of estimated brain weight across dog breeds. The dashed lines show the regression slopes from statistical models controlling for genetic relatedness between breeds. Each breed included in the analyses had at least 20 individuals complete a given task, and is represented by one diamond.

215   **(c) Individual-level analyses.** To examine how within-breed variation in cognition may influence

216   our results, we fit mixed-models predicting scores on each task as a function of breed-average

217   estimated brain weight on an individual level (Online Resource 1: Table 4). Results from these

218   individual-level analyses largely mirrored those from the main breed-level analyses: Estimated

219   brain weight was again a significant predictor of performance in each measure which primarily

220   indexed components of executive function (Delayed Memory: $\beta = 0.0015$, $\chi^2(1) = 11.06$, $p < 0.001$;

221   [Cunning] Watching: $\beta = 0.27$, $\chi^2(1) = 10.25$, $p = 0.001$; [Cunning] Not Watching: $\beta = 0.33$, $\chi^2(1)$

222    $= 15.34$, $p < 0.001$), as well as difference scores between conditions in the Cunning task ($\beta = -$

223   0.080, $\chi^2(1) = 13.40$, $p < 0.001$) and performance in Arm Pointing ($\beta = 0.00068$, $\chi^2(1) = 6.51$, $p =$

224   0.01). However, unlike results from the breed-level analyses, the association between estimated

225   brain weight and performance in Memory vs. Pointing fell slightly above the significance threshold

226   ($\beta = -0.0011$, $\chi^2(1) = 3.64$, $p = 0.056$), while a significant association emerged between estimated

227   brain weight and performance in Physical Reasoning ($\beta = 0.00092$, $\chi^2(1) = 4.00$, $p = 0.045$).

228   **(d) Body size.** As breed-average brain weights were estimated from breed-average body weights

229   in our main analyses, we expected to find many similar associations between cognition and body

230   size. Mixed-models predicting task scores as a function of CBARQ-reported breed-average body

231   weight generally revealed the same pattern of results as those using breed-average estimated brain

232   weight as the predictor; body weight was a significant predictor of performance in Delayed

233   Memory, Cunning, and the Watching and Not Watching conditions analyzed separately, but

234   associations between body weight and Arm Pointing ($p = 0.07$) and Memory vs. Pointing ($p =$

235   0.06) fell slightly above the significance threshold (Online Resource 1). In the majority of cases,

236   linear models using estimated brain weight as the predictor had a lower AIC and explained a larger

237   proportion of the variance in cognitive measures as compared to models using body weight as the

14

238   predictor, but differences in AIC and adjusted R^2 were generally small (Online Resource 1). Even

239   in studies using more direct measures of brain size rather than estimation, the challenge of

240   disentangling associations with absolute brain size and body size is evident as the two variables

241   are often very highly correlated (MacLean et al., 2014).

242   To explore whether the same associations between cognition and brain size would emerge

243   when estimating breed-average brain weight independently from body weight, we compiled breed-

244   average skull measurements from Boyko et al. (2010) for a subset of breeds (n = 27) for whom

245   data was available. To assess which skull measures best predicted brain weight, we first fit a

246   multiple regression model predicting known breed-average brain weights from Bronson (1979)

247   using breeds for which both skull measurements and brain weights were available (n = 12) as a

248   function of cranial depth, maximum cranial width, and least cranial width. As results from this

249   model showed that only cranial depth was a significant predictor of brain weight controlling for

250   the other predictors, we next fit a simple linear regression model predicting brain weight from

251   cranial depth alone. Breed-average cranial depth explained a greater proportion of the variance in

252   brain weight and had a lower model AIC ($\beta = 0.01$, $F(1, 10) = 119.4$, $p < 0.001$, adjusted $R^2 =$

253   0.92, AIC = 82.13) than did CBARQ-reported breed-average body weight in this same subset (β

254    $= 1.03$, $F(1, 10) = 62.83$, $p < 0.001$, adjusted $R^2 = 0.85$, AIC = 89.03), suggesting that cranial depth

255   was a better predictor of brain weight than body weight in this sample. We then used cranial depth

256   to predict breed-average brain weight across the 27 breeds for which cognitive data and skull

257   measurements were available. Lastly, we fit mixed-models (controlling for genetic relatedness

258   between breeds) predicting scores on each cognitive task as a function these new brain weight

259   estimates. Breed-average brain weight estimated from cranial depth significantly predicted

260   performance in each measure which primarily indexed components of executive function (Delayed

261   Memory: $\beta = 0.0014$, $\chi^2(1) = 4.91$, $p = 0.03$; [Cunning] Watching: $\beta = 0.43$, $\chi^2(1) = 4.51$, $p = 0.03$;

262   [Cunning] Not Watching: $\beta = 0.49$, $\chi^2(1) = 6.72$, $p = 0.01$), but did not significantly predict

263   performance in Arm Pointing ($\beta = -0.0002$, $\chi^2(1) = 0.09$, $p = 0.76$), Memory vs. Pointing ($\beta =$

264   0.0002, $\chi^2(1) = 0.02$, $p = 0.89$), or difference scores between conditions in the Cunning task ($\beta = -$

265   0.06, $\chi^2(1) = 0.69$, $p = 0.41$). Therefore, estimates of breed-average brain weight derived

266   independently of breed-average body weight were significantly associated with measures of short-

267   term memory and self-control, but not other cognitive measures.

268   The findings above reveal a range of associations between estimated brain weight and

269   breed differences in cognition. However, it remains possible that additional factors, which covary

270   with body weight and brain weight, may partially account for these associations. To address this

271   possibility, we conducted additional analyses with potentially confounding variables.

272   **(e) Perceptual factors.** Previous studies suggest that skull shape is associated with aspects of

273   visual perception in dogs. Specifically, brachycephalic dogs (defined by a high cephalic index

274   (CI), see Online Resource 1) are characterized by more forward-facing eyes and greater ocular

275   overlap (Gácsi, McGreevy, Kara, & Miklósi, 2009; Helton & Helton, 2010). Gácsi et al. (2009)

276   found that brachycephalic breeds were significantly better at following human pointing cues as

277   compared to dolichocephalic breeds (low CI), and suggested that this result may be partially

278   attributable to breed differences in visual perception. Our sample contained 50 breeds for which

279   CI measurements were reported in (McGreevy et al., 2013) or (Boyko et al., 2010), and in these

280   breeds, CI was significantly negatively correlated with estimated brain weight ($r = -0.43$, $p =$

281   0.002). Thus, explanations invoking breed differences in vision yield predictions opposite to what

282   we observed in measures of short-term memory, self-control, and gesture following. Indeed, in

283   breeds for which both cognitive and CI data were available, CI was significantly negatively

284   correlated with performance in measures of short-term memory and self-control (Delayed

285   Memory: r = -0.47, p = 0.02; [Cunning] Watching: r = -0.41, p = 0.02; [Cunning] Not Watching:

286   r = -0.52, p = 0.002), and was not significantly correlated with measures of gesture following (Arm

287   Pointing: r = -0.19, p = 0.24; Memory vs. Pointing: r = -0.04, p = 0.85). Additionally, because we

288   do not find consistent relationships between estimated brain weight and cognitive performance

289   across tasks incorporating highly similar experimental set-ups and identical stimulus presentation

290   distances, it is highly unlikely that breed differences in vision play a large role in the relationships

291   we observed.

292   **(f) Training history.** A second important consideration relates to possible effects of training

293   history on these cognitive measures. Using questionnaire data submitted to *Dognition.com*, we

294   found that breeds with larger brains were more likely to have attended at least one obedience class

295   (r = 0.71, p < 0.001), and were more likely to have been extensively trained (r = 0.75, p = 0.01).

296   Although this information was not available for the majority of our subjects (precluding inclusion

297   as a covariate in the main breed-level analyses), we fit mixed-models predicting scores on each

298   task as a function of breed-average estimated brain weight and owner-reported extent of training

299   history on an individual level including dogs for which both measures were available (Table 2).

300   These analyses revealed that controlling for training history, estimated brain weight was a

301   significant predictor of performance in each measure which primarily indexed components of

302   executive function (Delayed Memory: β = 0.0015, $\chi^2(1)$ = 4.22, p = 0.40; [Cunning] Watching: β

303   = 0.35, $\chi^2(1)$ = 12.95, p < 0.001; [Cunning] Not Watching: β = 0.38, $\chi^2(1)$ = 17.93, p < 0.001), but

304   was not a significant predictor of performance in any other measures (Yawning: β = -0.00043,

305    $\chi^2(1)$ = 0.21, p = 0.64; Eye Contact: β = -0.068, $\chi^2(1)$ = 1.17, p = 0.28; Arm Pointing: β = 0.00056,

306    $\chi^2(1)$ = 1.78, p = 0.18; Foot Pointing: β = -0.00020, $\chi^2(1)$ = 0.17, p = 0.68; Cunning: β = -0.028,

307      $\chi^2(1) = 0.25$, p = 0.62; Memory vs. Pointing: β = -0.00095, $\chi^2(1) = 0.91$, p = 0.34; Memory vs.

308   Smell: β = -0.00021, $\chi^2(1) = 0.078$, p = 0.78; Inferential Reasoning: β = 0.00082, $\chi^2(1) = 1.17$, p =

309   0.28; Physical Reasoning: β = 0.0011, $\chi^2(1) = 2.42$, p = 0.12). Therefore, as in the breed-level

310   analyses, estimated brain weight was a significant predictor of performance on measures of short-

311   term memory and self-control, even after controlling for training history on an individual level.

312   However, unlike results from the main breed-level analyses (but mirroring the pattern of results

313   obtained using cranial depth rather than body weight to estimate brain weight in a subset of our

314   sample), estimated brain weight was not a significant predictor of difference scores between

315   conditions in the Cunning task or of reliance on gesture following in Arm Pointing or Memory vs.

316   Pointing after controlling for training history. We also found that controlling for estimated brain

317   weight, training history was a significant predictor of performance in the Watching (β = 8.67, $\chi^2(1)$

318   = 31.08, p < 0.001) and Not Watching (β = 8.55, $\chi^2(1) = 30.02$, p < 0.001) conditions of the

319   Cunning task, as well as in Eye Contact (β = 3.60, $\chi^2(1) = 15.87$, p < 0.001), Arm Pointing (β =

320   0.024, $\chi^2(1) = 8.18$, p = 0.004), Memory vs. Pointing (β = -0.041, $\chi^2(1) = 5.94$, p = 0.015), and

321   Inferential Reasoning (β = 0.029, $\chi^2(1) = 3.96$, p = 0.047), but was not a significant predictor of

322   performance in the six remaining measures (Yawning: β = -0.018, $\chi^2(1) = 0.95$, p = 0.33; Foot

323   Pointing: β = 0.0097, $\chi^2(1) = 1.11$, p = 0.29; Cunning: β =0.35, $\chi^2(1) = 0.16$, p = 0.69; Memory vs.

324   Smell: β = -0.027, $\chi^2(1) = 3.55$, p = 0.059; Delayed Memory: β = 0.026, $\chi^2(1) = 3.46$, p = 0.063;

325   Physical Reasoning: β = 0.18, $\chi^2(1) = 1.71$, p = 0.19). It is important to note that in measures of

326   self-control (Watching and Not Watching conditions of Cunning), both estimated brain weight and

327   training history made independent significant contributions to task performance, the latter of which

328   is unsurprising given that owners verbally forbid subjects from taking visible food (a commonly

329   trained command) as a part of the task.

330   **Table 2**

Task	n	Estimated Brain Weight			Training History		
		β	χ²	p	β	χ²	p
Yawning	1567	-0.00043	0.21	0.64	-0.018	0.95	0.33
Eye Contact	1452	-0.068	1.17	0.28	3.60	15.87	**<0.001***
Arm Pointing	1145	0.00056	1.78	0.18	0.024	8.18	**0.004***
Foot Pointing	1102	-0.00020	0.17	0.68	0.0097	1.11	0.29
Cunning	905	-0.028	0.25	0.62	0.35	0.16	0.69
Watching Condition	905	0.35	12.95	**<0.001***	8.67	31.08	**<0.001***
Not Watching Condition	917	0.38	17.93	<0.001*	8.55	30.02	**<0.001***
Memory vs. Pointing	793	-0.00095	0.91	0.34	-0.041	5.94	**0.015***
Memory vs. Smell	749	-0.00021	0.078	0.78	-0.027	3.55	0.059
Delayed Memory	726	0.0015	4.22	**0.040***	0.026	3.46	0.063
Inferential Reasoning	632	0.00082	1.17	0.28	0.029	3.96	**0.047***
Physical Reasoning	608	0.0011	2.42	0.12	0.18	1.71	0.19

331   **Table 2.** Results from mixed linear models (controlling for breed-level genetic relatedness) predicting cognitive
332   performance from breed-average estimated brain weight and owner-reported training history for each task on an
333   individual level. The training history variable was derived from a questionnaire item asking owners, "How much
334   training has your dog received?" Owners responded on an ordinal scale including "None," "Little," "Some," and
335   "Substantial" as response options. Significant p-values are denoted in bold.

336   **(g) Functional breed group classification.** A third consideration is that modern dog breeds have

337   been selected for a variety of functional roles, with some roles (e.g. hunting and herding) requiring

338   extensive cooperation with humans (Coppinger & Schneider, 1995). Previous studies suggest that

339   dogs bred for cooperative roles may be more likely to follow human gestures (Udell, Ewald, Dorey,

340   & Wynne, 2014; Wobber, Hare, Koler-Matznick, Wrangham, & Tomasello, 2009). Thus, to

341   control for potential effects of breed group, we fit models including American Kennel Club (AKC)

342   breed group designation and estimated absolute brain weight as predictors of performance. For the

343   Memory vs. Pointing task, but none of the other measures significantly associated with estimated

344   brain weight in the main analyses, a log likelihood ratio test revealed that controlling for brain

345   weight, breed group was a significant predictor of performance ($\chi^2(6) = 1.35$, $p = 0.03$) but not

346   vice-versa ($\chi^2(1) = 0.04$, $p = 0.15$). AKC-classified "Sporting" and "Working" breeds were the

347   most likely to follow an arm-pointing gesture in this task (Sporting: mean = 0.60, SEM = 0.02;

348   Working: mean = 0.63, SEM = 0.02), while breeds in the "Terrier" and "Herding" groups were the

349   least likely (Terrier: mean = 0.70, SEM = 0.01; Herding: mean = 0.69, SEM = 0.01). While

350   increased tendencies to follow an arm-pointing gesture over memory in the Memory vs. Pointing

351   task may be better explained by differences in AKC breed group than by differences in brain size,

352   we find only mixed support for the idea that selection for cooperative roles is primarily responsible

353   for this result, as breeds belonging to the Herding group were among the least likely to follow

354   gestures in this task.

355   **4. Discussion**

356   Our findings support the hypothesis that increases in absolute brain size are associated with

357   aspects of executive function, even in the absence of primate-like neuroanatomy. This result raises

358   new questions about the cognitive consequences of evolutionary changes in brain size, and

359   suggests that even within a species, brain size is associated with some aspects of cognition. By

360   investigating intraspecific variance in a species characterized by high levels of morphological

361   diversity, this study circumvents some challenges inherent to previous interspecific comparisons.

362   Specifically, across species, differences in absolute brain volume can be confounded with changes

363   in the relative proportions of specific brain regions. This phenomenon can arise both due to

364   specialization of specific brain structures (mosaic brain evolution [Barton & Harvey, 2000; Barton

365   & Venditti, 2014; Gould et al., 2013]) resulting from heterogeneity in selection pressures on

366   neuroanatomical variation across taxa (Logan et al., 2018), or due to conserved developmental

367   processes involving the timing of neurogenesis, which yield disproportionate enlargement of late

368   developing structures (e.g. the neocortex) in larger-brained taxa (Finlay & Darlington, 1995; Kaas,

369   2000). Regarding the latter possibility, there are currently few data on the development of brain

370   structures in dogs, but preliminary data suggest that breed differences in brain volume are less

371   subject to these conserved developmental constraints which induce allometry (deviation from 1:1

372   scaling) between total brain volume and specific regions of the brain. Specifically, in contrast to

373   comparative mammalian samples, imaging studies have shown that there are no significant

374   differences in the proportional sizes of the cerebellum, forebrain, or brainstem across dog breeds

375   with widely varying total brain volumes (Thames et al., 2009), or in absolute size of the olfactory

376   lobe across breeds with widely varying skull shapes (Roberts et al., 2010). This finding is

377   consistent with the notion that allometric relationships which apply across species often do not

378   hold within species (Armstrong, 1990), leading researchers to suggest that the extraordinary

379   morphological variation of dogs makes this species an ideal candidate for investigating

380   intraspecific brain scaling and the cognitive implications thereof (Jardim-Messeder et al., 2017).

381   Importantly, even with a lack of isometric (i.e. 1:1) scaling between brain volume and the

382   number of neurons in the brain, larger dog brains are still expected to contain more neurons than

383   smaller dog brains. In the only comparison of dog neuron counts to date, Jardim-Messeder and

384   colleagues found that the cortex of a golden retriever with a body weight of 32kg contained 627

385   million neurons, while the cortex of an unknown breed with a body weight of 7.45kg contained

386   429 million neurons (Jardim-Messeder et al., 2017). Thus, if the number of neurons in the brain is

387   expected to predict taxonomic differences in executive function (Herculano-Houzel, 2017), our

388   findings are consistent with this hypothesis. However, because increases in volume are expected

389   to result in the addition of many fewer neurons in dog brains than primate brains, we would

390   theoretically expect differences in the slope of the relationship between brain volume and measures

391   of executive function between these taxonomic groups given adequate control of extraneous

392   variables.

393   A second major finding from this study is that the relationship between estimated brain

394   weight and breed differences in cognition varied widely across cognitive tasks. For example, we

395   found only limited evidence for an association between estimated brain weight and reasoning about

396   causal properties of the world, and no evidence for an association between estimated brain weight

397   and inferential reasoning, use of a novel communicative gesture (foot pointing), or measures of

398   eye contact with a human. After controlling for training history at an individual level, we also

399   found no evidence for an association between estimated brain weight and reliance on following

400   communicative pointing cues to locate food. This result supports domain-specific accounts of

401   cognition, and is consistent with previous comparative studies which have revealed links between

402   brain volume and executive function, but no association between brain volume and other domains

403   of cognition (MacLean et al., 2013). As suggested by domain specificity, absolute brain size is

404   therefore unlikely to be an informative predictor of all cognitive abilities. However, absolute brain

405   size may be particularly important for executive function, because these processes exert high-level

406   'supervisory' control over a variety of more specialized cognitive functions. Additionally, these

407   results suggest that the significant associations between estimated brain weight and measures of

408   executive function are unlikely to be artifacts of breed differences in motivation or perception, in

409   which case we would have expected similar associations for all tasks involving a search for food,

410   or requiring attention to visual stimuli in the frontal field.

411   One limitation of this study stems from the lack of individual-level brain weight data from

412   the dogs in our sample. While the scaling function used to estimate breed-average brain weights

413   described by Bronson (1979) explained an overwhelming proportion of the variance in brain

414   weight (93%) in Bronson's sample (26 breeds ranging from 3.6kg to 55.0kg in body weight), and

415   a comparable percentage (91%) when using C-BARQ breed-average body weight as a predictor,

416 we cannot rule out the possibility that brain-to-body size scaling in breeds absent from Bronson's

417 sample deviate from the scaling relationship used in our estimates. However, while estimates of

418 brain weight based on body weight are subject to prediction error, the effects of this error are

419 minimized in comparisons of taxa characterized by large differences in body size. Given the over

420 17-fold variation in body weight across breeds in our sample (range: 3.35kg – 59.75kg), and

421 confirmation of a strong link between body and brain weight in dogs (Bronson, 1979), it is highly

422 unlikely that prediction error substantially influenced our results. As expected given the strong

423 association between body and brain weight, the observed associations between cognition and

424 estimated absolute brain size are generally the same as those that exist between cognition and body

425 weight in our sample. However, we found the same links between absolute brain size and executive

426 function in a subset of our sample using brain weight estimated from skull measurements, rather

427 than body weight. Relatedly, the exact intraspecific neural scaling rules of dog brains remain

428 unknown, but it is of note that the two individuals examined in (Jardim-Messeder et al., 2017) fit

429 the interspecific neural scaling rules that apply across non-primate mammals. Future work can

430 address these limitations by examining how differences in cognition relate to variation in brain

431 size and neuron count on an individual level both within and across dog breeds. Similarly, without

432 independent measures of brain and body mass, we were unable to explore possible associations

433 between relative brain size and performance on the cognitive tasks.

434   In conclusion, our findings suggest that evolutionary relationships between executive

435 function and absolute brain size do not require primate-like neural scaling rules, that these

436 relationships may be independent of changes in the relative sizes of specific areas of the brain, and

437 that associations between brain size and cognition vary across cognitive domains. These findings

438 raise new questions about how evolutionary shifts in brain size influence cognition across taxa,

439   and suggest that dog breeds provide a powerful and highly tractable model for assessing the

440   cognitive consequences of neuroanatomical variation among close genetic relatives.

446   **Competing Interests**

447   BH is a founder of *Dognition.com* and a member of its Scientific Advisory Board. JC, JK,

448   and ÁM are also members of the *Dognition.com* Scientific Advisory Board.

449   **Author Contributions**

450   BH, JC, JK, ÁM, and ELM conceived and designed the experiments. DJH and ELM

451   analyzed the data. DJH, BH, JC, JK, ÁM, and ELM wrote the paper.

452   **Data Accessibility**

453   Data are available as electronic supplementary material.

458   **Compliance with Ethical Standards**

459   All animals included in this study were pet dogs tested by citizen scientists in their own

460   homes. The use of third party data from *Dognition.com* was approved by Duke University

461   IACUC protocol A138-11-06 and data were collected in accordance with relevant guidelines and

462   regulations.

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