

1 **Title: A farewell to EQ: A new brain size measure for comparative primate cognition**

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17

18 **Abstract**

19 Both absolute and relative brain size vary greatly among and within the major vertebrate
20 lineages. Scientists have long debated how larger brains in primates and hominins translate
21 into greater cognitive performance, and in particular how to control for the relationship
22 between the non-cognitive functions of the brain and body size. One solution to this
23 problem is to establish the slope of cognitive equivalence, that is the line connecting
24 organisms with an identical bauplan but different body sizes. Here, we suggest that
25 intraspecific slopes provide the best available estimate of this measure. This approach was
26 abandoned because slopes were too low by an unknown margin due to estimation error. We
27 control for the error problem by focusing on highly dimorphic primate species with large
28 sample sizes and fitting a line through the mean values for adult females and males. We
29 obtain the best estimate for the slope of ca 0.27, a value much lower than those constructed
30 using all mammal species, and close to the value expected based on the genetic correlation
31 between brain size and body size. We also find that the estimate of cognitive brain size
32 based on cognitive equivalence fits empirical cognitive studies better than the
33 encephalization quotient (EQ), which should therefore be avoided in future studies on
34 primates, and presumably mammals and birds in general. The use of residuals from the line
35 of cognitive equivalence may change conclusions concerning the cognitive abilities of
36 extant and extinct primate species, including hominins.

37

38 **Keywords:** encephalization quotient; cognitive equivalence; intelligence; mammals;
39 hominins

40

41 **Introduction**

42 Although recent ecological approaches to comparative cognition have focused on linking
43 performance in specific cognitive tasks to specific brain regions [e.g. Healy & Krebs 1996],
44 traditionally comparative cognition has relied on a presumed link between some summary
45 measure of cognitive performance and total brain size [Jerison 1973]. Scholars have
46 therefore long been searching for a neuroanatomical measure of overall cognitive ability,
47 both to compare living species and to estimate the cognitive abilities of extinct ones relative
48 to their extant relatives. The most intuitive measure is a species' brain size (or, especially for
49 extinct species, the highly similar cranial capacity: Isler et al. 2008). However, because
50 brains also control numerous non-cognitive somatic functions, most researchers have
51 agreed it cannot be used without controlling for these somatic functions.

52 Building on a century-long tradition, Jerison [1973] distinguished between the
53 somatic and the cognitive brain functions and proposed we can estimate the portion of the
54 brain dedicated to somatic functions, and so by subtraction arrive at the size of the
55 cognitive portion. Jerison fitted regression equations to the brain size-body size data of all
56 available species in many different mammalian lineages. Because this produced a
57 regression a slope close to 0.67 in a log-log plot, he interpreted this as reflecting a
58 fundamental physiological regularity linking brain size to the body's surface area and thus
59 the amount of proprioceptive inputs. This slope could therefore serve as the expected value
60 of the somatic portion of the brain, and the deviation from the regression line as the
61 estimate of the cognitive portion, i.e. cognitive brain size. Jerison then proposed the
62 encephalization quotient (EQ), the ratio of a species' actual brain size to its predicted brain
63 size based on the clade-specific brain-body regression line, to capture its relative cognitive

64 performance. The EQ has become a commonly used estimate of the cognitive abilities or
65 intelligence of animal species. Other researchers have argued the slope is actually
66 somewhat higher, linking it to metabolic turnover instead, and thus suggesting a slope of
67 0.75 [Martin 1981; Armstrong 1983], but did not question the fundamental EQ approach.

68 Most research on basic relationships between brain size, body size and cognitive
69 performance has been conducted on mammals, and in particular primates. This research
70 has produced various lines of evidence argue against the EQ approach. First, its use assumes
71 that there is no correlation between body size and cognitive performance, but in practice
72 there is a negative correlation between EQ and body size within mammalian orders (see
73 below). We should therefore see that bigger mammal species show poorer cognitive
74 performance than smaller relatives in the same order. However, the opposite appears to be
75 the case [Rensch 1973], suggesting a lower value of the slope. Second, a lower slope would
76 also be expected given the combined effect of two persistent macro-evolutionary trends: (i)
77 brains have increased relative to body size, a phenomenon we can call the Lartet-Marsh rule
78 [Jerison 1973], and (ii) body size did increase as well, a phenomenon known as Cope's rule
79 [Alroy 1998]. As a result, more recently evolved lineages will tend to have both larger body
80 sizes and a larger brain sizes [e.g. Halley & Deacon 2017], which artificially inflates the slope
81 of the regression through the total sample. Third, different mammalian lineages
82 unexpectedly show different regression slopes of brain size on body size [Martin & Harvey
83 1985].

84 These inconsistencies reveal the fundamental flaw in the EQ approach [Deacon
85 1990; Striedter 2005]: it assumes that one process (be it proprioception or metabolic
86 turnover) predominates in determining brain size to the extent that cognitive functions
87 produce only minor deviations, so we can estimate their strength by taking ratios or
88 residuals. Instead, we may expect a variety of processes to affect brain size, some of them
89 lineage-specific, and each potentially varying in strength across lineages. Nonetheless, EQs
90 continue to be used to compare mammalian taxa [e.g. Boddy et al. 2012], especially extinct
91 ones [e.g. Grabowski et al. 2016; Benoit et al. 2019].

92 Although EQ approaches are inadequate, no universally accepted alternative has
93 emerged. A major reason is that the notion of overall cognitive ability or performance
94 remained vague, making it harder to produce an alternative measure. In fact, modern
95 behavioral ecology generally assumes animals have bundles of domain-specific cognitive
96 adaptations [Shettleworth 2010]. Consequently, "overall" cognitive performance does not
97 exist and overall brain size does not necessarily provide any useful information when it
98 comes to understanding the animal's ecological niche or social organization. Instead,
99 researchers relate the relative size of specific brain regions to specific cognitive challenges
100 to look for patterns at that level in large comparative surveys. Examples include seed
101 caching and recovery [Healy & Krebs 1996; Garamszegi & Eens 2004] or the incidence of
102 feeding innovations [Timmermans et al. 2000] in birds.

103 Recently, however, brain size has regained standing as a relevant variable. First,
104 along with the unquestioned selective increase or decrease of certain brain parts in
105 response to specific pressures [Barton & Harvey 2000], mammalian brains are also
106 organized in fundamentally similar ways across animals of varying sizes, even across
107 lineages, with predictable allometric relationships among the sizes of the various brain
108 regions [Finlay & Darlington 1995; Finlay et al. 2001]. Indeed, many cognitive activities
109 correspond to concerted activity waves throughout the brain rather than being tied to one

110 particular region [Park & Friston 2013], suggesting that a decrease or increase in one
111 particular region under selection will affect the sizes of other parts and thus also the size of
112 the whole brain [Barton 2006]. Second, an important consequence of cognitive abilities that
113 tie together many brain regions is domain-general intelligence [Burkart et al. 2017]. This
114 concept has historically been applied mainly to humans, and many, implicitly or explicitly,
115 still consider it to be uniquely human. There is now mounting evidence, however, that at
116 least among various mammals [Burkart et al. 2017] and birds [Ashton et al. 2018], domain-
117 general intelligence can be recognized within species, and that different species vary
118 considerably in the strength of this domain-general ability [Deaner et al. 2006; Reader et al.
119 2011]. The latter finding allows empirical tests of the predictive value of EQs or conceptually
120 similar residuals. Broad comparative analyses of estimated domain-general cognitive
121 abilities have shown that EQ is a poor predictor of these abilities [Deaner et al. 2007; Reader
122 et al. 2011], and more limited analyses reached the same conclusion [Alba 2010; Rumbaugh
123 et al. 1996]. Moreover, as noted above, most large-bodied species have greater cognitive
124 abilities than expected based on their EQ values [Rensch 1973], which tend to decrease with
125 body size within orders. In conclusion, these more direct, cognition-based tests of EQ-based
126 approaches confirm that they do not predict cognitive abilities.

127

128 *Non-EQ approaches*

129 These conceptual and empirical problems with EQ measures indicate that we need
130 to control for body size in a different way. Some scholars have suggested that no control is
131 needed at all [e.g. Rensch 1973; Striedter 2005; Byrne 1995], but most accept that the
132 regulation of somatic functions requires at least some brain resources that are not also
133 available for cognitive functions. Two main alternatives have been proposed. The first set of
134 techniques is similar to the EQ approach, as it relies on broad interspecific comparisons.
135 Portmann [1946, 1947] proposed that Galliformes are the most primitive birds and
136 deviations from their interspecific regression equation should be used to estimate
137 encephalization. Stephan [1960] proposed the same procedure for mammals, using the
138 "basal insectivores" as the baseline. This produces a "progression index" for each species.
139 However, due to various conceptual and statistical problems [Deacon 1990] it has found
140 little application. This index also predicts primate cognitive performance only marginally
141 better than EQ and far worse than brain size per se [Gibson et al. 2001; Deaner et al. 2007],
142 although it is unknown how well it does for other mammals or birds.

143 Another interspecific approach uses ratios of different brain regions, assuming that
144 one, the numerator, is responsible for the brain's cognitive functions, and the other, the
145 denominator, is responsible for its somatic functions [Krompecher & Lipák 1966;
146 Passingham 1982]. This ratio then estimates the development of cognitive functions
147 relative to expectation. The most popular measure is the Neocortex Ratio, the size of the
148 neocortex relative to the rest of the brain [Dunbar 1992]. However, all ratio measures have
149 the fundamental drawback that they lack a clear neurobiological justification [Deacon 1990;
150 Deaner et al. 2000; Barton 2006], and the neocortex ratio was favored simply because it
151 yielded the best correlation with the putative selective pressure [Dunbar 1992]. Like most
152 other ratios, the neocortex ratio is clearly correlated with both overall brain and body size,
153 as expected based on the fundamental brain allometries [Finlay & Darlington 2001; Halley &
154 Deacon 2017]. Thus, its use depends entirely on the goodness of the fit with presumed
155 selective pressures, risking circularity. If this fit varies across taxa, we cannot tell whether a

156 poor fit reflects an imperfect neuroanatomical measure or different selective environments
157 [Stout 2018]. Moreover, the neocortex ratio does not differentiate between monkeys and
158 apes, which are known to differ in cognitive performance [Gibson et al. 2001]. Also, it does
159 not always predict actual cognitive performance in the primate sample as strongly as other
160 measures when we control for phylogenetic non-independence [e.g., Deaner et al. 2007].
161 We will therefore not further consider ratio measures (but see discussion).

162

163 *The slope of cognitive equivalence*

164 The aim of this paper is to revisit the main remaining alternative: estimating the
165 slope of cognitive equivalence. Its logic works as follows. We assume (1) that the cognitive
166 performance of adult individuals within a species does not depend on their body size, and
167 (2) that the intraspecific relationship between body size and brain size among adults
168 estimates the extra amount of brain tissue required to sustain the additional somatic
169 functions in larger individuals because there are no changes in bauplan and sensory-motor
170 abilities. Therefore, assuming that intraspecific variation in adult size is based on selection
171 on body size alone, the regression of brain size on body size should give us the slope of
172 cognitive equivalence. If analyses conducted on a range of species converge on a similar
173 slope, the cognitive brain size of a species can then be estimated as the residual of the
174 actual brain size of that species from a general line with that slope and some informative
175 intercept.

176 This is not a new idea. Many estimates of this slope from samples of conspecific
177 individuals of known body and brain mass have been made in the past. However, they vary
178 considerably. Summarizing previous work, Pilbeam & Gould [1974] noted values between
179 0.2 and 0.4. The range for individual mammal species with larger samples was somewhat
180 tighter, with average values between 0.23 and 0.25 (e.g. Hemmer 1971; Röhrs 1986) for
181 large intraspecific samples, but a median of 0.14 for primates [Martin & Harvey 1985] and
182 0.15 in a large recent analysis of birds and mammals [Tsuboi et al. 2018]. This considerable
183 variability exists because empirical slopes within species are usually underestimated [Pagel
184 & Harvey 1988] by varying margins. Thus, if we can remove this source of error, the this
185 measure's utility could be restored.

186 The variability in slope estimates can be explained as follows. The equation for the
187 slope of a regression is [Lande 1985]:

$$\text{Slope}(y, x) = \text{Corr}(y, x) \times \frac{\sigma(y)}{\sigma(x)}$$

188 where $\text{corr}(y, x)$ is the correlation between x and y , and σ is the standard deviation. Because
189 virtually all mammals show determinate growth, there is little variation in body and brain
190 size. As a result, variation due to measurement error can greatly affect the estimated slope
191 of the brain-body relation within a set of adults. We usually estimate the independent
192 variable, body size, by taking body mass, but there are good reasons to assume that this
193 estimate varies considerably due to error, even within individuals. In contrast, the response
194 variable, brain mass or endocranial volume (our estimate for brain size), varies far less. First,
195 during periods of starvation, brains continue to receive the same energy flow as during
196 times of plenty, whereas the rest of the body must make do with less. This phenomenon is
197 known as brain sparing [Wells 2010], resulting in a tiny reduction of brain mass and a
198 massive reduction in body mass. Second, during times of plenty, the body accumulates fat,
199 whereas the brain does not. Seasonal variation in body mass may therefore greatly exceed

200 the one in brain mass, except for a small number of species with seasonal variation in brain
201 mass [Dechmann et al. 2017]. Third, among females body mass varies across the
202 reproductive cycle, with higher values during pregnancy and lower values toward the end of
203 lactation. Finally, captivity, too, can increase differences in body weight between wild and
204 captive specimens, especially in slow-growing species [e.g. Isler et al. 2008; Leigh 1994].
205 Due to these various processes, variance in body mass at a given size can be up to four times
206 as high as in brain mass [Pagel & Harvey 1989], and the slope will inevitably be
207 underestimated, potentially by up to a factor two. To reduce this erroneous reduction in the
208 slope estimate, we should include a greater range of intraspecific body sizes in the analysis,
209 reduce the error in the estimation of each point by taking averages where possible, and use
210 only wild specimens.

211 One seemingly obvious way to achieve this is to use the means of higher units
212 (species, genera, families) as data points. This does indeed produce steeper slopes [Martin &
213 Harvey 1985]. However, while this so-called taxon-level effect is partly due to the reduction
214 of noise due to varying body mass, it also reflects the combined Cope-Marsh effects noted
215 above, which will also produce higher slopes for families and orders [Jerison 1973; Rowe et
216 al. 2011]. Therefore, because we cannot disentangle this taxon-level effect and the
217 estimation error effect, slopes obtained among related species or genera need not reflect
218 cognitive equivalence. However, this slope may still be useful, as it provides a convenient
219 upper limit to the actual slope of cognitive equivalence. The analysis of congeneric slopes by
220 Isler et al. [2008] using independent contrasts yielded a mean slope of 0.41 for primates,
221 suggesting the true slope lies somewhere between 0.15 and 0.40.

222 The best option thus remains to obtain intraspecific slopes that are affected as little
223 as possible by the error problem. We can achieve this by looking for species with large
224 variation in adult body size. Using data on dog breeds, which show 30-fold variation in body
225 size, Bronson [1979] obtained a slope of 0.27 based on averages per breed. This would seem
226 to provide an excellent estimate of the slope of cognitive equivalence, but since dog breeds
227 were produced by artificial selection, we cannot be sure that cognitive equivalence was
228 maintained across the whole size range [cf. Martin & Harvey 1985].

229 Here, we consider a variation on this theme. We focus on primates with clear sexual
230 dimorphism in body size, so as to minimize error due to the small range in adult body sizes.
231 Second, we take the means of males and females so as to reduce the error in individual data
232 points. And third, we only consider data from wild specimens. We then estimate the slope
233 by fitting a line through the female and male average (which we will refer to as the 2-point
234 slope). We predict that this 2-point slope will be steeper than the slope through all available
235 data points, and closer to the true, unbiased value.

236 This 2-point slope will be biased when the sexes differ in body composition, in which
237 case body mass is not a good estimate of actual (lean) body size [Schoenemann 2004]. In
238 humans (not in our sample), men's bodies are far leaner than women's bodies, even among
239 foragers [Wells 2010]. Obviously, the 2-point slope would then be overestimated. However,
240 such major sex differences in adiposity are not found among non-human primates, because
241 both arboreality and the high mobility under natural conditions will strongly limit adiposity
242 and thus reduce any such differences [Heldstab et al. 2016; Sterck et al. 2019]. By including
243 only animals taken from the wild, we largely eliminate this possible confounding effect.

244 The 2-point slope will also be biased when males and females experience differential
245 selection pressures on overall cognitive abilities, in particular due to sexual selection, which

246 by definition may affect the sexes differently. We do not expect this to be important
247 because we know of no studies of primate cognition that needed to control for sex [e.g.
248 Amici et al. 2012; Hopkins et al. 2014; Damerius et al. 2017; see also Arden & Adams 2016,
249 for dogs]. Likewise, for humans most experts agree that there is no gender difference in
250 intelligence, although some argue for a small difference [Irwing & Lynn 2005], which may
251 also reflect differential socialization. Moreover, for primates, Lindenfors et al. [2007] found
252 no evidence that sexual selection affected relative neocortex size, the largest part of
253 primate brains. Thus, this assumption seems warranted. However, for birds, Garamszegi et
254 al. [2005] found a weak positive effect of extra-pair copulation on female brain size.
255 Likewise, Kotrschal et al. [2012] found that males in an Icelandic population of three-spined
256 sticklebacks had far larger brains than females, although they could only speculate about
257 the selective agent (perhaps male-only parental care). This effect is less likely in our sample
258 because we focused on highly dimorphic species, thus excluding major variation in the
259 mating system. Nonetheless, to control for the possibility, we will compare species with
260 single-male versus multi-male mating. A final possible effect of sexual selection is that there
261 may be an upper limit to the males' ability to maintain cognitive equivalence as body mass
262 dimorphism increases, because females are thought to be at the ecologically optimal size
263 for a given niche. We therefore also examine the importance of dimorphism as a factor in
264 the slope.

265 Given these various assumptions and our inability to fully test all of them, it is
266 essential to seek external validation. Two opportunities exist. First, we can assess the
267 ecological validity, by asking whether the residual brain size values based on the new slope
268 actually predict cognitive abilities across species and do so better than alternative
269 neuroanatomical measures that have been proposed in the past. This test faces a major
270 hurdle, in that we do not know whether the relationship between the correct
271 neuroanatomical measures and cognitive performance is linear, more than linear or less
272 than linear. This problem is exacerbated by the fact that the performance measures are
273 often normalized or even ordinal. However, since the relationship is necessarily monotonic,
274 the correct measure should always preserve the rank order in cognitive performance.
275 Although the different neuroanatomical measures we compare are likely to show high rank
276 correlations among each other, we can nonetheless test their predictive value by assessing
277 the value of the rank correlations with cognitive performance. We found two published data
278 sets comparing species' cognitive performance for this analysis. A second way to validate
279 the slope value is to compare it with the strength of genetic correlations between brain size
280 and body size [Lande 1979]. We will do this in the discussion, once we have acquired our
281 estimate.

282 In this study, we therefore first determined the slopes of cognitive equivalence for
283 sexually dimorphic primate species. We used two samples (one using conservative and
284 another using more relaxed sample size criteria), and assessed the possible effects of
285 sample sizes, mating system, and sexual dimorphism. Next, we validated the slope we
286 obtained by comparing it with the genetic correlation between brain and body size and by
287 its rank correlation with published measures of species' cognitive abilities. Finally, we made
288 a first, preliminary assessment of the consequences of adopting this new measure of a
289 species' cognitive abilities, using extinct hominins.

290

291

292 **Materials and Methods**

293 We compiled data on cranial capacity and body mass of primates from the studies by
294 Heldstab et al. [2018, 2019]. We selected species with fairly large sample sizes ($N \geq 5$ for
295 each sex) to minimize error in estimating the mean body and brain size of males and
296 females. We only included wild-caught animals to avoid captivity effects on body mass
297 (usually fattening), and fully adult individuals, as evinced by the eruption of the third molar.
298 Finally, we set a minimal mass dimorphism at 1.20, because preliminary analysis revealed
299 wildly fluctuating estimated 2-point slopes at values close to monomorphism, as expected.
300 Overall, we had 18 primate species that met these criteria. The brain-body size slope was
301 then estimated for each species, as the slope of the line connecting the male and female
302 average (the 2-point slope), as well as the slope through all points. A second primate data
303 set was produced by including all species with at least 10 adult individuals and at least 2 of
304 each sex and mass dimorphism of at least 1.20. This data set contained 27 species. We
305 expected more variance in the estimate of the slope. We refer to these two data sets, as the
306 conservative and relaxed primate data set, respectively.

307 We examined the bivariate effects of various variables discussed above on the
308 estimated slope: mating system (single-male versus multi-male) and female brain size, as
309 well as sexual dimorphism (to assess whether it has a positive effect on estimated slope for
310 which we should control), sample size (likewise). We also used a model selection approach
311 to identify the best-fitting model.

312 For the validation part, we used published data sets to capture cognitive
313 performance: global cognitive performance [Deaner et al. 2007], and general intelligence
314 factor g_{st} from Reader et al. [2011].

315 The independent measures we used were:

- 316 1. body size (P , estimated as body mass in g);
- 317 2. brain size (E , estimated as endocranial volume, in cc, roughly corresponding
318 to mass in g: Isler et al. 2008);
- 319 3. Jerison's [1973] encephalization quotient ($E/[0.12 \times P^{0.667}]$),
- 320 4. An estimate of the cognitive brain based on cognitive equivalence (E -
321 $[0.065 \times P^{0.27}]$), where the exponent 0.27 is the midpoint value of the
322 empirically obtained intraspecific 2-point slopes in the first set of analyses,
323 and the intercept based on one of the smallest-brained mammals, *Sorex*
324 *minutus*, which has a 5 gram body mass and a 0.1 gram brain weight [Bauchot
325 & Stephan 1966]. This measure ensures that virtually all mammals have a
326 positive cognitive brain size.

327 Note that measure #4 is an absolute measure of the amount of brain tissue available
328 for cognitive tasks, whereas measure #3, the EQ, is a ratio. Thus, two species that differ
329 greatly in body size can have the same EQ, yet the larger of the two will have far higher
330 values of measure #4. Note, too, that measure #4 may be negative for ectothermic
331 vertebrates [cf. Jerison 1973], and thus may only be intuitive for birds and mammals.

332 As noted above, we used rank correlations to assess the fit of these measures.

333

334

335 **Results**

336 *Estimating the value of the slope of cognitive equivalence*

337 As expected, the 2-point slopes based on mean values per sex are better than those
338 based on all individual points. Using the conservative primate dataset, we found that the
339 slopes using all the data points (mean= 0.209; SEM = 0.020) were on average 30% less steep
340 than the 2-point slopes (mean= 0.268; SEM= 0.020). Likewise, the more conservative
341 dataset, with at least 5 adult individuals of each sex, gave more reliable slope estimates
342 (lower SEM) than the more relaxed data set, which also varied less with sexual dimorphism
343 (Table 1). Thus, the best estimate of the slope is 0.27.

344 The analyses of the possible effect of confounding variables were performed on the
345 conservative primate dataset only, again using only species with sexual dimorphism of
346 ≥ 1.20 , where the standard errors of the estimated slope values had stabilized. Our limited
347 sample size forced us to do bivariate tests. In these tests, we did not need to correct for
348 phylogenetic non-independence because the Pagel's λ values of the slopes [Pagel 1992]
349 were < 0.001 . We found no effect of sample size ($r = -0.041$, $N = 18$, $P = 0.87$) on the value of
350 the 2-point slope. Likewise, there was no effect of sexual dimorphism ($r = -0.093$, $P = 0.71$) or
351 of mating system (single-male versus multi-male; $t_{(16)} = -1.39$, $P = 0.18$). Moreover, none of
352 the various possible multivariate models showed anywhere near a significant result and
353 multiple models had close similarity in overall fit (not shown).

354

355 Table 1. Effect of changing the minimal cutoff point of sexual dimorphism (S.D. min) for
356 inclusion into the analysis of the 2-point slopes for the conservative and the relaxed primate
357 sample (S.E.M. = standard error of the mean; N= number of species)

358

S.D. min	Conservative sample			Relaxed sample		
	Slope	S.E.M.	N	Slope	S.E.M.	N
1.20	0.268	0.020	18	0.246	0.023	27
1.25	0.274	0.022	16	0.262	0.022	23
1.30	0.258	0.017	15	0.251	0.020	22
1.40	0.258	0.017	15	0.251	0.020	22
1.50	0.259	0.023	8	0.262	0.027	13

359

360

361 *Validating the value of the slope*

362 Table 2 provides the values of the Spearman rank correlations for the validation
363 studies for each of the five measures used. Overall, as expected because of the need to use
364 ranks only, the results are very close, and the confidence limits for the various measures
365 generally overlap. Nonetheless, in both cognitive performance measures (the Deaner et al.
366 [2007] and Reader et al. [2011] data), the EQ gives the lowest correlations, whereas the
367 cognitive brain estimate, absolute brain size and even body size do about equally well.

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373 **Table 2.** Validation analyses using multiple data sets of cognitive performance, using
374 Spearman rank correlations.

Predictor variable	r_s	p-value	95% CI	99% CI
<i>Deaner et al. (2007) N=24</i>				
ln (brain size)	0.811	$p < 0.001$	(0.507, 0.767)	(0.452, 0.795)
ln (body size)	0.845	$p < 0.001$	(0.452, 0.736)	(0.393, 0.767)
cognitive brain	0.809	$p < 0.001$	(0.602, 0.913)	(0.509, 0.933)
Jerison brain	0.542	$p = 0.007$	(0.178, 0.775)	(0.045, 0.823)
<i>Reader et al. (2011) N=28</i>				
ln (brain size)	0.512	$p = 0.005$	(0.172, 0.742)	(0.050, 0.793)
ln (body size)	0.515	$p = 0.005$	(0.176, 0.744)	(0.055, 0.794)
cognitive brain	0.517	$p = 0.005$	(0.179, 0.746)	(0.057, 0.795)
Jerison brain	0.408	$p = 0.031$	(0.042, 0.678)	(-0.081, 0.739)

375

376

377

378 Discussion

379 Value of the slope

380 We examined the proposition that there is a slope of cognitive equivalence, which
381 predicts the change in brain size, and thus cognitive abilities, corresponding to a change in
382 body size in which all the details of bauplan and sensory-motor abilities are kept constant.
383 Existing estimates of this slope suffer from the problem of measurement error, because
384 mammals generally have only a narrow range of body sizes, whereas their estimates (body
385 mass) can vary widely. We therefore used mean values for males and females in sexually
386 dimorphic species, which have a larger range of body sizes, to estimate the 2-point slope. In
387 general, this approach yielded steeper slopes than regressions through all available data
388 points, confirming the expected reduction in the effect of error on slope estimates, and
389 explaining why previous studies often found shallower slopes.

390 We found no effect of possible confounding variables, such as mating system or
391 dimorphism beyond 1.20. The slope of 0.27 obtained here is the same as the one found for
392 dogs, where breeds vary greatly in size [Bronson 1979], but, as expected, higher than the
393 value of 0.23 [Hemmer 1971] or 0.25 [Röhrs 1986] found in previous intraspecific mammal
394 studies with large samples that used all individual data rather than estimating 2-point
395 slopes.

396

397 Validation of the slope estimate

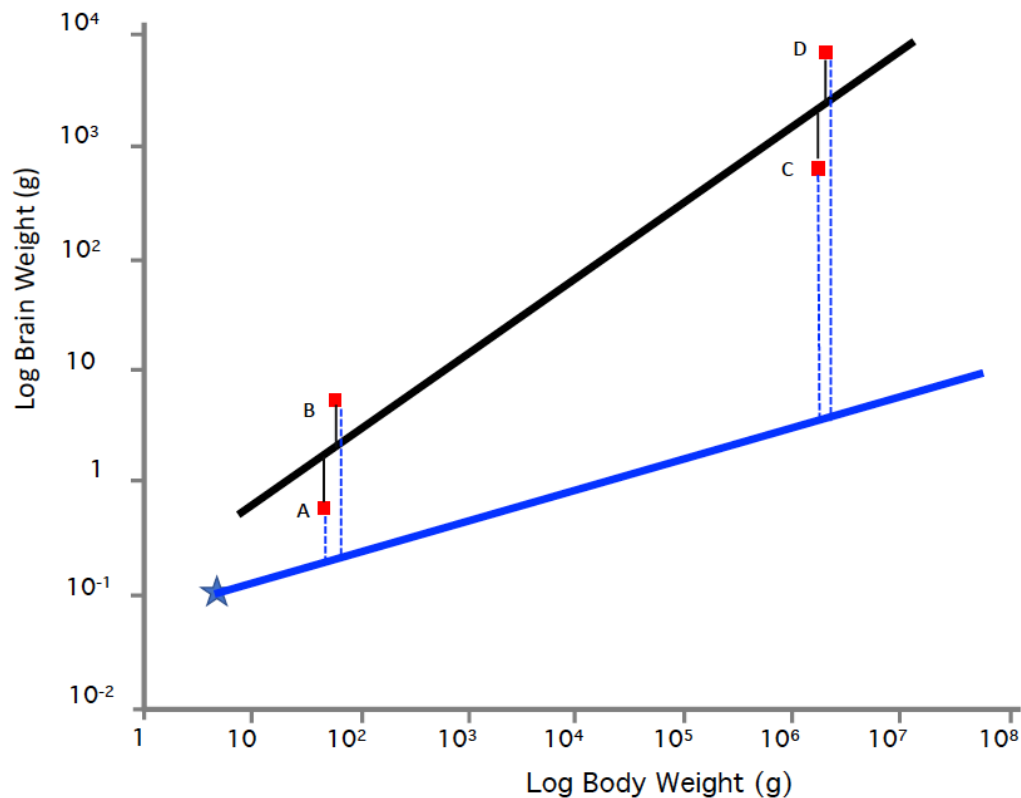
398 Based on selection experiments on body size in inbred mice lines, Lande [1979, 1985]
399 predicted a 0.36 slope of log (brain size) on log (body size), which would also hold when
400 body size changes by drift, and thus also when populations contain selectively neutral
401 genetic variation in body size. Slopes observed after selection experiments on body size in
402 rodents yielded values between 0.2 and 0.4 [Riska & Atchley 1985], but since these should
403 also be affected by the error problem, their true value may also be ≥ 0.25 . However, Lande
404 [1985] suggested that the genetic correlation between brain and body size is lower in
405 natural species. Indeed, Grabowski [2016] estimated it for samples of five primate species
406 taken from the wild, and found an average value of 0.254, which should be somewhat lower

407 than the true slope, given the error in body mass used to estimate genetic correlation
408 between brain and body. Thus, our estimate of 0.27 for the slope of cognitive equivalence is
409 quite consistent with these estimates of genetic correlation.

410 We therefore used a line of $P^{0.27}$ (where P is body size) as the estimate of the somatic
411 brain. For estimates of a species' cognitive brain we need to anchor the line (Fig. 1). To
412 achieve positive values for all species, we took the presumably smallest-brained mammal,
413 *Sorex minutus*, and forced the curve through its values (average body mass 5 g, average
414 brain mass 0.1 g [Bauchot & Stephan 1966]). This leads to the minimum estimated size of
415 the somatic brain as $E_s = 0.065 \times P^{0.27}$, and thus the following estimate of the cognitive brain
416 size: $E_c = E - E_s$, where E is the species' actual brain size. Figure 1 illustrates the procedure.

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420 Figure 1. Illustrating the difference between EQs and estimates of cognitive brain
421 size. The steep black line gives Jerison's curve for the average mammalian brain and the
422 shallow blue line the curve for the estimate of the somatic brain, which was anchored
423 using the smallest-brained mammal, *Sorex minutus* (blue star). Four hypothetical
424 species, red squares A-D, are included to illustrate the different measures. The black
425 vertical lines are the residuals from Jerison's line; EQ is the ratio of the value for a given
426 point and the value of the corresponding point on the black line. The blue dashed lines
427 are the estimates of the cognitive brain size.

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429 The most important result of the cognitive validation analyses was that the
430 alternative measures, including body size, all perform better than EQ. The EQ is the ratio of
431 observed to expected brain size, and in Fig. 1, the antilog of the residual from Jerison's line.

432 Thus, a very small mammal could have the same ratio as a very large mammal (as do
433 species B and D in Fig. 1), even if they differ dramatically in the absolute size of the
434 estimated cognitive brain (the antilog of the blue dashed vertical lines). Thus, the estimated
435 order of overall cognitive performance would increase as follows under the EQ: $A=C < B=D$.
436 Under the cognitive brain estimate deployed here it would be: $A < B < C < D$, the same order
437 as in absolute brain size, or (in this example) absolute body size of the species.

438 The close similarity in how well the various non-EQ measures predicted actual
439 estimates of overall cognitive abilities is not surprising. Absolute brain size is often a
440 reasonable predictor of specific cognitive abilities in studies that did not use the measure
441 based on cognitive equivalence [Benson-Amran et al. 2015; MacLean et al. 2014; Horschler
442 et al. 2019]. The two measures are closely correlated, and also of course show strong
443 correlations with body size. Indeed, also the neocortex ratio remains highly correlated with
444 body size [e.g. Stout 2018]. Although we did not include the neocortex ratio in this study, in
445 the dataset used by Dunbar [1992], which uses averages for genera and sexes, the
446 Spearman rank correlation between the two is 0.871 ($N= 38$, $P<0.001$) (non-linear
447 relationship). Thus, the discrepancies among the various alternative approaches (absolute
448 brain size, cognitive equivalence, neocortex ratio) are quite modest, and in practice we will
449 often not have the resolution needed to decide which of these is the best.

450 Nonetheless, although the low value of the slope of cognitive equivalence indicates
451 that only a modest correction for body size is needed, some correction for the somatic
452 functions of brains is conceptually necessary (despite proposals to abandon it altogether).
453 First, the cognitive abilities of extremely large animals would almost certainly be
454 overestimated. Second, sex differences in cognitive abilities would otherwise be inferred
455 that may well not exist. For instance, despite a clear gender difference in brain size [e.g. in
456 Martin [1986], men's mean is 1498 cc and women's mean 1326 cc), there is only a tiny (if
457 any) gender difference in intelligence in humans [Irwing & Lynn 2005]. The estimate based
458 on cognitive equivalence is therefore to be preferred.

459 It appears that this approach reduces the effect of body size on brain size much more
460 than has traditionally been considered necessary. It is not clear why this is. First, this
461 conclusion may be peculiar to primates, with their large brains for mammals, and thus large
462 neocortices [Finlay et al. 2001]. Where cognitive functions take up a large proportion of the
463 overall brain size, the relative importance of the somatic functions must become
464 concomitantly smaller. If so, we expect the slope to be lower for other mammalian orders.
465 Second, the size of the somatic brain may be small overall because neurons in many brain
466 regions can be involved in multiple networks simultaneously, thus blurring the distinction
467 between somatic and cognitive functions.

468 The analysis presented here is of course preliminary. It is based on primates only,
469 and on a limited number of species at that, and could not establish whether species
470 differences in slopes were true or merely reflected error. Future work should include all
471 mammals with non-trivial dimorphism in body size, while ensuring the use of fully adult,
472 wild specimens, with values not affected by advanced pregnancy or confounded by seasonal
473 variation in adiposity. Along with work on other vertebrates, this work may find that slopes
474 vary among lineages, and generate and test hypotheses on its causes.

475 Nevertheless, this study confirms that the effect of body size on the size of the
476 somatic brain (the 2-point slope) varies considerably between mammals (and presumably
477 birds [Tsuboi et al. 2018]) on the one hand, and ectothermic vertebrates (fishes,

478 amphibians, reptiles) on the other hand. The latter vary between 0.4 and 0.5 within species
479 (Tsuboi et al 2018). For fishes, Triki et al. [2021, preprint] obtained a mean intraspecific
480 slope of 0.49 that is independent of body size variation. Furthermore, Triki et al. [2021,
481 preprint] studied one fish species, the cleaner fish *Labroides dimidiatus* in more detail.
482 Individual performance in various cognitive tasks was not correlated with body size, so that
483 the intraspecific brain-body slope of 0.53 of this species indeed represents the slope of
484 cognitive equivalence. The causes of this clear difference between intraspecific slopes in
485 endotherms versus ectotherm vertebrates remain unexplained.

486 It might be objected that comparing distantly related taxa on their cognitive
487 performance based on brain measures only is not advised given the known differences in
488 neuron densities in the brains of different clades [Herculano-Houzel 2017] and the effect on
489 brain size of highly divergent bauplans. We fully endorse this view. Comparing cognitive
490 brain estimates among distantly related lineages may not be very revealing, and we should
491 be very careful. Nonetheless, this restriction does not argue in favor of reviving the EQ
492 approach.

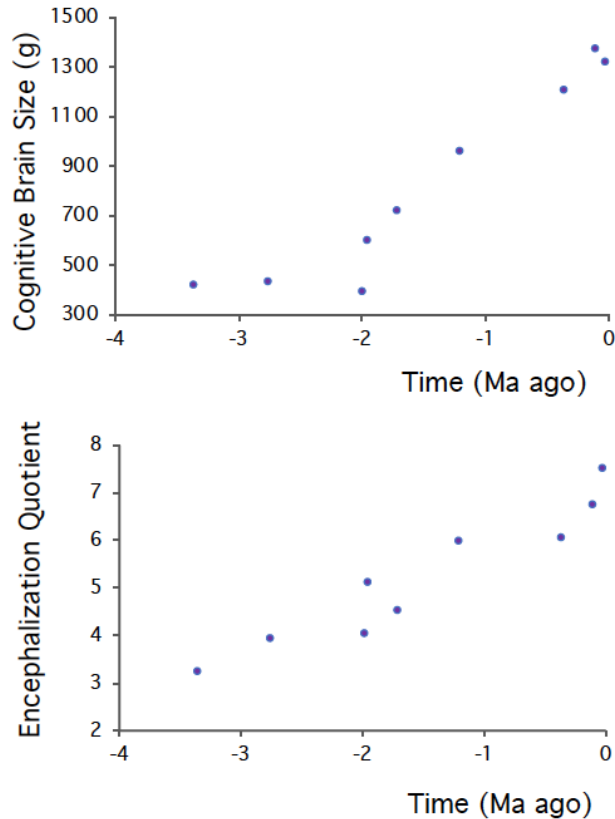
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494 ***Applications: An example***

495 Although a thorough application of the new method is beyond the scope of this
496 paper, we can get a first impression by comparing the cognitive brain estimate with
497 Jerison's [1973] EQ for extinct hominins thought to be in the main lineage contributing
498 representatives that formed our own species (thus excluding the robust australopithecines
499 and both *Homo floresiensis* and *H. naledi*). Because the new measure produces cognitive
500 brain size estimates rather close to overall brain size, the two techniques yield a rather
501 different picture (Figure 2). Jerison's EQ suggests a long period of a continuing, gradual
502 increase in cognitive abilities from 4 Ma until roughly 300 ka, followed by a sudden uptick.
503 The alternative EQ measure proposed by Grabowski et al. [2016], which is based on a
504 somewhat shallower slope, gives a similar picture, but without the sudden uptick in the last
505 300 ka (see their Fig. 2). The cognitive equivalence measure, in contrast, suggests cognitive
506 stasis between 4 Ma and 2 Ma, after which cognitive abilities steadily increased.

507 The paucity of material and the problems inherent in estimating body size from
508 incomplete remains advise caution. Still, it can be argued that the general pattern
509 suggested by the cognitive equivalence measure is closer to current understanding. Thus,
510 the material culture of hominins did not exceed that of the extant great apes [Wynn et al.
511 2011], the diversity and complexity of hominin material culture began in earnest around 2
512 Ma [e.g. Stout 2011], and there is no great increase in relative brain size within the human
513 species [Grabowski et al. 2016; Schoenemann 2013].

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Figure 2. The changes in cognitive brain size (a) and EQ (b) during hominin evolution. The dates are the median observed age (Ma before present). Data based on Grabowski [2016].

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Implications

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Comparative tests of adaptive hypotheses to explain brain size evolution in primates sometimes reach incompatible conclusions [Wartel et al. 2019], as do those on other mammals or birds [Healy & Rowe 2007]. Among the many reasons responsible for this impasse, one potentially prominent aspect is generally overlooked [Rogell et al. 2019]. These tests invariably include body mass as a control variable, and then try to explain the remaining variation in brain size, in effect letting the pattern of covariation among the variables decide the allometric slope. In practice, the high correlation between body size and the other potential explanatory variables may affect the outcome and interpretation of the results [Stout 2018].

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Thus, when we have a validated estimate of the size of the cognitive brain we can use this residual measure as the response variable, and so should get a fairer evaluation of the hypotheses trying to explain brain size evolution. In the end, this may be the most valuable contribution of the kind of analysis undertaken in this paper.

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544

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546

547 **Ethics note:** Data were compiled from published studies.

548

549 **Authors' contributions**

550 CvS provided the conceptual basis, and RB and ZT added major discussion; SH provided
551 data; SH and CvS did the analyses; all authors wrote the final version.

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