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The Evolution of Self-Control

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Classification: Biological Sciences – Psychological and Cognitive Sciences

Short title: The Evolution of Self-Control

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Abstract

27 Cognition presents evolutionary research with one of its greatest challenges. Cognitive
28 evolution has been explained at the proximate level by shifts in absolute and relative
29 brain volume and at the ultimate level by differences in social and dietary complexity.
30 However, no study has integrated the experimental and phylogenetic approach at the
31 scale required to rigorously test these explanations. Instead, previous research has largely
32 relied on various measures of brain size as proxies for cognitive abilities. We
33 experimentally evaluated these major evolutionary explanations by quantitatively
34 comparing the cognitive performance of 567 individuals representing 36 species on two
35 problem-solving tasks measuring self-control. Phylogenetic analysis revealed that
36 *absolute* brain volume best predicted performance across species and accounted for
37 considerably more variance than brain volume controlling for body mass. This result
38 corroborates recent advances in evolutionary neurobiology and illustrates the cognitive
39 consequences of cortical reorganization through increases in brain volume. Within
40 primates, dietary breadth but not social group size was a strong predictor of species
41 differences in self-control. Our results implicate robust evolutionary relationships
42 between dietary breadth, absolute brain volume, and self-control. These findings provide
43 a significant first step toward quantifying the primate cognitive phenome and explaining
44 the process of cognitive evolution.

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Significance Statement

Although scientists have identified surprising cognitive flexibility in animals and potentially unique features of human psychology, we know less about the selective forces that favor cognitive evolution, or the proximate biological mechanisms underlying this process. We tested 36 species in two problem solving tasks measuring self-control and evaluated the leading hypotheses regarding how and why cognition evolves. Across species, differences in absolute (not relative) brain volume best-predicted performance on these tasks. Within primates, dietary breadth also predicted cognitive performance, whereas social group size did not. These results suggest that increases in absolute brain size provided the biological foundation for evolutionary increases in self-control, and implicate species differences in feeding ecology as a potential selective pressure favoring these skills.

62 Introduction

63 Since Darwin, understanding the evolution of cognition has been widely regarded as one
64 of the greatest challenges for evolutionary research (1). Although researchers have
65 identified surprising cognitive flexibility in a range of species (2-40) and potentially
66 derived features of human psychology (41-61), we know much less about the major
67 forces shaping cognitive evolution (62-71). With the notable exception of Bitterman's
68 landmark studies conducted several decades ago (63, 72-74), most research comparing
69 cognition across species has been limited to small taxonomic samples (70, 75). With
70 limited comparable experimental data on how cognition varies across species, previous
71 research has largely relied on proxies for cognition (e.g. brain size) or meta-analyses
72 when testing hypotheses about cognitive evolution (76-92). The lack of cognitive data
73 collected with similar methods across large samples of species precludes meaningful
74 species comparisons that can reveal the major forces shaping cognitive evolution across
75 species, including humans (48, 70, 89, 93-98).

76 To address these challenges we measured cognitive skills for self-control in 36
77 species of mammals and birds (Fig 1) tested using the same experimental procedures, and
78 evaluated the leading hypotheses for the neuroanatomical underpinnings and ecological
79 drivers of variance in animal cognition. At the proximate level, both absolute (77, 99-
80 107) and relative brain size (108-112) have been proposed as mechanisms supporting
81 cognitive evolution. Evolutionary increases in brain size (both absolute and relative) and
82 cortical reorganization are hallmarks of the human lineage and are believed to index
83 commensurate changes in cognitive abilities (52, 105, 113-115). Further, given the high
84 metabolic costs of brain tissue (116-121) and remarkable variance in brain size across

85 species (108, 122), it is expected that the energetic costs of large brains are offset by the
86 advantages of improved cognition. The *cortical reorganization hypothesis* suggests that
87 selection for absolutely larger brains – and concomitant cortical reorganization – was the
88 predominant mechanism supporting cognitive evolution (77, 91, 100-106, 120). In
89 contrast, the *encephalization hypothesis* argues that an increase in brain volume relative
90 to body size was of primary importance (108, 110, 111, 123). Both of these hypotheses
91 have received support through analyses aggregating data from published studies of
92 primate cognition and reports of ‘intelligent’ behavior in nature – both of which correlate
93 with measures of brain size (76, 77, 84, 92, 110, 124).

94 With respect to selective pressures, both social and dietary complexity have been
95 proposed as ultimate causes of cognitive evolution. The *social intelligence hypothesis*
96 proposes that increased social complexity (frequently indexed by social group size) was
97 the major selective pressure in primate cognitive evolution (6, 44, 48, 50, 87, 115, 120,
98 125-141). This hypothesis is supported by studies showing a positive correlation
99 between a species’ typical group size and neocortex ratio (80, 81, 85-87, 129, 142-146),
100 cognitive differences between closely related species with different group sizes (130, 137,
101 147, 148), and evidence for cognitive convergence between highly social species (26, 31,
102 149-151). The *foraging hypothesis* posits that dietary complexity, indexed by field
103 reports of dietary breadth and reliance on fruit – a spatiotemporally distributed resource –
104 was the primary driver of primate cognitive evolution (152-155). This hypothesis is
105 supported by studies linking diet quality and brain size in primates (79, 81, 86, 142, 156),
106 and experimental studies documenting species differences in cognition that relate to
107 feeding ecology (94, 157-167).

108 While each of these hypotheses has received empirical support, a comparison of
109 the relative contributions of the different proximate and ultimate explanations requires:
110 (i) a cognitive dataset covering a large number of species tested using comparable
111 experimental procedures; (ii) cognitive tasks that allow valid measurement across a range
112 of species with differing morphology, perception and temperament; (iii) a representative
113 sample within each species to obtain accurate estimates of species-typical cognition; (iv)
114 phylogenetic comparative methods appropriate for testing evolutionary hypotheses; and
115 (v) unprecedented collaboration to collect these data from populations of animals around
116 the world (70).

117 Here, we present the first large-scale collaborative dataset and comparative
118 analysis of this kind, focusing on the evolution of self-control. We chose to measure self-
119 control – the ability to inhibit a prepotent but ultimately counterproductive behavior –
120 because it is a crucial and well-studied component of executive function and is involved
121 in diverse decision-making processes (168-170). For example, animals require self-
122 control when avoiding feeding or mating in view of a higher-ranking individual, sharing
123 food with kin, or searching for food in a new area rather than a previously rewarding
124 foraging site. In humans, self-control has been linked to health, economic, social, and
125 academic achievement, and is known to be heritable (171-173). In song sparrows, a
126 study using one of the tasks reported here found a correlation between self-control and
127 song repertoire size, a predictor of fitness in this species (174). In primates, performance
128 on a series of nonsocial self-control control tasks was related to variability in social
129 systems (175), illustrating the potential link between these skills and socioecology. Thus,

130 tasks that quantify self-control are ideal for comparison across taxa given these robust
131 behavioral correlates, heritable basis, and potential impact on reproductive success.

132 In this study we tested subjects on two previously implemented self-control tasks.
133 In the A not B task (27 species, N = 344), subjects were first familiarized with finding
134 food in one location (container A) for three consecutive trials. In the test trial, subjects
135 initially saw the food hidden in the same location (container A), but then moved to a new
136 location (container B) before they were allowed to search (Movie S1). In the cylinder
137 task (32 species, N = 439), subjects were first familiarized with finding a piece of food
138 hidden inside an opaque cylinder. In the following ten test trials, a transparent cylinder
139 was substituted for the opaque cylinder. To successfully retrieve the food, subjects
140 needed to inhibit the impulse to reach for the food directly (bumping into the cylinder) in
141 favor of the detour response they had used during the familiarization phase (Movie S2).

142 Thus, the test trials in both tasks required subjects to inhibit a prepotent motor
143 response (searching in the previously rewarded location or reaching directly for the
144 visible food), but the nature of the correct response varied between tasks. Specifically, in
145 the A not B task subjects were required to inhibit the response that was previously
146 successful (searching in location A) whereas in the cylinder task subjects were required
147 to perform the same response as in familiarization trials (detour response), but in the
148 context of novel task demands (visible food directly in front of the subject).

149 **Results**

150 Across species and accounting for phylogeny, performance on the two tasks was strongly
151 correlated ($R = 0.53$, $N = 23$, $p < 0.01$). Thus, species ($n = 23$) that participated in both
152 cognitive tasks were assigned a composite score averaging performance across tasks.

153 Because the two tasks assessed complementary but not identical abilities, the composite
154 score serves as a general index of self-control across tasks. Phylogenetic analyses
155 revealed that scores were more similar among closely related species, with the maximum
156 likelihood estimate of λ – a measure of phylogenetic signal – significantly greater than
157 zero in most cases (Table 1). For both tasks, scores from multiple populations of the same
158 species (collected by different researchers at different sites) were highly correlated
159 (cylinder task: $r = 0.95$, $n = 5$, $p = 0.01$; A not B task: $r = 0.87$, $n = 6$, $p = 0.03$; see SI).
160 To control for the non-independence of species level data, we used phylogenetic
161 generalized least squares (PGLS) to test the association between performance on the
162 cognitive tasks and the explanatory variables associated with each hypothesis. Our
163 neuroanatomical predictors included measures of absolute brain volume (endocranial
164 volume [ECV]), residual brain volume (residuals from a phylogenetic regression of ECV
165 predicted by body mass [ECV residuals]) and Jerison's (1973) encephalization quotient
166 (EQ; see Methods).

167 Across species, absolute brain volume (measured as ECV) was a robust predictor
168 of performance (Fig 2; Table 2) supporting the predictions of the *cortical reorganization*
169 *hypothesis*. ECV covaried positively with performance on the cylinder task and the
170 composite score and explained substantial variance in performance ($r^2 = 0.43-0.60$; Table
171 2). This association was much weaker for the A not B task, reflecting that the largest-
172 brained species (Asian elephant) had the lowest score on this measure (Fig 2; Table 2).
173 The same analysis excluding the elephant yielded a strong and significant positive
174 association between ECV and scores on the A not B task (Fig 2; Table 2). Across the
175 entire sample, residual brain volume was far less predictive than absolute brain volume: it

176 explained only 3% of variance in composite scores, and was a significant predictor of
177 performance in only one of the tasks (Table 2; SI; Fig 2). EQ was positively related to
178 composite scores across species ($\beta = 0.28$, $t_{21} = 3.23$, $p < 0.01$, $\lambda = 0$, $r^2 = 0.33$) but again
179 explained far less variance than absolute brain volume.

180 We conducted the same analyses using only primates (23 species, 309 subjects),
181 the best-represented taxonomic group in our dataset. Within primates, absolute brain
182 volume was the best predictor of performance across tasks and explained substantial
183 variation across species ($r^2 = 0.55-0.68$; Fig 3; Table 2). In contrast to the analysis across
184 all species, residual brain volume was predictive of performance on both tasks within
185 primates, although it explained much less variance than absolute brain volume ($r^2 = 0.18-$
186 0.30 ; Fig 3; Table 2). Within primates the analysis using EQ as a predictor of composite
187 scores was similar to that using ECV residuals ($\beta = 0.24$, $t_{13} = 1.65$, $p = 0.06$, $\lambda = 0.66$, r^2
188 $= 0.17$).

189 We also restricted the analyses to only the non-primate species in our sample (13
190 species, 258 subjects). Within the non-primate species, ECV was again the best predictor
191 of self-control, and was significantly and positively associated with composite scores and
192 scores on the cylinder task, but not the A not B task (Table 2). Removing the Asian
193 elephant from the analysis of the A not B task did not change this result ($\beta = 0.09$, $t_6 =$
194 1.37 , $p = 0.11$, $\lambda = 0$, $r^2 = 0.24$). Residual brain volume was not a significant predictor of
195 any of these measures (Table 2), and EQ was unrelated to composite scores ($\beta = -.01$, $t_6 =$
196 -0.08 , $p = 0.53$, $\lambda = 0.28$, $r^2 < 0.01$).

197 We used the experimentally derived measures of self-control to investigate the
198 two leading ecological hypotheses that have been proposed as catalysts of primate

199 cognitive evolution. We focused on primates because these species are best represented
200 in our dataset, and the ecological data have been systematically compiled and related to
201 neuroanatomical proxies for cognition in these species. As a measure of social
202 complexity, we tested the hypothesis that social group size, which covaries with
203 neocortex ratio in anthropoid primates (129), would predict performance in the self-
204 control tasks. To explore multiple variants of this hypothesis, we investigated both
205 species-typical population group size and foraging group size as predictor variables.
206 Neither measure of group size was associated with task performance (Fig 3; Table 2;
207 Table S7), echoing findings using observational data on behavioral flexibility (92). We
208 tested the foraging hypotheses by examining whether the degree of frugivory (% fruit in
209 diet) or dietary breadth (number of dietary categories reported to have been consumed by
210 each species (92)) predicts performance. The percent of fruit in a species' diet was not a
211 significant predictor of any of the cognitive measures (Fig 3; Table 2; Table S7).
212 However, dietary breadth covaried strongly with our measures of self-control (Fig 3;
213 Table 2; Table S7). Supplemental analyses involving home range size, day journey length,
214 the defensibility index, and substrate use revealed no significant associations (SI).

215 To provide an integrated test of variance explained by absolute brain volume and
216 dietary breadth, we fit a multiple regression including both terms as predictors of
217 primates' composite cognitive scores. This model explained 80% of variance in
218 performance between species with significant and positive coefficients for both absolute
219 ECV and diet breadth, controlling for the effects of one another (ECV: $t_{11} = 2.10$, $p =$
220 0.03 ; diet breadth: $t_{11} = 4.05$, $p < 0.01$; $\lambda = 0.56$, $r^2 = 0.80$). Thus, while correlated with
221 one another ($t = 2.83$, $p = 0.01$, $\lambda = 0$, $r^2 = 0.29$), both brain volume and dietary

222 complexity account for unique components of variance in primate cognition, together
223 explaining the majority of interspecific variation on these tasks. Interestingly, in this
224 model the independent effect for dietary breadth ($r^2=0.59$) was considerably larger than
225 that for brain volume ($r^2 = 0.28$).

226 We also assessed the extent to which our experimental data corroborate species-
227 specific reports of intelligent behavior in nature (92). Controlling for observational
228 research effort, our experimental measures covaried positively with reports of innovation,
229 extractive foraging, tool use, social learning, and tactical deception in primates (Table 2;
230 Table S7; SI). Our experimental measure also covaried with a ‘general intelligence’
231 factor ‘ g_s ’ (92) derived from these observational measures (Table 2; Table S7; SI).

232 Lastly, we used data from the extant species in our dataset to reconstruct
233 estimated ancestral states in the primate phylogeny. Maximum likelihood reconstruction
234 of ancestral states implies gradual cognitive evolution in the lineage leading to apes, with
235 a convergence between apes and capuchin monkeys (Fig 4; SI). Thus, in addition to
236 statistical inferences about ancestral species, this model reveals branches in the
237 phylogeny associated with rapid evolutionary change, convergence and divergence, and
238 the historical contexts in which these events occurred.

239 **Discussion**

240 Our phylogenetic comparison of three-dozen species supports the hypothesis that
241 the major proximate mechanism underlying the evolution of self-control is increases in
242 absolute brain volume. Our findings also implicate dietary breadth as an important
243 ecological correlate, and potential selective pressure for the evolution of these skills. In
244 contrast, residual brain volume was only weakly related – and social group size was

245 unrelated – to variance in self-control. The weaker relationship with residual brain
246 volume and lack of relationship with social group size is particularly surprising given the
247 common use of relative brain volume as a proxy for cognition and historical emphasis on
248 increases in social group size as a likely driver of primate cognitive evolution (85).

249 Why might absolutely larger brains confer greater cognitive advantages than
250 relatively larger brains? One possibility is that as brains get absolutely larger, the total
251 number of neurons increases, and brains tend to become more modularized, perhaps
252 facilitating the evolution of new cognitive networks (91, 101, 102). Indeed, recent data
253 suggest that human brains are notable mainly for their absolute volume, and otherwise
254 conform to the (re)organizational expectations for a primate brain of their volume (100,
255 104-107, 176, 177). Due to limited comparative data on more detailed aspects of
256 neuroanatomy (e.g. neuron counts, regional volumes, functional connectivity) our
257 analyses were restricted to measures derived from whole brain volumes. However, an
258 important question for future research will be whether finer measures of the
259 neuroanatomical substrates involved in regulating self-control (e.g. prefrontal cortex)
260 explain additional variation in cognition across species. For example, the best performing
261 species in our sample were predominantly anthropoid primates, species that have evolved
262 unique prefrontal areas that are thought to provide a cognitive advantage in foraging
263 decisions that rely on executive function (178-180). Nonetheless, other species without
264 these neuroanatomical specializations also performed well, raising the possibility that the
265 cognitive skills required for success in these tasks may be subserved by diverse but
266 functionally similar neural mechanisms across species (e.g., 181). Thus, while
267 evolutionary increases in brain volume create the potential for new functional areas or

268 cognitive networks, more detailed data from the fields of comparative and behavioral
269 neuroscience will be essential for understanding the biological basis of species
270 differences in cognition (e.g., (182-185)).

271 Within primates we also discovered that dietary breadth is strongly related to
272 levels of self-control. One plausible ultimate explanation is that individuals with the most
273 cognitive flexibility may be most likely to explore and exploit new dietary resources or
274 methods of food acquisition, which would be especially important in times of scarcity. If
275 these behaviors conferred fitness benefits, selection for these traits in particular lineages
276 may have been an important factor in the evolution of species differences in self-control.
277 A second possibility is that dietary breadth represents an ecological constraint on brain
278 evolution, rather than a selective pressure per se (116, 156, 186, 187). Accordingly,
279 species with broad diets may be most capable of meeting the metabolic demands of
280 growing and maintaining larger brains, with brain enlargement favored through a range
281 of ecological selective pressures (86). Nonetheless, after accounting for shared variance
282 between dietary breadth and brain volume, dietary breadth was still strongly associated
283 with performance on self-control tasks. Thus, it is likely that dietary breadth acts both as
284 a selective pressure and a metabolic facilitator of cognitive evolution. Given that foraging
285 strategies have also been linked to species differences in cognition in non-primate taxa
286 (94, 157-160, 162, 163, 167), it remains an important question whether dietary breadth
287 will have similar explanatory power in other orders of animals.

288 The data reported here likely represent relatively accurate estimates of species-
289 typical cognition because we collected data from large samples within each species
290 (mean $n = 15.3 \pm 2.0$ subjects per species, range = 6-66), scores from multiple

291 populations of the same species were highly correlated, and performance was not
292 associated with previous experience in cognitive tasks (SI). Thus, while populations may
293 vary to some extent (e.g. due to differences in rearing history or experimental experience),
294 these differences are small relative to the interspecific variation we observed. The
295 relationship between our experimental measures of self-control and observational
296 measures of behavioral flexibility also suggest that our measures have high ecological
297 validity, and underscore the complementary roles of observational and experimental
298 approaches for the study of comparative cognition.

299 Our tasks could be flexibly applied with a range of species because all species we
300 tested exhibited the perceptual, motivational, and motoric requirements for participation.
301 Thus, despite the fact that these species may vary in their reliance on vision, visual acuity,
302 or motivation for food rewards, all species met the same pretest criteria, assuring similar
303 proficiency with basic task demands before being tested. Nonetheless, in any comparative
304 cognitive test it is possible that features of individual tasks are more appropriate for some
305 species than others. One mechanism to overcome this challenge is through the approach
306 implemented here, in which (i) multiple tasks designed to measure the same underlying
307 construct are used, (ii) the correlation between tasks is assessed across species, and (iii) a
308 composite score averaging performance across tasks is used as the primary dependent
309 measure. In cases where data are limited to a single measure from a species, the results
310 must be interpreted extremely cautiously (e.g. performance of the Asian elephant on the
311 A not B task).

312 The relationship between self-control and absolute brain volume is unlikely to be
313 a non-adaptive byproduct of selection for increases in body size for several reasons. First,

314 a comparison of models using only body mass or ECV as the predictor of composite
315 scores yielded stronger support for the ECV model both in an analysis across all species
316 ($\Delta_{\text{AIC}} = 0.77$), and within primates ($\Delta_{\text{AIC}} = 3.12$). However, it is only within primates that
317 the change in AIC between the body mass and ECV models exceeded the 2-unit
318 convention for meaningful difference (188). Second, the number of neurons in primate
319 brains scales isometrically with brain size, indicating selection for constant neural density
320 and neuron size, a scaling relationship that contrasts with other orders of animals (100).
321 Thus, the relationship between absolute brain volume and self-control may be most
322 pronounced in the primate species in our sample, and may not generalize to all other
323 large-brained animals (e.g. whales, elephants), or taxa whose brains are organized
324 differently than primates (e.g. birds). Nonetheless, even when removing primate species
325 from the analysis, absolute brain volume remained the strongest predictor of species
326 differences in self-control. Third, ancestral state reconstructions indicate that both
327 absolute and relative brain volume have increased over time in primates, while body mass
328 has not (189). Lastly, although not as predictive as absolute brain volume, residual brain
329 volume was a significant predictor of self-control in several of our analyses. Thus,
330 multiple lines of evidence implicate selection for brain volume (and organization)
331 independent of selection for body size, and our data illustrate the cognitive consequences
332 of these evolutionary trends.

333 With the exception of dietary breadth we found no significant relationships
334 between several socioecological variables and measures of self-control. These findings
335 are especially surprising given that both the percentage of fruit in the diet and social
336 group size correlate positively with neocortex ratio in anthropoid primates (86, 142). Our

337 findings suggest that the effect of social and ecological complexity may be limited to
338 influencing more specialized, and potentially domain-specific forms of cognition (190-
339 198). For example, among lemurs, sensitivity to cues of visual attention used to
340 outcompete others for food covaries positively with social group size, while a nonsocial
341 measure of self-control does not (147). Therefore, our ability to evaluate the predicted
342 relationships between socioecology and cognition will depend on measures designed to
343 assess skills in specific cognitive domains (e.g. visual perspective-taking or spatial
344 memory). In addition, more nuanced measures of social and ecological complexity (e.g.
345 coalitions or social networks) may be necessary to detect these relationships (199).

346 Overall, our results present a critical step toward understanding the cognitive
347 implications of evolutionary shifts in brain volume and dietary complexity. They also
348 underscore the need for future cognitive studies investigating how ecological factors
349 drive cognitive evolution in different psychological domains. These experimental
350 measures will be particularly important given that even the most predictive
351 neuroanatomical measures failed to account for more than 30% of cognitive variance
352 across species in this study. With a growing comparative database on the cognitive skills
353 of animals, we will gain significant insights into the nature of intelligence itself, and the
354 extent to which changes in specific cognitive abilities have evolved together, or
355 mosaically, across species. This increased knowledge of cognitive variation among living
356 species will also set the stage for stronger reconstructions of cognitive evolutionary
357 history. These approaches will be especially important given that cognition leaves so few
358 traces in the fossil record. In the era of comparative genomics and neurobiology, this

359 research provides a critical first step toward mapping the primate cognitive phenome and
360 unraveling the evolutionary processes that gave rise to the human mind.

361 **Methods**

362 In the A not B task, subjects were required to resist searching for food in a
363 previous hiding place when the food reward was visibly moved to a novel location.
364 Subjects watched as food was hidden in one of three containers positioned at the exterior
365 of a three-container array and were required to correctly locate the food in this container
366 on three consecutive familiarization trials before advancing to the test. In the test trial,
367 subjects initially saw the food hidden in the same container (container A), but then
368 watched as the food was moved to another container at the other end of the array
369 (container B; Movie S1). Subjects were then allowed to search for the hidden food, and
370 the accuracy of the first search location was recorded. This procedure differs slightly
371 from the original task used by Piaget (200) in which test trials involved the immediate
372 hiding of the reward in location B, without first hiding the reward in location A. Our
373 method followed the procedure of Amici et al. (175), and similarly we conducted one test
374 trial per subject. For the A not B task, our dependent measure was the percentage of
375 individuals that responded correctly on the test trial within each species.

376 In the cylinder task, subjects were first familiarized with finding a piece of food
377 hidden inside an opaque cylinder. Subjects were required to successfully find the food by
378 detouring to the side of the cylinder on 4/5 consecutive trials before advancing to the test.
379 In the following ten test trials, a transparent cylinder was substituted for the opaque
380 cylinder. To successfully retrieve the food, subjects needed to inhibit the impulse to reach
381 for the food directly (bumping into the cylinder) in favor of the detour response they had
382 used during the familiarization (Movie S2). Although subjects may have initially failed

383 to perceive the transparent barrier on the first test trial, they had ample opportunity to
384 adjust their behavior through visual, auditory and tactile feedback across the ten test trials.
385 For the cylinder task our dependent measure was the percentage of test trials that a
386 subject performed the correct detour response, which was averaged across individuals
387 within species to obtain species means.

388 In both tasks, all species were required to meet the same pretest criteria,
389 demonstrating a basic understanding of the task, and allowing meaningful comparison of
390 test data across species. Although the number of trials required to meet these criteria
391 varied between species, we found no significant relationship between the number of
392 pretest trials and test performance on either task (A not B: $t_{25} = -1.83$, $\lambda = 0.52$, $p = 0.08$;
393 Cylinder Task: $t_{30} = -1.14$, $\lambda = 0.69$, $p = 0.26$). For analyses involving brain volume, log
394 endocranial volume (ECV) was used as the measure of absolute brain volume and we
395 extracted residuals from a PGLS model of log ECV predicted by log body mass as our
396 primary measure of relative brain volume (ECV residuals; SI). As an additional measure
397 of relative brain size we incorporated Jerison's (1973) encephalization quotient (EQ),
398 calculated as: $EQ = \text{brain mass} / 0.12 * \text{body mass}^{0.67}$. Although EQ and a residuals
399 approach both measure deviation from an expected brain to body scaling relationship,
400 they differ in that EQ measures deviation from a previously estimated allometric
401 exponent using a larger dataset of species, whereas ECV residuals are derived from the
402 actual scaling relationship within our sample, while accounting for phylogeny.

403 To control for the non-independence of species level data, we used PGLS to test
404 the association between performance on the cognitive tasks and the explanatory variables
405 associated with each hypothesis. We predicted that brain volume, group size, and

406 measures of dietary complexity would covary positively with cognitive performance.
407 Thus, each of these predictions was evaluated using directional tests following the
408 conventions ($\delta = 0.01$, $\alpha = 0.04$) recommended by Rice & Gaines (201), which allocates
409 proportionally more of the null distribution in the predicted direction, while retaining
410 statistical power to detect unexpected patterns in the opposite direction. We incorporated
411 the parameter λ in the PGLS models to estimate phylogenetic signal and regression
412 parameters simultaneously, using a maximum likelihood procedure (202, 203).

413

414 **Acknowledgements**

415 We thank Natalie Cooper and Sunil Suchindran for statistical advice. We thank Jeff
416 Stevens and two anonymous reviewers for comments on drafts of this manuscript. This
417 work was supported by the National Evolutionary Synthesis Center (NESCent) through
418 support of a working group lead by Charles Nunn and Brian Hare. NESCent is supported
419 by the NSF #EF-0905606. For training in phylogenetic comparative methods, we thank
420 the AnthroTree Workshop (supported by NSF BCS-0923791). Additional author support
421 and acknowledgments are listed in the SI.

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References

- 429 1. Darwin C (1871) *The descent of man, and selection in relation to sex* (D.
430 Appleton and company, New York,) p 2 v.
- 431 2. Beran MJ & Beran MM (2004) Chimpanzees remember the results of one-by-one
432 addition of food items to sets over extended time periods. *Psychological Science*
433 15(2):94-99.
- 434 3. Bourjade M, Thierry B, Call J, & Dufour V (2012) Are monkeys able to plan for
435 future exchange? *Animal Cognition* 15(5):783-795.
- 436 4. Bugnyar T & Heinrich B (2005) Ravens, *corvus corax*, differentiate between
437 knowledgeable and ignorant competitors. *Proceedings of the Royal Society B-*
438 *Biological Sciences* 272(1573):1641-1646.
- 439 5. Call J & Tomasello M (2008) Does the chimpanzee have a theory of mind? 30
440 years later. *Trends in Cognitive Sciences* 12(5):187-192.
- 441 6. Cheney DL & Seyfarth RM (1990) *How monkeys see the world: Inside the mind*
442 *of another species* (University of Chicago Press, Chicago) p 377.
- 443 7. Cheney DL & Seyfarth RM (2007) *Baboon metaphysics : The evolution of a*
444 *social mind* (University of Chicago Press, Chicago) p 348.
- 445 8. Chittka L & Niven J (2009) Are bigger brains better? *Current Biology*
446 19(21):R995-R1008.
- 447 9. de Waal FB (2008) Putting the altruism back into altruism: The evolution of
448 empathy. *Annual Review of Psychology* 59:279-300.
- 449 10. Fragaszy DM & Perry S (2003) *The biology of traditions : Models and evidence*
450 (Cambridge University Press, Cambridge, UK ; New York) p 456.

- 451 11. Gacsi M, Miklosi A, Varga O, Topal J, & Csanyi V (2004) Are readers of our
452 face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent
453 recognition of human's attention. *Animal Cognition* 7(3):144-153.
- 454 12. Galef BG & Laland KN (2005) Social learning in animals: Empirical studies and
455 theoretical models. *Bioscience* 55(6):489-499.
- 456 13. Leavens DA & Hopkins WD (1998) Intentional communication by chimpanzees:
457 A cross-sectional study of the use of referential gestures. *Developmental*
458 *psychology* 34(5):813.
- 459 14. Liedtke J, Werdenich D, Gajdon G, Huber L, & Wanker R (2011) Big brains are
460 not enough: Performance of three parrot species in the trap-tube paradigm. *Animal*
461 *Cognition* 14(1):143-149.
- 462 15. Maestriperi D (2003) *Primate psychology* (Harvard University Press, Cambridge,
463 Mass. ; London) p 619.
- 464 16. Matsuzawa T (2001) *Primate origins of human cognition and behavior* (Springer,
465 Tokyo ; New York) p 587.
- 466 17. Miklósi Á (2008) *Dog behaviour, evolution, and cognition* (OUP Oxford).
- 467 18. Range F, Horn L, Bugnyar T, Gajdon GK, & Huber L (2009) Social attention in
468 keas, dogs, and human children. *Animal Cognition* 12(1):181-192.
- 469 19. Schmitt V, Pankau B, & Fischer J (2012) Old world monkeys compare to apes in
470 the primate cognition test battery. *PLoS One* 7(4):e32024.
- 471 20. Udell MaR, Dorey NR, & Wynne CDL (2010) What did domestication do to
472 dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews of*
473 *the Cambridge Philosophical Society* 85:327-345.

- 474 21. Wasserman E, Kiedinger R, & Bhatt R (1988) Conceptual behavior in pigeons:
475 Categories, subcategories, and pseudocategories. *Journal of Experimental*
476 *Psychology: Animal Behavior Processes* 14(3):235.
- 477 22. Webb B (2012) Cognition in insects. *Philosophical Transactions of the Royal*
478 *Society of London. Series B, Biological sciences* 367:2715-2722.
- 479 23. Weir AA, Chappell J, & Kacelnik A (2002) Shaping of hooks in new caledonian
480 crows. *Science* 297(5583):981-981.
- 481 24. Wright AA, Santiago HC, Sands SF, Kendrick DF, & Cook RG (1985) Memory
482 processing of serial lists by pigeons, monkeys, and people. *Science*
483 229(4710):287-289.
- 484 25. Arnold K & Zuberbühler K (2006) Language evolution: Semantic combinations
485 in primate calls. *Nature* 441(7091):303-303.
- 486 26. Benson-Amram S & Holekamp KE (2012) Innovative problem solving by wild
487 spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences*
488 279(1744):4087-4095.
- 489 27. Cook RG, Brown MF, & Riley DA (1985) Flexible memory processing by rats:
490 Use of prospective and retrospective information in the radial maze. *Journal of*
491 *Experimental Psychology: Animal Behavior Processes* 11(3):453.
- 492 28. Suddendorf T & Corballis MC (2010) Behavioural evidence for mental time
493 travel in nonhuman animals. *Behavioural Brain Research* 215(2):292-298.
- 494 29. MacLean EL & Hare B (2012) Bonobos and chimpanzees infer the target of
495 another's attention. *Animal Behaviour* 83(2):345-353.

- 496 30. Melis AP, Hare B, & Tomasello M (2006) Chimpanzees recruit the best
497 collaborators. *Science* 311(5765):1297-1300.
- 498 31. Emery NJ & Clayton NS (2004) The mentality of crows: Convergent evolution of
499 intelligence in corvids and apes. *Science* 306(5703):1903-1907.
- 500 32. Pepperberg IM & Pepperberg IM (2009) *The alex studies: Cognitive and*
501 *communicative abilities of grey parrots* (Harvard University Press).
- 502 33. Bekoff M, Allen C, & Burghardt GM eds (2002) *The cognitive animal :*
503 *Empirical and theoretical perspectives on animal cognition* (MIT Press,
504 Cambridge, Mass.), p 504.
- 505 34. Brannon EM & Terrace HS (1998) Ordering of the numerosities 1 to 9 by
506 monkeys. *Science* 282(5389):746-749.
- 507 35. Hampton RR, Zivin A, & Murray EA (2004) Rhesus monkeys (*macaca mulatta*)
508 discriminate between knowing and not knowing and collect information as needed
509 before acting. *Animal Cognition* 7(4):239-246.
- 510 36. Kaminski J, Call J, & Fischer J (2004) Word learning in a domestic dog: Evidence
511 for "fast mapping". *Science* 304(5677):1682-1683.
- 512 37. Mendes N, Hanus D, & Call J (2007) Raising the level: Orangutans use water as a
513 tool. *Biology Letters* 3(5):453-455.
- 514 38. Horner V & Whiten A (2005) Causal knowledge and imitation/emulation
515 switching in chimpanzees (*Pan troglodytes*) and children (*homo sapiens*). *Animal*
516 *cognition* 8(3):164-181.
- 517 39. Inoue S & Matsuzawa T (2007) Working memory of numerals in chimpanzees.
518 *Current Biology* 17(23):R1004-R1005.

- 519 40. Kaminski J, Call J, & Tomasello M (2008) Chimpanzees know what others know,
520 but not what they believe. *Cognition* 109(2):224-234.
- 521 41. Hare B (2011) From hominoid to hominid mind: What changed and why? *Annu.*
522 *Rev. Anthropol.* 40:293-309.
- 523 42. Penn DC, Holyoak KJ, & Povinelli DJ (2008) Darwin's mistake: Explaining the
524 discontinuity between human and nonhuman minds. *Behavioral and Brain*
525 *Sciences* 31(2):109-130; discussion 130-178.
- 526 43. Tomasello M (1999) *The cultural origins of human cognition* (Harvard University
527 Press, Cambridge, Mass.) pp vi, 248 p.
- 528 44. Whiten A & Erdal D (2012) The human socio-cognitive niche and its
529 evolutionary origins. *Philosophical Transactions of the Royal Society B:*
530 *Biological Sciences* 367(1599):2119-2129.
- 531 45. Shettleworth SJ (2012) Modularity, comparative cognition and human uniqueness.
532 *Philosophical transactions of the Royal Society of London. Series B, Biological*
533 *sciences* 367(1603):2794-2802.
- 534 46. Boyd R & Richerson PJ (2009) Culture and the evolution of human cooperation.
535 *Philos. Trans. R. Soc. B-Biol. Sci.* 364(1533):3281-3288.
- 536 47. Csibra G & Gergely G (2009) Natural pedagogy. *Trends in Cognitive Sciences*
537 13:148-153.
- 538 48. Fitch WT, Huber L, & Bugnyar T (2010) Social cognition and the evolution of
539 language: Constructing cognitive phylogenies. *Neuron* 65(6):795-814.

- 540 49. Haun D, Rapold C, Call J, Janzen G, & Levinson S (2006) Cognitive cladistics
541 and cultural override in hominid spatial cognition. *Proceedings of the National*
542 *Academy of Sciences* 103(46):17568-17573.
- 543 50. Herrmann E, Call J, Hernandez-Lloreda MV, Hare B, & Tomasello M (2007)
544 Humans have evolved specialized skills of social cognition: The cultural
545 intelligence hypothesis. *Science* 317(5843):1360-1366.
- 546 51. Hill K, Barton M, & Hurtado AM (2009) The emergence of human uniqueness:
547 Characters underlying behavioral modernity. *Evolutionary Anthropology*
548 18(5):187-200.
- 549 52. Hill K, Kaplan H, Lancaster J, & Hurtado A (2000) A theory of human life
550 history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology*
551 9(4):156-185.
- 552 53. Kagan J (2004) The uniquely human in human nature. *Daedalus* 133(4):77-88.
- 553 54. Melis AP & Semmann D (2010) How is human cooperation different?
554 *Philosophical Transactions of the Royal Society B: Biological Sciences*
555 365(1553):2663.
- 556 55. Meltzoff AN (1999) Origins of theory of mind, cognition and communication.
557 *Journal of communication disorders* 32(4):251-269.
- 558 56. Moll H & Tomasello M (2007) Cooperation and human cognition: The
559 vygotskian intelligence hypothesis. *Philos. Trans. R. Soc. B-Biol. Sci.*
560 362(1480):639-648.

- 561 57. Penn D & Povinelli D (2007) On the lack of evidence that non-human animals
562 possess anything remotely resembling a 'theory of mind'. *Philos Trans R Soc Lond*
563 *B Biol Sci* 362(1480):731-744.
- 564 58. Penn DC & Povinelli DJ (2007) Causal cognition in human and nonhuman
565 animals: A comparative, critical review. *Annu Rev Psychol* 58:97-118.
- 566 59. Dean LG, Kendal RL, Schapiro SJ, Thierry B, & Laland KN (2012) Identification
567 of the social and cognitive processes underlying human cumulative culture.
568 *Science* 335(6072):1114-1118.
- 569 60. Jensen K, Call J, & Tomasello M (2007) Chimpanzees are rational maximizers in
570 an ultimatum game. *Science* 318(5847):107-109.
- 571 61. Fehr E & Fischbacher U (2004) Third-party punishment and social norms.
572 *Evolution and Human Behavior* 25(2):63-87.
- 573 62. Beach FA (1950) The snark was a boojum. *American Psychologist* 5:115-124.
- 574 63. Bitterman ME (1965) Phyletic differences in learning. *American Psychologist*
575 20(6):396-410.
- 576 64. Griffin DR (1978) Prospects for a cognitive ethology. *Behavioral and Brain*
577 *Sciences* 1(4):527-538.
- 578 65. Hodos W & Campbell CB (1969) Scala naturae - why there is no theory in
579 comparative psychology. *Psychol. Rev.* 76(4):337-350.
- 580 66. Macphail EM (1987) The comparative psychology of intelligence. *Behavioral and*
581 *Brain Sciences* 10(4):645-656.

- 582 67. Platt ML & Spelke ES (2009) What can developmental and comparative cognitive
583 neuroscience tell us about the adult human brain? *Current Opinion in*
584 *Neurobiology* 19(1):1-5.
- 585 68. Shettleworth SJ (1993) Where is the comparison in comparative cognition?:
586 Alternative research programs. *Psychological Science* 4(3):179-184.
- 587 69. Shettleworth SJ (2009) The evolution of comparative cognition: Is the snark still a
588 boojum? *Behavioural Processes* 80(3):210-217.
- 589 70. MacLean EL, et al. (2012) How does cognition evolve? Phylogenetic comparative
590 psychology. *Animal Cognition* 15(2):223-238.
- 591 71. Haun D, Jordan FM, Vallortigara G, & Clayton NS (2010) Origins of spatial,
592 temporal and numerical cognition: Insights from comparative psychology. *Trends*
593 *in Cognitive Sciences* 14(12):552-560.
- 594 72. Bitterman ME (1965) Evolution of intelligence. *Scientific American* 212(1):92-
595 100.
- 596 73. Bitterman ME (1975) The comparative analysis of learning. *Science*
597 188(4189):699-709.
- 598 74. Bitterman ME (1960) Toward a comparative psychology of learning. *American*
599 *Psychologist* 15(11):704-712.
- 600 75. Reader SM (2014) Evolution of cognition. *Oxford bibliographies in evolutionary*
601 *biology*, ed Losos JB (Oxford University Press, New York).
- 602 76. Shultz S & Dunbar RIM (2010) Species differences in executive function
603 correlate with hippocampus volume and neocortex ratio across nonhuman
604 primates. *Journal of Comparative Psychology* 124(3):252-260.

- 605 77. Deaner RO, Isler K, Burkart J, & van Schaik C (2007) Overall brain size, and not
606 encephalization quotient, best predicts cognitive ability across non-human
607 primates. *Brain Behavior and Evolution* 70(2):115-124.
- 608 78. Roth G & Dicke U (2005) Evolution of the brain and intelligence. *Trends in*
609 *Cognitive Sciences* 9(5):250-257.
- 610 79. Barton RA (1998) Visual specialization and brain evolution in primates.
611 *Proceedings of the Royal Society of London Series B-Biological Sciences*
612 265(1409):1933-1937.
- 613 80. Barton RA (1999) The evolutionary ecology of the primate brain. *Comparative*
614 *primate socioecology*, ed Lee PC (Cambridge University Press, Cambridge), pp
615 167-203.
- 616 81. Barton RA (2006) Primate brain evolution: Integrating comparative,
617 neurophysiological, and ethological data. *Evolutionary Anthropology* 15(6):224-
618 236.
- 619 82. Beauchamp G & Fernandez-Juricic E (2004) Is there a relationship between
620 forebrain size and group size in birds? *Evolutionary Ecology Research* 6(6):833-
621 842.
- 622 83. Deaner R, van Schaik C, & Johnson V (2006) Do some taxa have better domain-
623 general cognition than others? A meta-analysis of nonhuman primate studies.
624 *Evolutionary Psychology* 4:149-196.
- 625 84. Deaner RO, Nunn CL, & van Schaik CP (2000) Comparative tests of primate
626 cognition: Different scaling methods produce different results. *Brain Behavior*
627 *and Evolution* 55(1):44-52.

- 628 85. Dunbar RI (1998) The social brain hypothesis. *Evolutionary Anthropology*
629 6(5):178-190.
- 630 86. Dunbar RI & Shultz S (2007) Understanding primate brain evolution. *Philos.*
631 *Trans. R. Soc. B-Biol. Sci.* 362(1480):649-658.
- 632 87. Dunbar RIM (2003) The social brain: Mind, language, and society in evolutionary
633 perspective. *Annu. Rev. Anthropol.* 32:163-181.
- 634 88. Gibson KR (2002) Evolution of human intelligence: The roles of brain size and
635 mental construction. *Brain, Behavior and Evolution* 59(1-2):10-20.
- 636 89. Healy SD & Rowe C (2007) A critique of comparative studies of brain size.
637 *Proceedings of the Royal Society B-Biological Sciences* 274(1609):453-464.
- 638 90. Shultz S & Dunbar R (2010) Encephalization is not a universal
639 macroevolutionary phenomenon in mammals but is associated with sociality.
640 *Proceedings of the National Academy of Sciences* 107(50):21582-21586.
- 641 91. Smaers J & Soligo C (2013) Brain reorganization, not relative brain size,
642 primarily characterizes anthropoid brain evolution. *Proceedings of the Royal*
643 *Society B: Biological Sciences* 280(1759).
- 644 92. Reader SM, Hager Y, & Laland KN (2011) The evolution of primate general and
645 cultural intelligence. *Philos. Trans. R. Soc. B-Biol. Sci.* 366(1567):1017-1027.
- 646 93. Nunn CL (2011) *The comparative method in evolutionary anthropology and*
647 *biology* (University of Chicago Press).
- 648 94. Balda RP, Kamil AC, & Bednekoff PA (1996) Predicting cognitive capacities
649 from natural histories: Examples from four corvid species. *Current Ornithology*
650 13:33-66.

- 651 95. Czeschlik T (1998) Animal cognition – the phylogeny and ontogeny of cognitive
652 abilities. *Animal Cognition* 1(1):1-2.
- 653 96. Garland T & Adolph SC (1994) Why not to do 2-species comparative-studies -
654 limitations on inferring adaptation. *Physiol. Zool.* 67(4):797-828.
- 655 97. Gomez JC (2005) Species comparative studies and cognitive development. *Trends*
656 *in Cognitive Sciences* 9(3):118-125.
- 657 98. Papini MR (2002) Pattern and process in the evolution of learning. *Psychol. Rev.*
658 109(1):186-201.
- 659 99. Sherwood CC, *et al.* (2006) Evolution of increased glia–neuron ratios in the
660 human frontal cortex. *Proceedings of the National Academy of Sciences*
661 103(37):13606-13611.
- 662 100. Herculano-Houzel S, Collins CE, Wong P, & Kaas JH (2007) Cellular scaling
663 rules for primate brains. *Proceedings of the National Academy of Sciences*
664 104(9):3562-3567.
- 665 101. Finlay BL & Darlington RB (1995) Linked regularities in the development and
666 evolution of mammalian brains. *Science* 268(5217):1578-1584.
- 667 102. Kaas JH (2000) Why is brain size so important: Design problems and solutions as
668 neocortex gets bigger or smaller. *Brain and Mind* 1(1):7-23.
- 669 103. Holloway RL (1966) Cranial capacity and neuron number: A critique and
670 proposal. *American Journal of Physical Anthropology* 25(3):305-314.
- 671 104. Herculano - Houzel S (2011) Brains matter, bodies maybe not: The case for
672 examining neuron numbers irrespective of body size. *Annals of the New York*
673 *Academy of Sciences* 1225(1):191-199.

- 674 105. Herculano-Houzel S (2012) The remarkable, yet not extraordinary, human brain
675 as a scaled-up primate brain and its associated cost. *Proceedings of the National*
676 *Academy of Sciences* 109(Supplement 1):10661-10668.
- 677 106. Herculano-Houzel S (2009) The human brain in numbers: A linearly scaled-up
678 primate brain. *Frontiers in Human Neuroscience* 3.
- 679 107. Azevedo FAC, *et al.* (2009) Equal numbers of neuronal and nonneuronal cells
680 make the human brain an isometrically scaled-up primate brain. *J. Comp. Neurol.*
681 513(5):532-541.
- 682 108. Jerison HJ (1973) *Evolution of the brain and intelligence* (Academic Press, New
683 York,) p 482.
- 684 109. Kappelman J (1996) The evolution of body mass and relative brain size in fossil
685 hominids. *Journal of Human Evolution* 30(3):243-276.
- 686 110. Lefebvre L, Reader SM, & Sol D (2004) Brains, innovations and evolution in
687 birds and primates. *Brain Behavior and Evolution* 63(4):233-246.
- 688 111. Sol D, Bacher S, Reader SM, & Lefebvre L (2008) Brain size predicts the success
689 of mammal species introduced into novel environments. *The American Naturalist*
690 172(s1):S63-S71.
- 691 112. Sol D, Duncan RP, Blackburn TM, Cassey P, & Lefebvre L (2005) Big brains,
692 enhanced cognition, and response of birds to novel environments. *Proc. Natl.*
693 *Acad. Sci. U. S. A.* 102(15):5460-5465.
- 694 113. Rightmire GP (2004) Brain size and encephalization in early to mid - pleistocene
695 homo. *American Journal of Physical Anthropology* 124(2):109-123.
- 696 114. Lovejoy CO (1981) The origin of man. *Science* 211(4480):341-350.

- 697 115. Seyfarth RM & Cheney DL (2002) What are big brains for? *Proceedings of the*
698 *National Academy of Sciences* 99(7):4141-4142.
- 699 116. Aiello LC & Wheeler P (1995) The expensive-tissue hypothesis: The brain and
700 the digestive system in human and primate evolution. *Current Anthropology*
701 36(2):199-221.
- 702 117. Isler K & van Schaik CP (2006) Metabolic costs of brain size evolution. *Biology*
703 *Letters* 2(4):557-560.
- 704 118. Barrickman NL, Bastian ML, Isler K, & van Schaik CP (2008) Life history costs
705 and benefits of encephalization: A comparative test using data from long-term
706 studies of primates in the wild. *Journal of Human Evolution* 54(5):568-590.
- 707 119. Bennett PM & Harvey PH (1985) Brain size, development and metabolism in
708 birds and mammals. *Journal of Zoology* 207:491-509.
- 709 120. Charvet CJ & Finlay BL (2012) Embracing covariation in brain evolution: Large
710 brains, extended development, and flexible primate social systems. *Progress in*
711 *Brain Research* 195:71-87.
- 712 121. Isler K & van Schaik CP (2009) The expensive brain: A framework for explaining
713 evolutionary changes in brain size. *Journal of Human Evolution* 57(4):392-400.
- 714 122. Martin RD (1981) Relative brain size and basal metabolic rate in terrestrial
715 vertebrates. *Nature* 293(5827):57-60.
- 716 123. Jerison HJ & Barlow H (1985) Animal intelligence as encephalization.
717 *Philosophical Transactions of the Royal Society of London. B, Biological*
718 *Sciences* 308(1135):21-35.

- 719 124. Byrne RW & Corp N (2004) Neocortex size predicts deception rate in primates.
720 *Proceedings of the Royal Society of London Series B-Biological Sciences*
721 271(1549):1693-1699.
- 722 125. Byrne RW & Whiten AW (1988) *Machiavellian intelligence : Social expertise*
723 *and the evolution of intellect in monkeys, apes, and humans* (Clarendon Press,
724 Oxford) pp xiv, 413.
- 725 126. Jolly A (1966) Lemur social behavior and primate intelligence. *Science* 153:501-
726 506.
- 727 127. Humphrey NK (1976) The social function of intellect. *Growing points in ethology*,
728 eds Bateson P & Hinde R (Cambridge University Press, Cambridge), pp 303-317.
- 729 128. de Waal FBM & Tyack PL (2003) *Animal social complexity : Intelligence,*
730 *culture, and individualized societies* (Harvard University Press, Cambridge,
731 Mass.) pp xiv, 616.
- 732 129. Dunbar RI & Shultz S (2007) Evolution in the social brain. *Science*
733 317(5843):1344-1347.
- 734 130. Bond AB, Kamil AC, & Balda RP (2003) Social complexity and transitive
735 inference in corvids. *Animal Behaviour* 65(3):479-487.
- 736 131. Byrne RW & Bates LA (2007) Sociality, evolution and cognition. *Current*
737 *Biology* 17(16):R714-723.
- 738 132. Cunningham E & Janson C (2007) A socioecological perspective on primate
739 cognition, past and present. *Animal Cognition* 10(3):273-281.
- 740 133. Dunbar RIM (1996) *Grooming, gossip and the evolution of language* (Faber and
741 Faber, London) p 230.

- 742 134. Emery N (2005) The evolution of social cognition. *The cognitive neuroscience of*
743 *social behaviour*, eds Easton A & Emery N (Routledge), pp 115-156.
- 744 135. Holekamp KE (2007) Questioning the social intelligence hypothesis. *Trends in*
745 *Cognitive Sciences* 11(2):65-69.
- 746 136. Kummer H, Daston L, Gigerenzer G, & Silk J (1997) The social intelligence
747 hypothesis. *Human by nature: Between biology and the social sciences*, eds
748 Weingart P, Mitchell SD, Richerson PJ, & Maasen S (Lawrence Erlbaum
749 Associates, Mahwah, NJ), pp 157-179.
- 750 137. MacLean EL, Merritt DJ, & Brannon EM (2008) Social organization predicts
751 transitive reasoning in prosimian primates. *Animal Behaviour* 76(2):479-486.
- 752 138. Paz-y-Miño CG, Bond AB, Kamil AC, & Balda RP (2004) Pinyon jays use
753 transitive inference to predict social dominance. *Nature* 430(7001):778-781.
- 754 139. Reader SM & Laland KN (2002) Social intelligence, innovation, and enhanced
755 brain size in primates. *Proceedings of the National Academy of Sciences*
756 99(7):4436-4441.
- 757 140. Barrett L, Henzi P, & Rendall D (2007) Social brains, simple minds: Does social
758 complexity really require cognitive complexity? *Philos. Trans. R. Soc. B-Biol. Sci.*
759 362(1480):561-575.
- 760 141. Seyfarth RM, Cheney DL, & Bergman TJ (2005) Primate social cognition and the
761 origins of language. *Trends in Cognitive Sciences* 9(6):264-266.
- 762 142. Barton RA (1996) Neocortex size and behavioural ecology in primates.
763 *Proceedings of the Royal Society of London. Series B, Biological sciences*
764 263(1367):173-177.

- 765 143. Kudo H & Dunbar RIM (2001) Neocortex size and social network size in
766 primates. *Animal Behaviour* 62(4):711-722.
- 767 144. Dunbar RIM & Shultz S (2007) Evolution in the social brain. *Science*
768 317(5843):1344-1347.
- 769 145. Pérez-Barbería FJ, Shultz S, & Dunbar RIM (2007) Evidence for coevolution of
770 sociality and relative brain size in three orders of mammals. *Evolution*
771 61(12):2811-2821.
- 772 146. Shultz S & Dunbar RIM (2007) The evolution of the social brain: Anthropoid
773 primates contrast with other vertebrates. *Proceedings of the Royal Society of*
774 *London Series B-Biological Sciences* 274(1624):2429-2436.
- 775 147. MacLean EL, et al. (2013) Group size predicts social but not nonsocial cognition
776 in lemurs. *PLoS One* 8(6):e66359.
- 777 148. Sandel AA, MacLean E, & Hare B (2011) Evidence from four lemur species that
778 ringtailed lemur social cognition converges with that of haplorhine primates.
779 *Animal Behaviour* 81(5):925-931.
- 780 149. Bugnyar T, Stowe M, & Heinrich B (2004) Ravens, *corvus corax*, follow gaze
781 direction of humans around obstacles. *Proceedings of the Royal Society of London*
782 *Series B-Biological Sciences* 271(1546):1331-1336.
- 783 150. Plotnik JM, De Waal FB, & Reiss D (2006) Self-recognition in an Asian elephant.
784 *Proceedings of the National Academy of Sciences* 103(45):17053-17057.
- 785 151. Holekamp KE, Sakai ST, & Lundrigan BL (2007) Social intelligence in the
786 spotted hyena (*crocuta crocuta*). *Philosophical Transactions of the Royal Society*
787 *B: Biological Sciences* 362(1480):523-538.

- 788 152. Milton K (1981) Distribution patterns of tropical plant foods as an evolutionary
789 stimulus to primate mental development. *American Anthropologist* 83(3):534-548.
- 790 153. Clutton-Brock TH & Harvey PH (1980) Primates, brains and ecology. *Journal of*
791 *Zoology* 190(MAR):309-323.
- 792 154. Barton RA (2012) Embodied cognitive evolution and the cerebellum.
793 *Philosophical Transactions of the Royal Society B: Biological Sciences*
794 367(1599):2097-2107.
- 795 155. Zuberbühler K & Janmaat K (2010) Foraging cognition in non-human primates.
796 *Primate Neuroethology*:64-83.
- 797 156. Fish JL & Lockwood CA (2003) Dietary constraints on encephalization in
798 primates. *American Journal of Physical Anthropology* 120(2):171-181.
- 799 157. Shettleworth SJ (2010) *Cognition, evolution, and behavior* (Oxford ; New York :
800 Oxford University Press, 2010.) 2nd Ed.
- 801 158. Balda RP & Kamil AC (1989) A comparative study of cache recovery by 3 corvid
802 species. *Animal Behaviour* 38:486-495.
- 803 159. Barkley CL & Jacobs LF (2007) Sex and species differences in spatial memory in
804 food-storing kangaroo rats. *Animal Behaviour* 73:321-329.
- 805 160. Bednekoff PA, Balda RP, Kamil AC, & Hile AG (1997) Long-term spatial
806 memory in four seed-caching corvid species. *Animal Behaviour* 53(2):335-341.
- 807 161. Heilbronner SR, Rosati AG, Stevens JR, Hare B, & Hauser MD (2008) A fruit in
808 the hand or two in the bush? Divergent risk preferences in chimpanzees and
809 bonobos. *Biology Letters* 4(3):246-249.

- 810 162. Krebs JR (1990) Food-storing birds - adaptive specialization in brain and
811 behavior. *Philos. Trans. R. Soc. Lond. Ser. B-Biol. Sci.* 329(1253):153-160.
- 812 163. Krebs JR, Sherry DF, Healy SD, Perry VH, & Vaccarino AL (1989) Hippocampal
813 specialization of food-storing birds. *Proceedings of the National Academy of*
814 *Sciences* 86(4):1388-1392.
- 815 164. Platt ML, Brannon EM, Briese TL, & French JA (1996) Differences in feeding
816 ecology predict differences in performance between golden lion tamarins
817 (*leontopithecus rosalia*) and wied's marmosets (*callithrix kuhli*) on spatial and
818 visual memory tasks. *Animal Learning & Behavior* 24(4):384-393.
- 819 165. Rosati AG, Stevens JR, Hare B, & Hauser MD (2007) The evolutionary origins of
820 human patience: Temporal preferences in chimpanzees, bonobos, and human
821 adults. *Current Biology* 17(19):1663-1668.
- 822 166. Rosati AG, Stevens JR, & Hauser MD (2006) The effect of handling time on
823 temporal discounting in two new world primates. *Animal Behaviour* 71(6):1379-
824 1387.
- 825 167. Shettleworth SJ (1990) Spatial memory in food-storing birds. *Philos. Trans. R.*
826 *Soc. B-Biol. Sci.* 329(1253):143-151.
- 827 168. Hare TA, Camerer CF, & Rangel A (2009) Self-control in decision-making
828 involves modulation of the vmPFC valuation system. *Science* 324(5927):646-648.
- 829 169. Hauser MD (1999) Perseveration, inhibition and the prefrontal cortex: A new look.
830 *Current Opinion in Neurobiology* 9(2):214-222.

- 831 170. Tangney JP, Baumeister RF, & Boone AL (2004) High self - control predicts
832 good adjustment, less pathology, better grades, and interpersonal success. *Journal*
833 *of Personality* 72(2):271-324.
- 834 171. Moffitt TE, *et al.* (2011) A gradient of childhood self-control predicts health,
835 wealth, and public safety. *Proceedings of the National Academy of Sciences*
836 108(7):2693-2698.
- 837 172. Mischel W, Shoda Y, & Rodriguez ML (1989) Delay of gratification in children.
838 *Science* 244(4907):933-938.
- 839 173. Bezdjian S, Baker LA, & Tuvblad C (2011) Genetic and environmental influences
840 on impulsivity: A meta-analysis of twin, family and adoption studies. *Clin.*
841 *Psychol. Rev.* 31(7):1209-1223.
- 842 174. Boogert NJ, Anderson RC, Peters S, Searcy WA, & Nowicki S (2011) Song
843 repertoire size in male song sparrows correlates with detour reaching, but not with
844 other cognitive measures. *Animal Behaviour* 81(6):1209-1216.
- 845 175. Amici F, Aureli F, & Call J (2008) Fission-fusion dynamics, behavioral flexibility,
846 and inhibitory control in primates. *Current Biology* 18(18):1415-1419.
- 847 176. Sherwood CC, *et al.* (2006) Evolution of increased glia-neuron ratios in the
848 human frontal cortex. *Proc. Natl. Acad. Sci. U. S. A.* 103(37):13606-13611.
- 849 177. Smaers J, *et al.* (2011) Primate prefrontal cortex evolution: Human brains are the
850 extreme of a lateralized ape trend. *Brain, Behavior and Evolution* 77(2):67-78.
- 851 178. Genovesio A, Wise SP, & Passingham RE (2014) Prefrontal–parietal function:
852 From foraging to foresight. *Trends in Cognitive Sciences* 18(2):72-81.

- 853 179. Preuss TM (1995) Do rats have prefrontal cortex? The rose-woolsey-akert
854 program reconsidered. *Journal of Cognitive Neuroscience* 7(1):1-24.
- 855 180. Passingham RE & Wise SP (2012) *The neurobiology of the prefrontal cortex:
856 Anatomy, evolution, and the origin of insight* (Oxford University Press).
- 857 181. De Kort SR & Clayton NS (2006) An evolutionary perspective on caching by
858 corvids. *Proceedings of the Royal Society B: Biological Sciences* 273(1585):417-
859 423.
- 860 182. Rilling JK, Glasser MF, Jbabdi S, Andersson J, & Preuss TM (2011) Continuity,
861 divergence, and the evolution of brain language pathways. *Frontiers in
862 Evolutionary Neuroscience* 3.
- 863 183. Mantini D, Corbetta M, Romani GL, Orban GA, & Vanduffel W (2013)
864 Evolutionarily novel functional networks in the human brain? *The Journal of
865 Neuroscience* 33(8):3259-3275.
- 866 184. Rilling JK, *et al.* (2008) The evolution of the arcuate fasciculus revealed with
867 comparative dti. *Nat. Neurosci.* 11(4).
- 868 185. Mars RB, Sallet J, Neubert F-X, & Rushworth MF (2013) Connectivity profiles
869 reveal the relationship between brain areas for social cognition in human and
870 monkey temporoparietal cortex. *Proceedings of the National Academy of Sciences*
871 110(26):10806-10811.
- 872 186. MacLean EL, Barrickman NL, Johnson EM, & Wall CE (2009) Sociality, ecology,
873 and relative brain size in lemurs. *Journal of Human Evolution* 56(5):471-478.

- 874 187. Allen KL & Kay RF (2012) Dietary quality and encephalization in platyrrhine
875 primates. *Proceedings of the Royal Society B: Biological Sciences* 279(1729):715-
876 721.
- 877 188. Burnham KP & Anderson DR (2002) *Model selection and multi-model inference:*
878 *A practical information-theoretic approach* (Springer).
- 879 189. Montgomery SH, Capellini I, Barton RA, & Mundy NI (2010) Reconstructing the
880 ups and downs of primate brain evolution: Implications for adaptive hypotheses
881 and homo floresiensis. *BMC Biology* 8(1):9.
- 882 190. Gigerenzer G (1997) The modularity of social intelligence. *Machiavellian*
883 *intelligence ii: Extensions and evaluation*, eds Whiten A & Byrne RA (Cambridge
884 University Press, Cambridge), pp 264-288.
- 885 191. Geary DC & Huffman KJ (2002) Brain and cognitive evolution: Forms of
886 modularity and functions of mind. *Psychological bulletin* 128(5):667.
- 887 192. Cosmides L (1989) The logic of social-exchange - has natural-selection shaped
888 how humans reason - studies with the wason selection task. *Cognition* 31(3):187-
889 276.
- 890 193. Fodor JA (1983) *The modularity of mind : An essay on faculty psychology* (MIT
891 Press, Cambridge, Mass.) p 145.
- 892 194. Hirschfeld LA & Gelman SA (1994) *Mapping the mind: Domain specificity in*
893 *cognition and culture* (Cambridge University Press).
- 894 195. Cosmides L & Tooby J (1994) Origins of domain specificity: The evolution of
895 functional organization. *Mapping the mind: Domain specificity in cognition and*
896 *culture*:85-116.

- 897 196. Leslie AM (1994) Tamm, toby, and agency: Core architecture and domain
898 specificity. *Mapping the mind: Domain specificity in cognition and culture*:119-
899 148.
- 900 197. Gelman R & Williams EM (1998) Enabling constraints for cognitive development
901 and learning: Domain specificity and epigenesis. *Handbook of child psychology*,
902 ed Damon W (John Wiley & Sons In., Hoboken, NJ), Vol 2: Cognition,
903 perception and language, pp 575-630.
- 904 198. Amici F, Barney B, Johnson VE, Call J, & Aureli F (2012) A modular mind? A
905 test using individual data from seven primate species. *PLoS One* 7(12):e51918.
- 906 199. Silk J, Cheney D, & Seyfarth R (2013) A practical guide to the study of social
907 relationships. *Evolutionary Anthropology: Issues, News, and Reviews* 22(5):213-
908 225.
- 909 200. Piaget J (1954) *The construction of reality in the child* (Basic Books, New York).
- 910 201. Rice WR & Gaines SD (1994) 'Heads i win, tails you lose' : Testing
911 directional alternative hypotheses in ecological and evolutionary research. *Trends*
912 *Ecol. Evol.* 9(6):235-237.
- 913 202. Freckleton RP, Harvey PH, & Pagel M (2002) Phylogenetic analysis and
914 comparative data: A test and review of evidence. *American Naturalist*
915 160(6):712-726.
- 916 203. Pagel M (1999) Inferring the historical patterns of biological evolution. *Nature*
917 401(6756):877-884.

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920 Table 1. Phylogenetic signal in the cognitive data. λ (ML) indicates the maximum
 921 likelihood estimate for λ , a statistical measure of phylogenetic signal (203). P-values are
 922 based on a likelihood ratio test comparing the model with the maximum likelihood
 923 estimate of λ to a model where λ is fixed at 0 (the null alternative representing no
 924 phylogenetic signal).

Data source	Dependent Measure	λ (ML)	Log Likelihood		p value
			$\lambda = \text{ML}$	$\lambda = 0$	
All species	Cylinder Score	0.83	-2.14	-4.13	0.05
	A not B Score	0.72	-12.60	-14.90	0.03
	Composite Score	0.76	-2.00	-3.47	0.09
Primates	Cylinder Score	0.95	-0.62	-3.63	0.01
	A not B Score	0.48	-6.05	-7.54	0.08
	Composite Score	0.86	-0.98	-3.32	0.03

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939 Table 2. The relationship between brain volume, socioecology, observational measures
 940 of cognition, and performance on the cognitive tasks. The sign of the t-statistic indicates
 941 the direction of the relationship between variables. Data regarding social learning,
 942 innovation, extractive foraging, tool use, tactical deception (all of which covary), and
 943 primate ‘g_s’ scores were adjusted for research effort and obtained from Reader et al. (92)
 944 and Byrne & Corp (124). PCA 1 is equivalent to the ‘g_s’ score calculated by Reader et al.
 945 (92) restricted to species in this dataset. We used the arcsine square-root transformed
 946 mean proportion of correct responses for each species as the dependent measure in all
 947 analyses, as this best met the statistical assumptions of our tests. Socioecological data
 948 were log transformed (group size) or arcsine square root transformed (proportion fruit in
 949 diet) for analysis.

950

Data Source	Explanatory Variable	Dependent Measure	t	df	p	r ²	λ	
All Species	Absolute Brain Volume	Cylinder	4.79	30	< 0.01	0.43	0.00	
		A not B	1.03	25	0.16	0.04	0.69	
		A not B (no elephant)	5.44	24	< 0.01	0.55	0.00	
	Residual Brain Volume	Composite	Composite	5.67	21	< 0.01	0.60	0.00
			Cylinder	2.31	30	0.01	0.15	0.98
			A not B	0.05	25	0.96	< 0.01	0.72
		A not B (no elephant)	A not B (no elephant)	0.33	24	0.37	< 0.01	0.58
			Composite	0.78	21	0.22	0.03	0.67
			Cylinder	3.30	10	< 0.01	0.52	0.00
Non-Primates	Absolute Brain Volume	A not B	-0.59	7	0.71	0.05	0.00	
		Composite	2.54	6	0.02	0.52	0.00	
		Cylinder	1.12	10	0.14	0.11	0.69	
	Residual Brain Volume	A not B	-1.83	7	0.95	0.32	0.00	
		Composite	-0.58	6	0.71	0.05	0.25	
		Cylinder	5.01	18	< 0.01	0.58	0.00	
Primates	Absolute Brain Volume	A not B	4.39	16	< 0.01	0.55	0.00	
		Composite	5.27	13	< 0.01	0.68	0.00	
		Cylinder	2.26	18	0.02	0.22	0.93	
	Residual Brain Volume	A not B	2.64	16	0.01	0.30	0.00	
		Composite	1.69	13	0.06	0.18	0.60	
		Cylinder	-0.75	13	0.77	0.04	0.83	
Primates	Population Group Size		-0.33	13	0.63	0.01	0.82	
	Foraging Group Size		0.11	13	0.46	< 0.01	0.85	
	Percent Fruit in Diet		5.62	12	< 0.01	0.72	0.75	
	Dietary Breadth		2.63	9	0.03	0.44	0.00	
	Social Learning		1.99	9	0.08	0.31	0.00	
	Innovation	Composite	3.10	9	0.01	0.52	0.00	
	Extractive Foraging		3.12	9	0.01	0.52	0.00	
	Tool Use		4.06	9	< 0.01	0.65	0.00	
	Tactical Deception		3.61	9	< 0.01	0.59	0.00	
	g _s		3.61	9	< 0.01	0.59	0.00	
	PCA 1		3.61	9	< 0.01	0.59	0.00	

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953 Figure Captions

954 *Figure 1.* A phylogeny of the species included in this study. Branch lengths are
955 proportional to time except where long branches have been truncated by parallel diagonal
956 lines (split between mammals and birds ~292 MY). MY = millions of years.

957

958 *Figure 2.* Cognitive scores as a function of log endocranial volume (ECV) and residual
959 brain volume (ECV residuals). In both tasks and in the composite measure, ECV was a
960 significant predictor of self-control. Relative brain volume universally explained less
961 variance. Plots show statistically transformed data (see Methods for details). The gray
962 dashed line shows an alternate model excluding the elephant from analysis. OW = Old
963 World, NW = New World.

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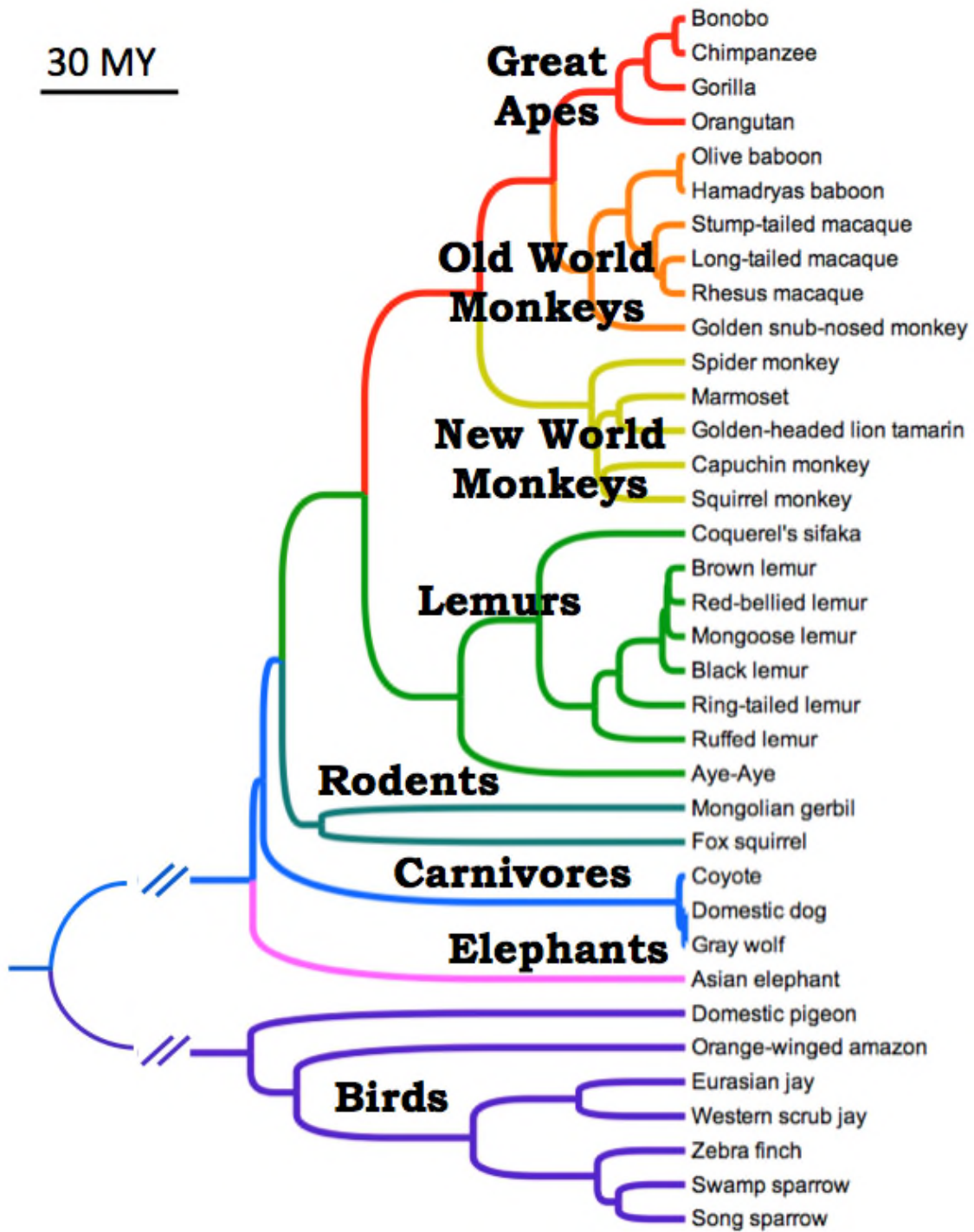
965 *Figure 3.* Cognitive scores for primates as a function of A) absolute and residual
966 endocranial volume (ECV), B) foraging and population social group size, and C)
967 frugivory and dietary breadth. Absolute ECV, residual ECV and dietary breadth covaried
968 positively with measures of self-control. Plots show statistically transformed data (see
969 Methods and Table 2 for details). OW = Old World, NW = New World.

970

971 *Figure 4.* Ancestral state reconstruction of cognitive skills for self-control. We generated
972 the maximum likelihood estimates for ancestral states along the primate phylogeny using
973 data from the composite measure (average score across tasks for species that participated
974 in both tasks). The red circles along the tips of the phylogeny are proportional to the

975 extant species' composite scores (larger circles represent higher scores). The blue circles
976 at the internal nodes of the phylogeny represent the estimated ancestral states for the
977 composite score, with the estimated value indicated within circles at each node.
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979 Figure 1.



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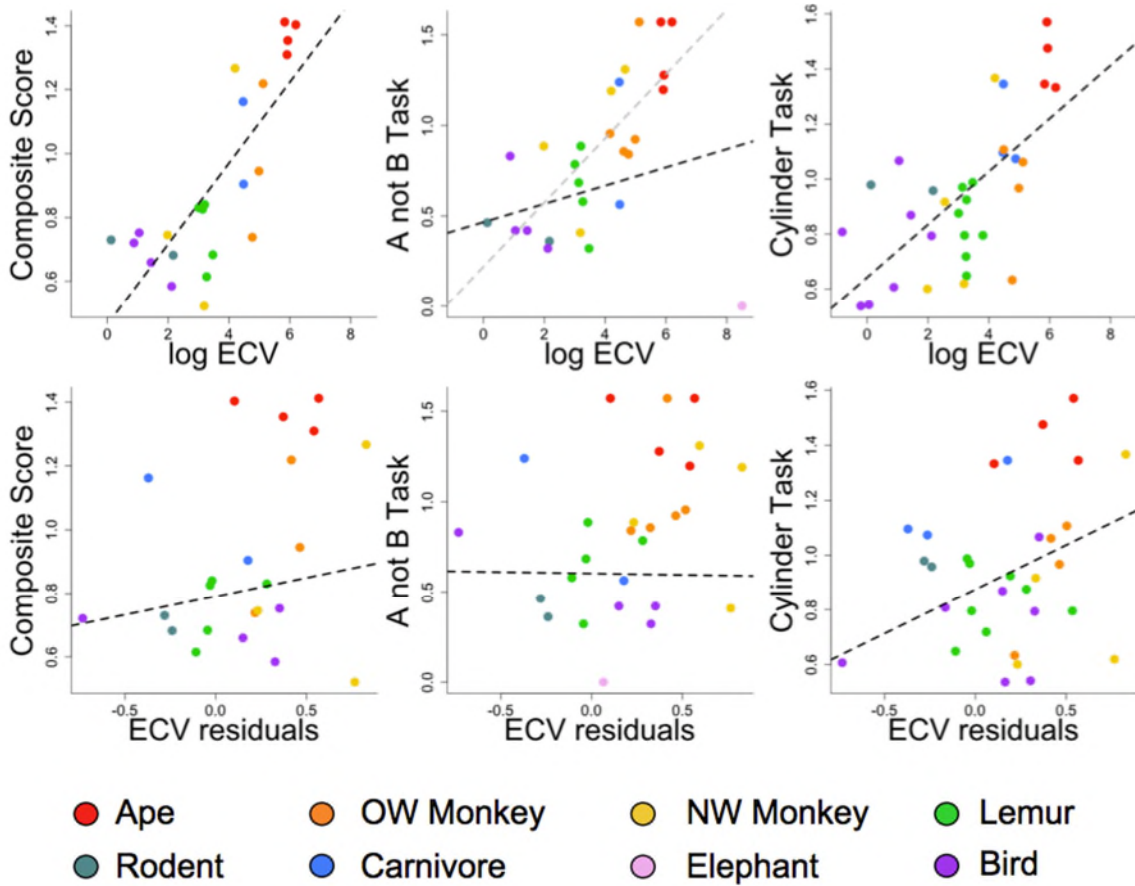
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984 Figure 2.

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Figure 3.

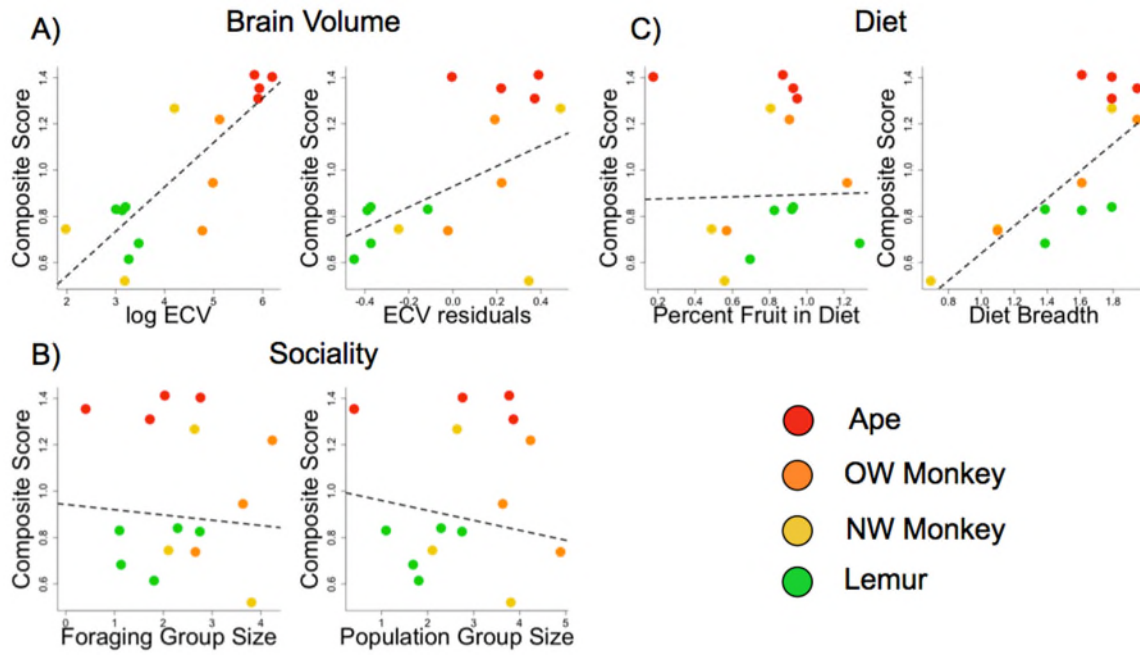


Figure 4.

