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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

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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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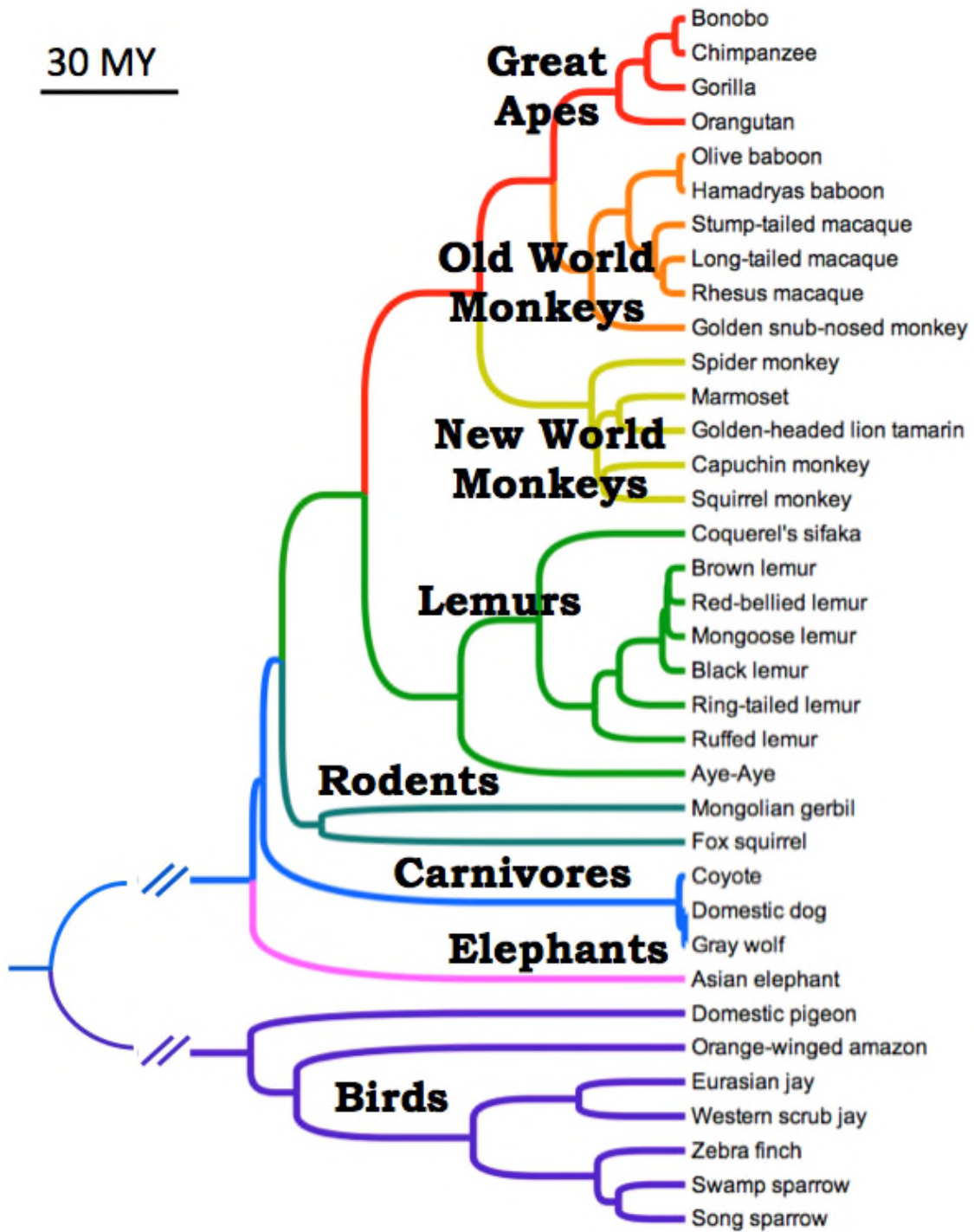
965 *Figure 3.* Cognitive scores for primates as a function of A) absolute and residual
966 endocranial volume (ECV), B) foraging and population social group size, and C)
967 frugivory and dietary breadth. Absolute ECV, residual ECV and dietary breadth covaried
968 positively with measures of self-control. 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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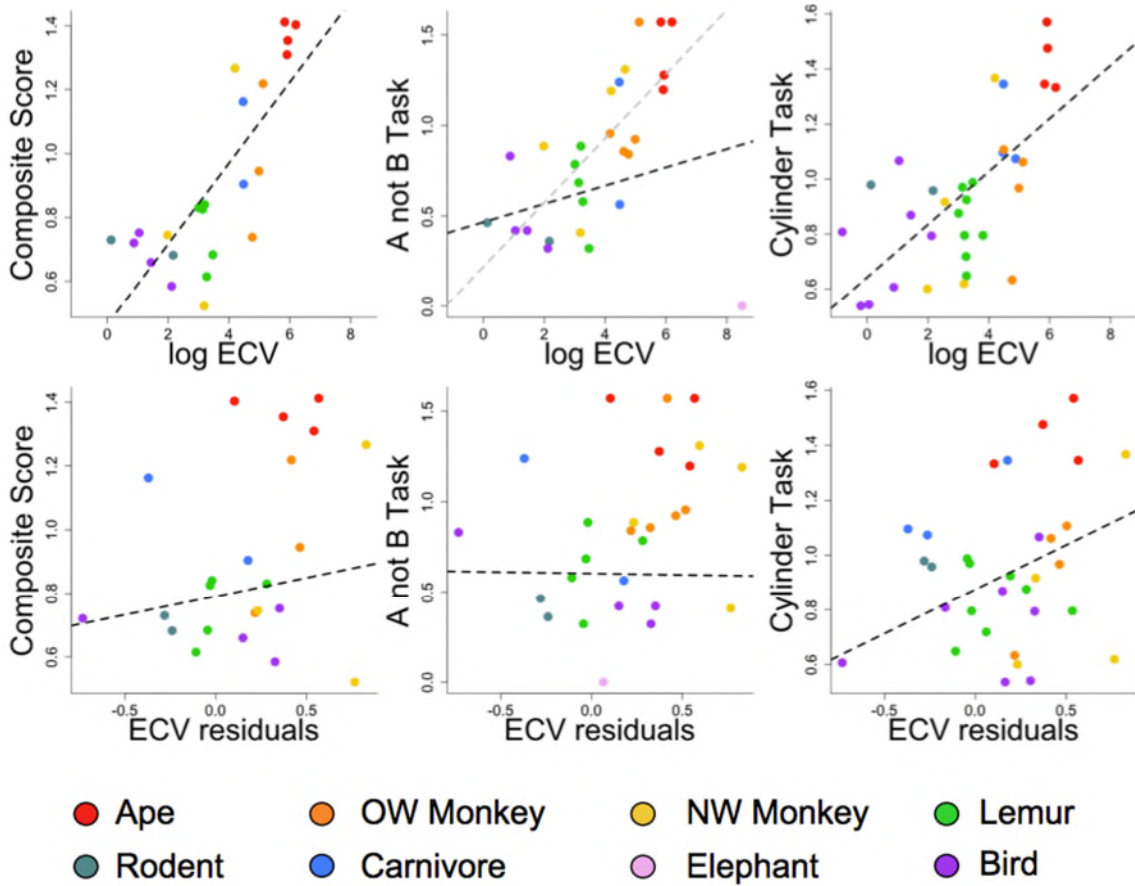
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984 Figure 2.

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Figure 3.

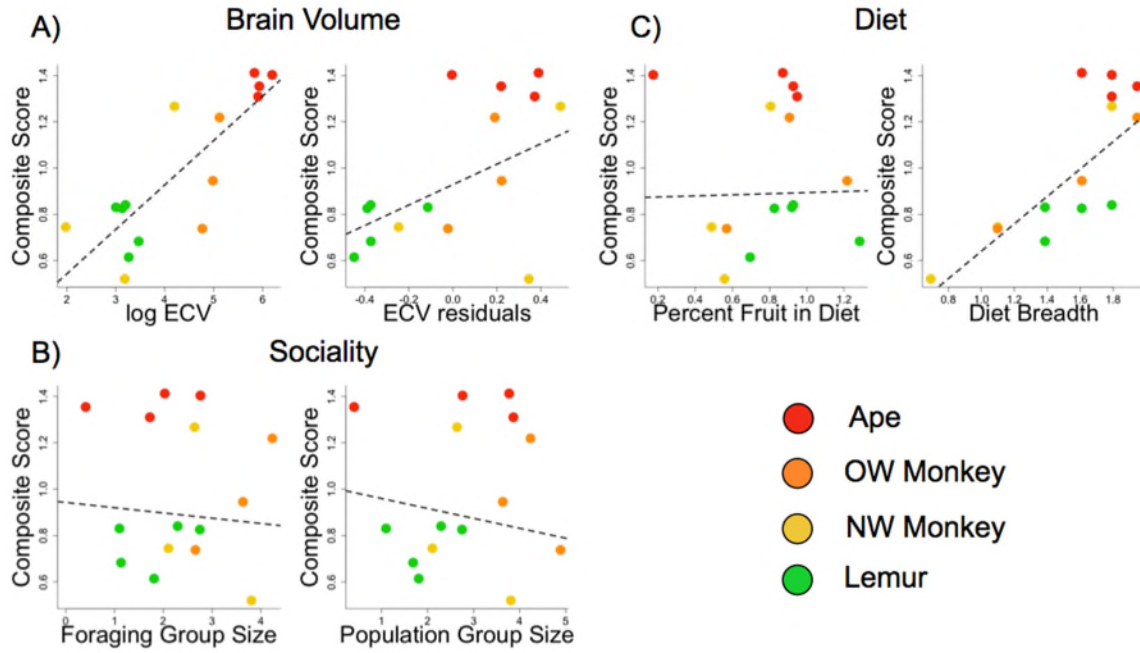


Figure 4.

