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The co-evolution of innovation and technical intelligence in primates

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1 **The co-evolution of innovation and technical**
2 **intelligence in primates**

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10 **Keywords:** innovation, social learning, tool use, intelligence, primate cognition, brain evolution

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13 **Summary**

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15 In birds and primates the frequency of behavioural innovation has been shown to covary with absolute and
16 relative brain size, leading to the suggestion that large brains allow animals to innovate, and/or that selection
17 for innovativeness, together with social learning, may have driven brain enlargement. We examined the
18 relationship between primate brain size and both technical (i.e. tool using) and non-technical innovation,
19 deploying a combination of phylogenetically informed regression and exploratory causal graph analyses.
20 Regression analyses revealed that absolute and relative brain size correlated positively with technical
21 innovation, and exhibited consistently weaker, but still positive, relationships with non-technical innovation.
22 These findings mirror similar results in birds. Our exploratory causal graph analyses suggested that technical
23 innovation shares strong direct relationships with brain size, body size, social learning rate and social group
24 size, while non-technical innovation did not exhibit a direct relationship with brain size. Nonetheless, non-
25 technical innovation was linked to brain size indirectly via diet and life-history variables. Our findings
26 support 'technical intelligence' hypotheses in linking technical innovation to encephalization, in the restricted
27 set of primate lineages where technical innovation has been reported. Our findings also provide support for a
28 broad co-evolving complex of brain, behaviour, life history, social and dietary variables, providing secondary
29 support for social and ecological intelligence hypotheses. The ability to gain access to difficult-to-extract, but
30 potentially nutrient-rich, resources through tool use may have conferred on some primates adaptive
31 advantages, leading to selection for brain circuitry that underlies technical proficiency.

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33 **1. Introduction**

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4 34 The extraordinary ecological and demographic success of humanity is commonly linked to our capacity for
5 35 innovation. We humans would appear to possess an unprecedented capability to devise novel solutions to
6 36 life's challenges, to express these solutions in our behaviour, tools and technology, and to propagate
7 37 innovation through social learning. Our engineering and technology have allowed us to inhabit even the most
8 38 hostile environments. Genetic studies suggest that this capability is longstanding, with hundreds, possibly
9 39 thousands, of human genes subject to positive selection over the last 100kyr, with a primary hypothesis for
10 40 why many of these alleles spread being adaptive responses to human learning and cultural activities [1-3]. For
11 41 instance, the domestication of plants and animals and associated consumption of novel foods seemingly
12 42 selected for alleles expressed in human digestion, as well as in resistance to animal-borne diseases [1-3].

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17 43 While humans may be exceptional innovators, we are far from the only species that devises novel
18 44 behaviour patterns. Recent research reveals that many animals will invent new behaviours or modify existing
19 45 behaviours (e.g. devise more efficient foraging techniques), that such innovation is taxonomically widespread,
20 46 and that there is considerable inter- and intra-specific variation in innovation rates [4]. Innovation has been
21 47 hypothesized to be an important influence on the success and evolution of many nonhuman animals,
22 48 particularly in populations faced with novel challenges such as anthropogenic change [4-6]. Evidence from
23 49 comparative and experimental studies supports this contention. For example, comparative studies of birds
24 50 have linked rates of behavioural innovation with range expansion [7-9], with rates of evolutionary
25 51 diversification [10, 11], and with dietary and habitat generalism [12, 13]. Experimental studies have associated
26 52 novel problem solving with fitness components such as mating success and offspring survival [14-16].

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32 53 These observations raise a number of questions: How did the ability to innovate evolve? How are the
33 54 aforementioned relationships between innovation and variables such as invasion success, fitness, and
34 55 speciosity causally related? What neurocognitive processes underpin innovation? And to what extent can
35 56 innovation be treated as a unitary phenomenon [4]? Might it, for instance, make better sense to subdivide
36 57 innovation into different categories, perhaps controlled by different neurocognitive processes, or to recognize
37 58 that different aspects of innovation may have quite distinctive evolutionary histories and taxonomic
38 59 distributions?

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43 60 To date, both theoretical arguments and empirical evidence have supported the idea that innovation
44 61 will be largely the product of domain-general cognitive abilities [4, 17, 18]. For example, comparative analysis
45 62 of observational reports of innovation across primate species reveal that innovation rate covaries together
46 63 with other observational measures thought to indicate general cognitive ability, such as rates of social
47 64 learning, tool use, and tactical deception [18, 19], as well as with experimental tests of learning and problem-
48 65 solving [20-22]. Similarly, experimentally induced and other novel behaviour in corvids (e.g. [23, 24]) supports
49 66 the idea that innovations appear when existing, domain-general abilities are applied to a novel problem.
50 67 However, there is some evidence that innovation may carry specific costs, such as exposure to
51 68 environmentally-transmitted parasites [19]. Behaviour patterns described as innovations encompass a huge
52 69 range of behaviour, likely involving multiple psychological processes [25; 26]. A potentially useful approach is
53 70 to subdivide innovation into different categories and to examine to what extent the same processes predict
54 71 these different categories of innovation.

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72 Here, we present comparative analyses based on an observational database of primate innovation
73 used in several previous studies (e.g. [18-21, 27, 28]). Innovation rates for different primate species are
74 estimated by surveying published literature for reports of innovation, an approach pioneered in studies of
75 foraging innovation in birds [22, 28-31]. The major advantage of this approach is that it provides quantitative
76 data on a large number of species, circumventing the longstanding challenge of designing experimental tests
77 that are fair to all species [18, 25, 32]. Multiple potentially confounding variables have been examined, with
78 little support for the method being subject to persistent or sizable biases over-and-above those that are readily
79 controlled for (e.g. research effort) [22]. The fact that similar patterns have been uncovered in both birds and
80 primates [22], and between this quantitative measure of innovativeness and performance in experimental tests
81 [18], enhances the validity of the approach. The method, interpreted appropriately, thus provides a useful
82 broad-scale complement to the in-depth data that can be obtained by experimental or observational study of
83 one or a few species [18, 20, 25, 33].

84 A long-held assumption is that innovation is a marker of intelligence, and more extensive or complex
85 innovation is thought to be facilitated by brain enlargement, particularly expansion of forebrain regions such
86 as the primate prefrontal cortex that are linked to creativity and problem solving [34]. Innovation has long
87 been proposed as a driver of brain evolution [5, 20, 35]. Examination of the links between innovation and brain
88 evolution provide a first step into understanding the neural underpinnings of innovation, and whether neural
89 changes accompany enhanced innovative propensities. Above we raised the question as to whether it would
90 be informative to divide innovation into different subcategories, potentially controlled by different
91 neurocognitive processes and driven by different selection pressures. One observation that prompts this
92 question is a recent analysis of avian foraging innovation [36], which divided foraging innovations into
93 'technical' innovations and 'food-type' innovations. Overington *et al.* [36] characterised 'technical' innovations
94 as those involving novel foraging techniques, such as innovative predatory techniques, commensal foraging,
95 tool use, and extractive foraging, and hence might be regarded as exerting some additional demands on the
96 cognitive capabilities of the animal associated with the extraction and exploitation of the novel resource.
97 Conversely, in birds, non-technical innovations are those where a novel food source is exploited without the
98 use of any novel technique ('food type' innovations), typically deploying established feeding methods that
99 seemingly exert few additional cognitive demands on the innovator over-and-above the recognition of the
100 novel resource as food. While both technical and food-type innovations covaried with brain size, Overington
101 *et al.* found that technical innovations exhibited a far stronger relationship with brain size, and explained a
102 greater proportion of variance in residual brain size than food-type innovations. These authors suggested that
103 the ability to extract valuable resources through novel technical foraging skills may require more advanced
104 cognition than merely introducing novel food items into their diet, and argued that technical innovation may
105 have driven brain evolution through selection for the neural underpinnings of technical proficiency. Thus
106 Overington *et al.*'s results were interpreted as supporting a technical intelligence hypothesis, suggesting that
107 increased brain size allows individuals to use innovation to modify their technical skills.

108 Here we explore the generality and robustness of Overington *et al.*'s [36] conclusions by investigating
109 whether similar relationships between innovation and brain evolution are observed in nonhuman primates.

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4 110 We take a broadly similar approach by subdividing our primate innovation dataset into technical innovations
5 111 and non-technical innovations. We focus particularly on innovations that require tool use as this is a core
6 112 element of technical intelligence hypotheses [37], one of several hypotheses put forward to explain the
7 113 evolution of enhanced cognition and brain enlargement [20, 38-41]. In a second set of analyses, we examine a
8 114 broader definition of technical innovation, including both innovative tool use and innovative extractive
9 115 foraging, reflecting arguments that extractive foraging played a role in primate cognitive evolution [42, 43].
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11 117 Our analyses examine the relationship between technical innovation, non-technical innovation, and
12 118 both absolute and relative brain size, as well as several factors that have been shown to covary with brain size
13 119 and/or innovation rate, including body size, life history variables, social group size, diet breadth and rates of
14 120 social learning. While there is potential utility in examining individual brain components and their relation to
15 121 behavioural innovation, currently insufficient data are available when innovation is sub-divided. Moreover,
16 122 recent work on the co-evolution of different brain areas suggests that many components change in volume
17 123 together as a network [44, 45]. This suggests that a focus on large brain areas or the entire brain may be
18 124 appropriate, particularly for broad categories of behaviour such as innovation that are plausibly reliant on
19 125 domain-general capabilities, and involve many cognitive and other processes and many parts of the brain.

20 126 Our objectives are twofold: (i) to determine the extent to which different classes of innovation covary
21 127 with brain size in primates, and (ii) to examine how technical and non-technical innovation co-evolve with
22 128 other behavioural and socioecological traits. We address these objectives deploying a powerful combination of
23 129 comparative phylogenetic analyses [46], phylogenetically-informed causal graphs [47] and non-linear
24 130 statistical approaches, to examine potential evolutionary drivers and infer causal relations. We conduct
25 131 analyses on datasets including all primate innovations recorded and also, to facilitate more precise
26 132 comparison with Overington *et al.* [36], who examined foraging innovation, on datasets limited to foraging
27 133 behaviour. The analyses shed new light on how and why innovative propensities evolved.

29 134 2. Methods

30 135 2.1. Brain data

31 136 Species means for brain size and body mass were obtained from Isler *et al.* [48]. Isler *et al.* compiled
32 137 endocranial volumes for 3813 museum specimens, at least 88% wild-caught, for 167 primate species.
33 138 Endocranial volume (ECV) provides a good estimate of brain volume which is easily convertible into brain
34 139 mass [49]. We complemented the dataset with body mass and brain mass for four additional species: *Callicebus*
35 140 *moloch*, *Cercopithecus talapoin* (from [50]), *Saguinus imperator* and *Callithrix geoffroyi* (from [51]). Brain mass in
36 141 these species was converted into ECV [49] before being added to the dataset. Endocranial volume (ECV) and
37 142 body mass were natural log-transformed prior to analysis to normalise distributions. Below we refer to ECV
38 143 as 'brain size' and to body mass as 'body size'.
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40 145 2.2. Behavioural data

41 146 Behavioural data were drawn from Reader *et al.* [18]. Reader *et al.* surveyed over 4000 published articles for
42 147 examples of innovation, social learning, tool use, and extractive foraging in living non-human primates, using
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4 149 keywords (e.g. 'novel' or 'traditional') to classify behaviour patterns (e.g. as 'innovation' or 'social learning').
5 150 Full details of the database and discussion of its merits, disadvantages, reliability and validity are given in
6 151 Reader *et al.* [18] and the papers cited therein. The observation frequencies for each of the four behavioural
7 152 measures were calculated as the total number of reported examples of each class. Initially, we examined each
8 153 innovation report and categorized it as a 'technical' innovation (involving tool use) or a 'non-technical'
9 154 innovation (not involving tool use; data will be archived online in the Dryad depository). We go on to conduct
10 155 further analyses in which 'technical innovation' is broadened to include both innovative tool use and
11 156 innovative extractive foraging. We also restricted a subset of analyses to foraging innovations only (strictly,
12 157 innovations that occur in a foraging context), deploying the classification in Reader & Laland [27]. We used
13 158 the number of published articles on each species in the *Zoological Record* (taken from [18]) as a measure of
14 159 research effort. We corrected the behavioural measures for differences in research effort by including research
15 160 effort as an independent variable in statistical analyses [52].
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162 2.3. Diet breadth, life history and social group size

163 163 Data on diet breadth (the number of food types typically eaten, out of a maximum of 13 different categories)
164 164 were obtained from Reader *et al.* [18]. Social group size and six life-history variables (gestation length,
165 165 interbirth interval, weaning age, age of sexual maturity, age at first birth and maximum longevity) were
166 166 extracted from the PanTheria dataset for the 167 species with brain data, with these measures available and
167 167 complete for 71 species [53]. In pairwise PGLS analyses, the six life-history variables were found to be
168 168 significantly positively correlated ($p < 0.05$). In order to extract a single dimension of life-history to use later as
169 169 a predictor in an exploratory analysis of causality, these six variables were natural log-transformed and used
170 170 to create a composite 'life-history' variable using phylogenetically controlled principal components analysis
171 171 (PPCA; [54]). The PPCA extracted a single component, which explained 78% of the variance in the data, and
172 172 all variables loaded positively on this component, with loadings from 0.58 to 0.90 ($\lambda = 0.84$). This composite
173 173 life-history variable was used in subsequent analyses. Social group size was natural log-transformed for
174 174 normalization. Diet breadth did not require transformation.
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176 2.4. Phylogeny

177 177 For the phylogenetic analyses, we used the 10k Trees project dated consensus tree (version 3) [55], and
178 178 matched primate species from the brain dataset and the behavioural dataset with species in the tree, taking
179 179 into consideration changes in nomenclature (ESM).
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181 2.5. Data analyses

182 182 A total of 167 primate species were represented in the phylogenetic tree and had published brain and
183 183 innovation data (strepsirrhines: 39 species, tarsids: 3 species, platyrrhines: 49 species, catarrhines: 76 species).
184 184 Data on life history, social group size and diet breadth were only available for 71 species in the innovation and
185 185 brain dataset (19 strepsirrhines, 1 tarsid, 21 platyrrhines and 30 catarrhines), and thus analyses involving these
186 186 variables were restricted to these 71 species. A substantial number of the 167 species had no recorded
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4 187 innovations. The fact that a species has zero recorded innovations when this is unexpected for a given research
5 188 effort may be informative, but it is also possible that species with no innovation reports have been studied
6 189 differently to those with innovation reports [25]. Thus, we also conducted analyses excluding those species
7 190 with zero innovation reports in our database. This “innovators” sample covered 48 species with available
8 191 brain data.

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11 192 To account for non-independence of species-level data, we used phylogenetic generalized least square
12 193 regressions (PGLS), with phylogenetic signal (Pagel’s λ) estimated by maximum likelihood (henceforth
13 194 $\lambda=ML$). Analyses were run in R version 3.0.2 [56] using the “caper” [57] and “phytools” packages [58]. Models
14 195 explored the relationship between brain size and innovation, treating innovation rates as response variables,
15 196 and including research effort as a covariate. Analyses that examined the relationship between relative brain
16 197 size and innovation included body mass. We also ran analyses examining absolute brain size, without body
17 198 mass as a covariate, to allow comparison of absolute versus relative brain measures of brain size as predictors
18 199 of cognitive differences, an open question in the field [21].

20 200 We ran additional analyses (ESM) to take into account the fact that a large number of species in our
21 201 database had zero recorded innovations. We ran a binomial regression predicting the probability that an
22 202 innovation is observed in each paper based on research effort (conducted using the method “glm” in R [56]).
23 203 We also present the results of using a zero-inflated Poisson (ZIP) model, which provides an alternative
24 204 method for controlling for the large number of species with zero recorded innovations [59]. However, the ZIP
25 205 model may not be suitable when there are a small number of observations for some entries (over 58% of the
26 206 species had under 20 papers recorded in the *Zoological Record* survey), meaning that the results of these models
27 207 should be interpreted with caution. Both the binomial model and the zero-inflated Poisson models also help
28 208 control for the observed heteroscedasticity in the data (if the number of observations for a species is large, we
29 209 should expect greater absolute variance in the number of reported innovations). However, binomial and ZIP
30 210 models that incorporate phylogenetic information are not well-established methodologies. Thus we used non-
31 211 phylogenetic methods for these analyses.

32 212 Exploratory causal graphs were used to further examine interrelationships between variables. Causal
33 213 graphs were generated by examining the phylogenetic partial correlation between variables, taking into
34 214 account the remaining variables (using PGLS). For a set of variables $A = \{A_1, \dots, A_n\}$, this method assesses the
35 215 relationship between A_i and A_j , by examining the correlation between the residuals of a phylogenetic linear
36 216 model of A_i predicted by the remaining variables (i.e. A_k for all k except for A_i and A_j) and A_j predicted by the
37 217 remaining variables. In order to guard against the premature rejection of causal relations between variables
38 218 we take the conservative stance of treating the correlation as potentially significant if $p < 0.1$, in which case an
39 219 edge between A_i and A_j is added to the causal graph. This method allows us to visualize the significant
40 220 relationships between variables when taking into account the presence of other variables, similar to other path
41 221 analysis methods [47, 60]. Edges were not oriented (i.e. directed) as we reasoned that biological evolution in
42 222 this domain frequently encompasses feedback processes between traits [18, 61].

43 223 Although this method uses the full set of covariates (all A_k) to assess independence, which may
44 224 reduce statistical power, we find that the results of this procedure are the same as a more complex algorithm

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4 225 (Whalen *et al.*, in preparation) which uses only connected variables. Our new method can be seen as an
5 226 exploratory automation of von Hardenberg and González-Voyer [62], building on Pearl's PC algorithm [63].
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7 227 For PGLS models within a given causal graph, λ is estimated by maximum likelihood, in order to account for
8 228 differing levels of phylogenetic signal across each linear model. . However, given that previous approaches
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10 229 have assumed a fixed common value for λ for all paths [62], we also analyse graphs with λ fixed at 0 or 1,
11 230 which represent the extreme values of λ , and thereby provide a strong check as to whether our conclusions are
12 231 robust to different values of phylogenetic signal. The values on the edge of each graph represent the p-value,
13 232 i.e. the significance of the relationship between variables when taking into account the influence of only
14 233 connected variables.
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18 235 3. Results

19 236
20 237 Where technical innovation was restricted to tool use, of the 584 reports of innovation, 45% were classified as
21 238 technical innovations and 55% as non-technical innovations (Figure 1). In the broader categorization of
22 239 technical innovation that included novel extractive-foraging behaviour patterns, 60% were classified as
23 240 technical innovations and 40% as non-technical innovations.
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28 242 3.1. Comparative phylogenetic analyses for all species

29 243 Total innovation rate (i.e., technical and non-technical combined) was found to be positively correlated with
30 244 absolute but not relative brain size in primates (Table 1). That is, there was a significant positive correlation
31 245 between innovation rate and brain volume, but this relationship was no longer significant when body mass
32 246 was taken into account.

33 247 Technical (i.e. involving tool use) and non-technical innovation rates correlated positively with each
34 248 other (PGLS: $\lambda=0$, $r=0.61$, $\beta=0.49\pm 0.09$, $p<0.0001$). A similar correlation was observed using a broader
35 249 classification of technical innovation, including innovative extractive foraging (PGLS: $\lambda=0.06$, $r=0.53$,
36 250 $\beta=0.44\pm 0.10$, $p<0.0001$). However, despite this positive correlation, different relationships were observed
37 251 between brain size and technical versus non-technical innovation rates. Technical innovation rate was
38 252 significantly correlated with absolute but not relative brain size, and we observed a stronger relationship with
39 253 brain size than that observed for total innovation rate. Similar results were found for technical innovation
40 254 including extractive foraging (Table 1). In contrast, non-technical innovation rate was not significantly
41 255 correlated with either absolute brain size or relative brain size (Table 1). The model including brain size as a
42 256 predictor of technical innovation, with research effort as a covariate, showed a higher correlation coefficient
43 257 ($r=0.13$) than the model predicting non-technical innovation ($r=0.07$), with a similar pattern observed using the
44 258 broader classification of technical innovation including extractive foraging ($r=0.14$ vs $r=0.08$).
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57 260 3.2. Controlling for zero-inflation

58 261 To address the concern that our PGLS results were biased by the large number of primate species with no
59 262 innovations (zero inflation), we conducted ZIP and binomial analyses. ZIP models on our 167-species sample
60 263 confirmed that zero scores on all measures of innovation were more likely in those species where research

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4 264 effort was low (Table S1). We found that the number of innovations observed correlated significantly with
5 265 research effort, body mass, and relative brain size using all innovation classifications. In contrast, absolute
6 266 brain size correlated with only two innovation measures, total innovation rate and technical innovation
7 267 including extractive foraging. Technical innovation was more strongly related to brain size than was non-
8 268 technical innovation, using both absolute and relative brain size measures and for all classifications of
9 269 technical innovation (see Block A in Table S1). Comparison of AIC values between models with and without
10 270 body size found better support for models that included body size (i.e., relative brain size models).

11 271 We also ran a set of analyses using a binomial model, which predicted the likelihood that a given
12 272 paper in the data set contained an innovation. Binomial models for all species showed that all innovation rates
13 273 (including total innovations, technical innovations and non-technical innovations) exhibited strong positive
14 274 correlations with both absolute and relative brain size ($p < 0.0001$, Table S2). Technical innovation was more
15 275 strongly related to both absolute and relative brain size than was non-technical innovation. These results are
16 276 consistent with the results of the ZIP model, and again, comparison of AIC values between models with and
17 277 without body size found better support for models that included body size.

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19 279 *3.3 Innovators only analyses*

20 280 Confirmation of zero inflation in the full species dataset provides further justification for repeating the
21 281 analysis using the reduced dataset of innovators (see Table 1). Amongst our sample of innovators (48 species),
22 282 we found strong correlations between total innovation rate and both absolute and relative brain size.
23 283 Technical innovation also exhibited strong correlations with both absolute and relative brain size, and these
24 284 relationships were stronger than those for total innovations. Non-technical innovation correlated significantly
25 285 with absolute brain size only, and this correlation was weaker than the one observed between technical
26 286 innovations and absolute brain size. Brain size was a better predictor of technical innovation than a predictor
27 287 of non-technical innovation (technical innovation: $r=0.14$; non-technical innovation: $r=0.10$; technical
28 288 innovation with extractive foraging: $r=0.26$, non-technical innovation without extractive foraging: $r=0.05$).
29 289 Using the binomial models, we again observed strong and significant correlations between all innovation rates
30 290 and absolute and relative brain size (see Table S2), and stronger relationships were observed between
31 291 technical innovation rates and brain size measures than between non-technical innovation rates and brain size.

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33 293 *3.4 Comparisons with Overington et al.: Foraging innovations*

34 294 To facilitate a closer comparison with Overington *et al.* [36], extractive foraging innovations were included in
35 295 technical innovation, and PGLS analyses were restricted to foraging innovations only. This reduced the
36 296 available pool of innovations considerably, and because of the aforementioned problems with zero-innovation
37 297 scores, the 167-species analysis was not appropriate. In the innovators only sample, technical innovation
38 298 correlated significantly with both absolute and relative brain size, but non-technical innovation did not
39 299 correlate with either (Table 1). In the ZIP and binomial models, technical innovation was again more strongly
40 300 correlated with brain size measures than was non-technical innovation (Tables S1, S2).

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42 302 *3.5 Causal graphs*

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4 303 We constructed three phylogenetically informed causal graphs, using total innovations, technical innovations
5 304 and non-technical innovations. In all sets of causal graphs, the findings for total innovations resemble those
6 305 for non-technical innovations, and can be contrasted with those for technical innovation. Also, in all of our
7 306 analyses, brain size, body size, the life-history composite measure and social group size shared multiple direct
8 307 connections (“edges”) with each other, suggesting that these variables have evolved together (Figure 2).

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11 308 Technical innovation rate shared direct edges with brain size in the best-supported graphs (λ =ML:
12 309 $p=0.043$, Fig. 2a; $\lambda=0$: $p=0.014$, $\lambda=1$: $p=0.009$, see Fig. S1), which indicates that these two variables are directly
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14 310 correlated even when the other variables are taken into account. Technical innovation rate also was directly
15 311 related to social learning rate ($p<0.0001$), body size ($p=0.039$) and social group size ($p<0.0001$). PGLS analyses
16 312 showed that these associations were all positive (brain size: $\lambda=0.84$, $r=0.27$, $p=0.014$; body size: $\lambda=0.85$, $r=0.20$,
17 313 $p=0.050$; social learning: $\lambda=0$, $r=0.77$, $p<0.0001$; Table S3). However, the relationship between technical
18 314 innovation and social group size was not statistically significant in the PGLS model ($\lambda=0.91$, $r=0.02$, $p=0.88$).
19 315 These edges are also strong when λ was set to 0 or 1 ($\lambda=0$: social learning rate: $p<0.0001$, body size: $p=0.041$,
20 316 social group size: $p<0.0001$; $\lambda=1$: social learning rate: $p<0.0001$, body size: $p=0.007$, social group size: $p<0.0001$,
21 317 see Figure S1a).

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26 318 Non-technical innovation shared a direct edge with social learning rate alone (λ =ML: $p<0.0001$, Fig.
27 319 2b; $\lambda=0$: $p<0.0001$, $\lambda=1$: $p<0.0001$, Fig. S1b). PGLS analysis showed that the correlation between these two
28 320 variables was positive ($\lambda=0$, $r=0.66$, $p<0.0001$). Any relationships between non-technical innovation rates with
29 321 other variables in the graph, including brain size, were mediated by social learning and diet breadth.

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32 322 Technical innovation rate including extractive foraging shared direct edges with social learning rate
33 323 ($p<0.0001$), and social group size ($p=0.020$) in the graphs with λ =ML (Fig. 2c), as well as in the graphs with $\lambda=0$
34 324 and $\lambda=1$ (Fig. S1c), but the direct relationship with brain size was lost ($p>0.1$). PGLS analyses showed that the
35 325 correlation of this measure of technical innovation with social learning was positive ($\lambda=0$, $r=0.76$, $p<0.0001$),
36 326 but the relationship with social group size was not significant ($\lambda=0.728$, $r=0.11$, $p=0.17$).

37 38 39 40 41 327 42 328 4. Discussion

43 329 The innovativeness of a species, defined as the frequency with which novel behaviour patterns are generated
44 330 (controlling for research effort) covaries with diverse measures of absolute and relative brain size in both birds
45 331 and primates [18, 22]. In birds, brain size covaries more strongly with technical than with non-technical
46 332 innovation [36], suggesting a potentially important distinction between these types of novel behaviour. Our
47 333 findings in nonhuman primates were broadly consistent with those of Overington *et al.* [36]. Phylogenetic
48 334 analyses comprising all primate innovations found that absolute (but not relative) brain size correlated
49 335 positively and strongly with both technical innovation and total innovations but showed a non-significant
50 336 relationship with non-technical innovation. However, PGLS analyses do not account for the zero-inflated
51 337 distribution of innovation counts across species. When this is controlled for, either by deploying zero-inflated
52 338 Poisson or binomial models, or by reducing the sample to ‘innovator’ species, we find that total innovation
53 339 measures covary significantly with absolute and relative brain size, and that technical innovation always
54 340 exhibits a stronger relationship with brain size than non-technical innovation.

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4 341 Exploratory causal graph analyses painted a similar picture, where technical innovation shared a
5 342 direct edge with brain size (Fig. 2a), whilst the number of non-technical innovations did not. Rather, non-
6 343 technical innovation was linked to brain size via social learning, diet and life-history variables (Fig. 2b).
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8 344 Technical innovation also shared very strong direct edges with social learning, body size and social group
9 345 size. However, when we add extractive foraging to technical innovation the direct relationship with brain size
10 346 was lost (Fig. 2c). This implies that tool use, more so than extractive foraging, may be the relevant factor
11 347 underlying the direct relationship between technical innovation and brain size.

14 348 This direct connection between technical innovation and brain size provides support for 'technical
15 349 intelligence' hypotheses (e.g. [37]) in suggesting that in some primate lineages the ability to invent novel
16 350 technical behaviours, specifically those involving tools, may have favoured encephalization, more than the
17 351 ability to generate novel behaviours per se. Overington *et al.* [36] restrict their analyses to foraging innovations
18 352 alone, and used a somewhat broader definition of technical innovations, with technical innovations referring
19 353 to novel foraging techniques, not just tool use. Our analyses tell a similar story to those of Overington *et al.* As
20 354 in birds, the ability to gain access to difficult-to-extract, but potentially nutrient-rich, resources through tool
21 355 use and technical skill may have conferred adaptive advantages, leading to selection for brain regions and
22 356 circuitry that underlie technical flexibility and proficiency in some primate lineages. This pattern holds when
23 357 our PGLS analyses were restricted to foraging innovations.

29 358 We also observed strong connections in causal graph analyses between primate technical innovation
30 359 and both social learning and social group size (although the group size-technical innovation link was not
31 360 significant in a PGLS analysis), suggesting co-evolution of elements of social, technical and ecological
32 361 intelligence, as has been previously argued (e.g. [64]). Those primates that score highly for innovation and tool
33 362 use (e.g. the great apes, capuchins, macaques) are also renowned for their social learning [18, 64], and there is
34 363 now extensive experimental evidence demonstrating that primates can acquire many tool using methods
35 364 through social learning [61]. Indeed, a robust finding of both our causal graph analyses and our previous
36 365 work [18, 19] is that innovation and social learning evolve together, a conclusion that holds here for both
37 366 technical and non-technical innovation.

42 367 The direct connections between technical innovation and social group size, as well as between social
43 368 learning and social group size, conflict with previous analyses that found no relation between social group
44 369 size and total innovation rate or social learning rate [18, 65]. This could reflect the effect of examining technical
45 370 innovations alone, additional power in the current analyses or sample, or the effect of the additional variables
46 371 incorporated in the present analyses. Theoretical work, however, suggests that the observed relationships of
47 372 group size with reported technical innovation rates may be no artefact. A wide variety of theoretical studies
48 373 now link the size of cultural repertoires with social group size, as larger populations provide a more stable
49 374 repository for the retention of innovations than do smaller groups, as well as more potential innovators [66-
50 375 69]. These links between technical innovation and both social learning incidence and social group size are, of
51 376 course, consistent with several social intelligence hypotheses [20, 38-41], which supports the suggestion that
52 377 these explanations are not mutually exclusive [18, 66]. The consistently observed edge in our path analyses

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4 378 linking social group size and brain size supports the established finding that social intelligence is an important
5 379 driver of brain evolution [20, 38-41].

6 380 Our causal graph analyses linked non-technical innovation to measures of diet breadth via social
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8 381 learning, a finding that evokes ecological intelligence explanations, in which primate intelligence is favoured
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10 382 by the challenge of locating and extracting diverse and constantly changing foods (e.g. [42, 43, 71, 72]).
11 383 However, as Overington *et al.* [36] reported for birds, while larger-brained, innovative primate species may be
12 384 more likely to incorporate novel foods into their diets, and while this ability may be ecologically important,
13 385 our findings imply that the relationship between innovativeness and brain size in primates is more likely to be
14 386 primarily driven by technical innovations.

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17 387 Although the absence of an edge between non-technical innovation and brain size in the best-
18 388 supported causal graph ostensibly rules out a direct coevolutionary relationship between these variables, it
19 389 does not preclude a more diffuse coevolutionary interaction. What the causal graph analysis implies is that if
20 390 there is a causal influence of non-technical innovation on brain evolution it occurs through changes in social
21 391 learning, diet and life-history. One plausible interpretation of these findings is that through social
22 392 transmission many primates learn to exploit novel foods, and the resources so gleaned both aid survival and
23 393 fuel brain growth. Cultural drive explanations [5, 20, 35, 41, 73] are relevant here, as they propose that
24 394 selection for innovativeness and/or efficient social learning drove the evolution of encephalization in
25 395 primates. However, given that most primate species in our sample exhibited zero innovations, we emphasize
26 396 that any causal role for innovation, be it technical or non-technical, in driving encephalization is likely to be,
27 397 only part of the story, and restricted to a subset of primate lineages.

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30 398 We emphasize that our causal graph analyses merely establish significant direct versus diffuse
31 399 coevolutionary relationships between variables, and we explicitly avoid attempting to infer the directionality
32 400 of edges. We adopt this conservative stance as we anticipate that feedback between coevolving traits is highly
33 401 likely, indeed at least as likely as the unidirectional evolution of one trait in response to changes in the other.
34 402 Hence, while our analyses are consistent with the interpretations that in some primate lineages (i) technical
35 403 innovation drove brain enlargement, or (ii) that large brains (which evolved for reasons unconnected to
36 404 innovation) are facultatively expressed in innovative behaviour, we suggest (iii) that technical innovation and
37 405 brain size coevolved in certain taxa, with each driving enhancements in the other. In addition, while it is likely
38 406 that technical innovation is more cognitively complex than non-technical innovation, a suggestion that our
39 407 findings may appear to support, there are reasons to be cautious in drawing this conclusion as technical
40 408 innovations may differ from other innovations in ways other than tool use.

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43 409 Given the fact that both brains and innovations can perform many functions, a complete analysis
44 410 would require numerous interacting variables to be investigated. Moreover, it remains an open question as to
45 411 whether innovation is a driving causal factor in our evolutionary analyses, or whether the innovations
46 412 observed in our survey are simply the by-products of broader psychological processes. Reports of technical
47 413 innovation are relatively sparsely distributed across the primates, and close relatives often differ considerably
48 414 in innovation rates. This could reflect the difficulty in gathering a comprehensive sample of primate
49 415 innovation, but also points to technical innovation being just a part of a larger story. Even focused on the
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4 416 restricted set of variables considered in our analyses, the emergent picture is one in which there are multiple
5 417 drivers of the evolution of the primate brain and intelligence that feed back on each other in complex,
6 418 nonlinear ways. It would seem that innovativeness in primates, like intelligence and cognition more generally,
7 419 is not to be explained by a single prime mover, but rather by a complex of factors that encompass technical,
8 420 social and ecological intelligence.
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14 423 Additional Information

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19 426 anonymous reviewers.
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22 428 Data Accessibility

23 429 The datasets supporting this article have been uploaded as part of the Supplementary Material and will be available via
24 430 the Dryad depository.
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27 432 Authors' Contributions

28 433 AN and SMR compiled the data; AN, AW and SES analysed the data; AN, SMR and KNL took the lead in writing the
29 434 article, with contributions from AW and SES. All authors gave final approval for publication.
30
31 435

32 436 Competing Interests

33 437 We have no competing interests.
34
35 438

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41 442 References

- 42
43 1. Wang ET, Kodama G, Baldi P, Moyzis RK. 2006 Global landscape of recent inferred Darwinian selection for *Homo sapiens*. *Proc. Natl. Acad. Sci. USA* **103**, 135-140.
44
45 2. Voight BF, Kudravalli S, Wen X, Pritchard JK. 2006 A map of recent positive selection in the human genome. *PLoS Biol.* **4**, e72
46
47 3. Laland KN, Odling-Smee FJ, Myles S. 2010 How culture shaped the human genome: bringing genetics and the human sciences together. *Nat. Rev. Genet.* **11**, 137-148.
48
49 4. Reader SM, Laland KN, (Eds) 2003. *Animal Innovation*. Oxford University Press.
50
51 5. Wilson AC. 1985 The Molecular Basis of Evolution. *Sci. Am.* **253**, 148-157.
52
53 6. Sih A. 2013 Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Anim. Behav.* **85**, 1077-1088.
54
55 7. Sol D. 2003 Behavioral flexibility: a neglected issue in the ecological and evolutionary literature? In: *Animal Innovation*, SM Reader, KN Laland, (Eds) pp. 63-82. Oxford, UK: Oxford University Press.
56
57 8. Sol D, Lefebvre L, Timmermans S. 2002 Behavioral flexibility and invasion success in birds. *Anim. Behav.* **63**: 495-502.
58
59 9. Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L. 2005 Big brains, enhanced cognition, and response of birds to novel environments. *Proc. Natl. Acad. Sci. USA* **102**, 5460-5465.
60
61 10. Nicolakakis N, Sol D, Lefebvre L. 2003. Behavioural flexibility predicts species richness in birds, but not extinction risk. *Anim. Behav.* **65**, 445-452.
62
63 11. Sol D, Stirling G, Lefebvre L. 2005 Behavioral drive or behavioral inhibition in evolutionary diversification: the case of subspecies diversification in Holarctic Passerines. *Evolution* **59**, 2669-2677.
64
65 12. Overington SE, Griffin A, Sol D, Lefebvre L. 2011 Are innovative species ecological generalists? A test in North American birds. *Behav. Ecol.* **22**, 1286-1293.
66
67 13. Ducatez S, Clavel J, Lefebvre L. 2015 Ecological generalism and behavioral innovation in birds. Technical intelligence or the simple incorporation of new foods? *J. Anim. Ecol.* **84**, 79-89.
68
69 14. Cauchard L, Boogert NJ, Lefebvre L, Dubois F, Doligez B. 2013 Problem solving performance is correlated with reproductive success in a wild bird population. *Anim. Behav.* **85**, 19-26. (doi:10.1016/j.anbehav.2012.10.

- 005).
 15. Cole EF, Morand-Ferron J, Hinks A, Quinn JL. 2012 Cognitive ability influences life history variation in the wild. *Curr. Biol.* **22**, 1808-1812.
 16. Keagy J, Savard J-F, Borgia G. 2009 Male satin bowerbird problem-solving ability predicts mating success. *Anim. Behav.* **78**, 809-817.
 17. Chiappe D, MacDonald K. 2005 The evolution of domain-general mechanisms in intelligence and learning. *J. Gen. Psychol.* **132**, 5-40.
 18. Reader SM, Hager Y, Laland KN. 2011 The evolution of primate general and cultural intelligence. *Phil. Trans. R. Soc. B* **366**, 1017-1027.
 19. McCabe CM, Reader SM, Nunn CL. 2015 Infectious disease, behavioural flexibility and the evolution of culture in primates. *Phil. Trans. R. Soc. B* **282**, 20140862.
 20. Reader SM, Laland KN. 2002 Social intelligence, innovation and enhanced brain size in primates. *Proc. Nat. Acad. Sci. USA* **99**, 4436-4441.
 21. MacLean EL, Hare B, Nunn CL, Addessi E, Amici F, et al. 2014 The evolution of self-control. *Proc. Nat. Acad. Sci. USA* **111**, 2140-2148.
 22. Lefebvre L, Reader SM, Sol D. 2004 Brains, innovations and evolution in birds and primates. *Brain Behav. Evol.* **63**, 233-246.
 23. Bird CD, Emery NJ. 2009 Rooks use stones to raise the water level to reach a floating worm. *Curr. Biol.* **19**, 1410-1414. (doi:10.1016/j.cub.2009.07.033).
 24. Lefebvre L, Nicolakakis N, Boire D. 2002 Tools and brains in birds. *Behavior* **139**, 939-973. (doi:10.1163/156853902320387918).
 25. Reader SM, MacDonald K. 2003 Environmental variability and primate behavioural flexibility. In: *Animal Innovation*, SM Reader, KN Laland, (Eds) pp. 83-116. Oxford, UK: Oxford University Press.
 26. Tebbich *et al.*, this volume
 27. Reader SM, Laland KN. 2001 Primate innovation: sex, age and social rank differences. *Int. J. Primatol.* **22**, 787-805.
 28. Fernandez HBF, Woodley MA, te Nijenhuis J. 2014 Differences in cognitive abilities among primates are concentrated on G: Phenotypic and phylogenetic comparisons with two meta-analytical databases. *Intelligence* **46**, 311-322.
 29. Lefebvre L, Whittle P, Lascaris E, Finkelstein A. 1997 Feeding innovations and forebrain size in birds. *Anim. Behav.* **53**, 549-560.
 30. Lefebvre *et al.*, this volume
 31. Sol *et al.*, this volume
 32. Maclean EL, Matthews LJ, Hare BA, Nunn CL, Anderson RC, et al. 2012 How does cognition evolve? Phylogenetic comparative psychology *Anim. Cogn.* **15**, 223-238.
 33. Lefebvre L. 2011 Taxonomic counts of cognition in the wild. *Biol. Lett.* **7**, 631-633. (doi: 10.1098/rsbl.2010.0556).
 34. Dietrich A. 2004. The cognitive neuroscience of creativity. *Psych. Bull. Rev.* **11**, 1011-1026.
 35. Wyles JS, Kunkel JG, Wilson AC 1983. Birds, behavior, and anatomical evolution. *Proc. Nat. Acad. Sci. USA* **80**, 4394-4397.
 36. Overington SE, Morand-Ferron J, Boogert NJ, Lefebvre L. 2009 Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Anim. Behav.* **78**, 1001-1010.
 37. Byrne RW. 1997 The technical intelligence hypothesis: An additional evolutionary stimulus to intelligence? In: *Machiavellian Intelligence II: Extensions and Evaluations*, pp. 289-311. Cambridge, UK: Cambridge University Press.
 38. Byrne RW, Whiten A 1988. *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*. Oxford, UK: Oxford University Press.
 39. Dunbar RIM. 1995 Neocortex size and group size in primates: a test of the hypothesis. *J. Hum. Evol.* **28**, 287-296.
 40. Whiten A, Byrne RW. 1997 *Machiavellian Intelligence II. Extensions and Evaluations*. Cambridge, UK: Cambridge University Press.
 41. van Schaik CP, Burkart JM. 2011 Social learning and evolution: the cultural intelligence hypothesis. *Phil. Trans. R. Soc. B* **366**, 1008-1016.
 42. Milton K. 1988 Foraging behaviour and the evolution of primate intelligence. In: *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*. RW Byrne, A Whiten, (Eds). pp. 271-84. Oxford, UK: Oxford University Press.
 43. Parker ST, Gibson KR. 1977 Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *J. Hum. Evol.* **6**, 623-641.
 44. Barton RA. 2006 Primate brain evolution: integrating comparative, neurophysiological, and ethological data. *Evol. Anthro.* **15**, 224-236.
 45. Barton RA, Harvey PH. 2000 Mosaic evolution of brain structure in mammals. *Nature* **405**, 1055-1058.
 46. Freckleton RP, Harvey PH, Pagel MD. 2002 Phylogenetic analysis and comparative data: A test and review of evidence. *Am. Nat.* **160**, 712-726.
 47. Shipley B 2000. *Cause and Correlation in Biology: A User's Guide to Path Analysis, Structural Equations and Causal Inference*. Cambridge, UK: Cambridge University Press.
 48. Isler K, Kirk CE, Miller JMA, Albrecht GA, Gelvin BR, Martin RD. 2008 Endocranial volumes of primate species: scaling analyses using a comprehensive and reliable data set. *J. Hum. Evol.* **55**, 967-978. (10.1016/j.jhevol.2008.08.004).
 49. Rehkamper G, Frahm HD, Zilles K. 1991. Quantitative development of brain and brain structures in birds (Galliformes and Passeriformes) compared to that in mammals (Insectivores and Primates). *Brain Behav. Evol.* **37**, 125-143.
 50. Stephan H, Frahm HD, Baron G. 1981. New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatologica* **35**, 1-29.
 51. Myers P, Espinosa R, Parr CS, Jones T, Hammond GS, Dewey TA. 2015 The Animal Diversity Web (online). (Accessed at <http://animaldiversity.org>.)
 52. Freckleton R. 2009 The seven deadly sins of comparative analysis. *J. Evol. Biol.* **22**:1367-75.
 53. Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, Orme DL, et al. 2009 PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**, 2648-2648. (doi: 10.1890/08-1494.1).
 54. Revell LJ. 2009 Size-correction and principal components for interspecific comparative studies. *Evolution* **63**, 3258-3268. (doi: 10.1111/j.1558-5646.2009.00804.x).
 55. Arnold C, Matthews LJ, Nunn CL. 2010 The 10k trees website: A new online resource for primate phylogeny. *Evol. Anthropol.* **19**, 114-118. (doi: 10.1002/evan.20251).
 56. R Core Team 2013 R: *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
 57. Orme C, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2011 CAPER: comparative analysis of phylogenetics and evolution in R, R package v. 0.4. See: <http://CRAN.R-project.org/package=caper> (accessed 25 October 2011).
 58. Revell LJ. 2012 Phytools: an R package for phylogenetic comparative biology (and other things). *Method. Ecol. Evol.* **3**, 217-223.
 59. Zeileis A, Kleiber C, Jackman S. 2008 Regression Models for Count Data in R. *J. Stat. Softwr.* **27**(8).
 60. Baba K, Shibata R, Sibuya M. 2004 Partial correlation and conditional correlation as measures of conditional independence. *Aust. NZ J. Stat.* **46**:657-64
 61. Hoppitt W, Laland KN. 2013 *Social Learning: An Introduction to Mechanisms, Methods, and Models*. Princeton, NJ: Princeton University Press.
 62. von Hardenberg A, González-Voyer A. 2013 Disentangling evolutionary cause-effect relationships with phylogenetic confirmation path analysis. *Evol.* **67**:378-87
 63. Pearl J. 2009 *Causality*. Cambridge University Press
 64. Cheney DL, Seyfarth RM. 2007 Baboon Metaphysics: The

- 1 Evolution of a Social Mind.
Chicago, IL: University of
2 Chicago Press.
- 3 65. Reader SM, Lefebvre L. 2001 Social
4 learning and sociality. *Behav.*
5 *Brain Sci.* **24**, 353-355.
- 6 66. Henrich J. 2004 Demography and
7 cultural evolution: why adaptive
8 maladaptive losses in
9 Tasmania. *Am. Antiq.* **69**, 197-
10 221.
- 11 67. Lewis H, Laland KN. 2012
12 Transmission fidelity is the key
13 to the build-up of cumulative
14 culture. *Phil. Trans. R. Soc. B*
15 **367**, 2171-2180.
- 16 68. Powell A, Shennan S, Thomas MG.
17 2009 Late Pleistocene
18 demography and the
19 appearance of modern human
20 behavior. *Science* **324**, 1298-
21 1301.
- 22 69. Muthukrishna & Henrich, this volume
- 23 70. Deaner RO, van Schaik C, Johnson V.
24 2006 Do some taxa have better
25 domain-general cognition than
26 others? A meta-analysis of
27 nonhuman primate studies.
28 *Evol. Psychol.* **4**, 149-196.
- 29 71. Gibson KR. 1986 Cognition, brain size
30 and the extraction of embedded
31 food resources. In: *Primate*
32 *Ontogeny, Cognition and Social*
33 *Behavior*. JG Else, PC Lee,
34 (Eds). pp. 93-103. Cambridge,
35 UK: Cambridge University
36 Press.
- 37 72. Harvey PH, Krebs JR. 1990 Comparing
38 brains. *Science* **249**, 140-146.
- 39 73. Whiten A, van Schaik CP. 2007 The
40 evolution of animal 'cultures'
41 and social intelligence. *Phil.*
42 *Trans. R. Soc. B* **363**, 603-620.

Figure and table captions

Table 1. PGLS analyses of the relationship between innovation rates as the outcome variable and brain size as a factor, controlling for an estimate of research effort on each species (number of publications in a survey of the Zoological Record). For each innovation rate measure we ran a model assessing the effect of relative brain size, by including body mass as a cofactor (top of each pair of rows), and absolute brain size, by not including body mass as a cofactor (lower of each pair of rows; body mass results are thus marked not applicable [NA] for these rows). All models were strongly significant ($p < 0.001$). Significant relationships between innovation rate and body mass or brain size are in bold.

Figure 1. Number of reports of innovation, tool use and extractive foraging in our survey of non-human primates. Of the 584 reports of innovation (shaded), 264 or 45% were classified as 'technical innovation' (i.e. innovative tool use) and 320 or 55% were classified as 'non-technical innovation'. In a second set of analyses, we used a broader definition of technical innovation that included novel tool use and novel extractive foraging behaviour patterns. With this broader definition, 351 or 60% were classified as 'technical innovation' and 223 or 40% were classified as 'non-technical innovation'.

Figure 2. Best-supported graphs using phylogenetic exploratory path analyses including either (a) technical innovation rate, (b) non-technical innovation rate, or (c) technical innovation rate including extractive foraging [EF], together with social learning rate, brain size, body size, a life history composite measure, social group size and diet breadth. Edges, i.e. lines, between pairs of variables indicate significant correlations between these variables while taking their correlation with the other variables into account. P-values are indicated for those edges. Analyses of total innovation rate (i.e. technical and non-technical innovations combined) gives very a similar picture to Fig 2b. Dotted boxes indicate tightly covarying suites of variables

Tables

		Brain measure	Model		Research Effort		Body mass		Brain size	
			λ	r	β	p	β	p	β	p
All (167 species)	Innovation	Relative	0.58	0.55	0.33	<0.0001	-0.10	0.61	0.37	0.19
		Absolute	0.58	0.56	0.33	<0.0001	NA	NA	0.23	0.016
	Technical innovation	Relative	0.81	0.37	0.12	0.0002	-0.09	0.60	0.36	0.12
		Absolute	0.81	0.38	0.12	0.0002	NA	NA	0.25	0.005
	Non-technical innovation	Relative	0	0.58	0.30	<0.0001	-0.01	0.91	0.07	0.64
		Absolute	0	0.58	0.30	<0.0001	NA	NA	0.06	0.16
	Technical innovation with extractive foraging	Relative	0.71	0.52	0.24	<0.0001	0.00	1.00	0.28	0.27
		Absolute	0.71	0.52	0.24	<0.0001	NA	NA	0.28	0.003
	Non-technical innovation without extractive foraging	Relative	0	0.50	0.22	<0.0001	-0.04	0.74	0.11	0.46
		Absolute	0	0.51	0.22	<0.0001	NA	NA	0.06	0.11
Innovators (48 species)	Innovation	Relative	0	0.79	0.58	<0.0001	-0.48	0.11	0.98	0.015
		Absolute	0	0.78	0.56	<0.0001	NA	NA	0.37	0.0002
	Technical innovation	Relative	0.31	0.73	0.54	<0.0001	-0.82	0.027	1.52	0.027
		Absolute	0.33	0.70	0.49	<0.0001	NA	NA	0.49	0.001
	Non-technical innovation	Relative	0	0.64	0.41	0.0001	-0.17	0.59	0.45	0.26
		Absolute	0	0.65	0.40	0.0001	NA	NA	0.24	0.012
	Technical innovation with extractive foraging	Relative	0.32	0.77	0.59	<0.0001	-0.60	0.08	1.28	0.006
		Absolute	0.26	0.76	0.56	<0.0001	NA	NA	0.51	0.0002
	Non-technical innovation without extractive foraging	Relative	0	0.53	0.34	0.004	-0.35	0.32	0.69	0.14
		Absolute	0	0.53	0.33	0.005	NA	NA	0.24	0.027
	Foraging innovation	Relative	0	0.72	0.29	<0.0001	-0.48	0.14	0.88	0.040
		Absolute	0	0.69	0.29	<0.0001	NA	NA	0.28	0.006
	Technical foraging innovation with extractive foraging	Relative	0.15	0.73	0.52	<0.0001	-0.68	0.041	1.23	0.006
		Absolute	0	0.71	0.48	<0.0001	NA	NA	0.31	0.003
Non-technical foraging innovation without extractive foraging	Relative	0	0.45	0.27	0.004	-0.13	0.63	0.27	0.46	
	Absolute	0	0.46	0.27	0.004	NA	NA	0.10	0.23	

Figures

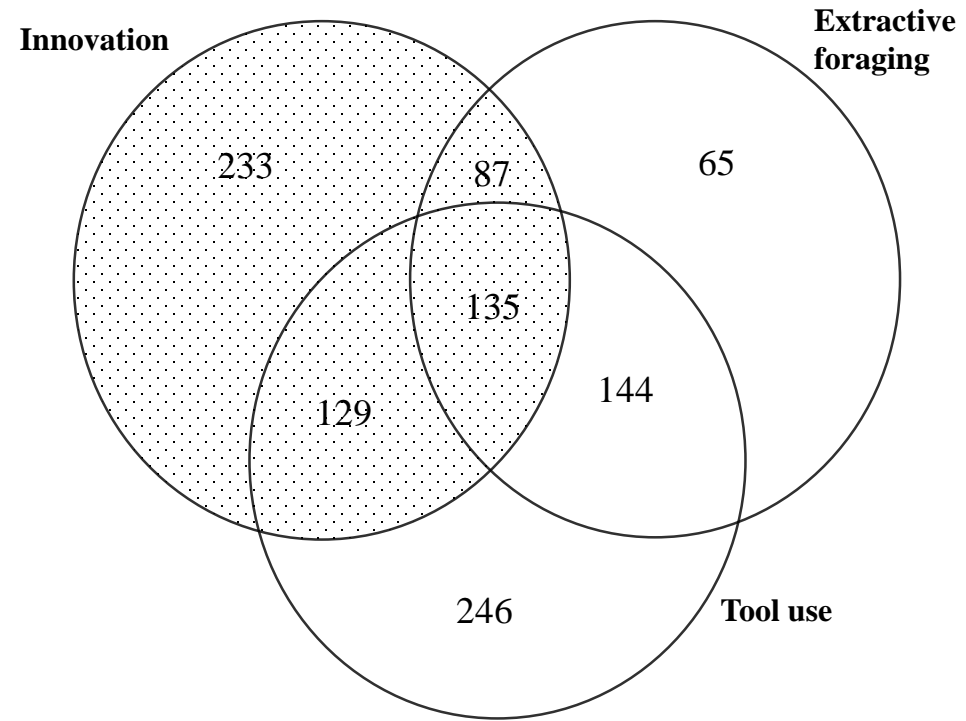
Figures are provided in two PDF files (NavarreteFigure1.pdf, NavarreteFigure2.pdf).

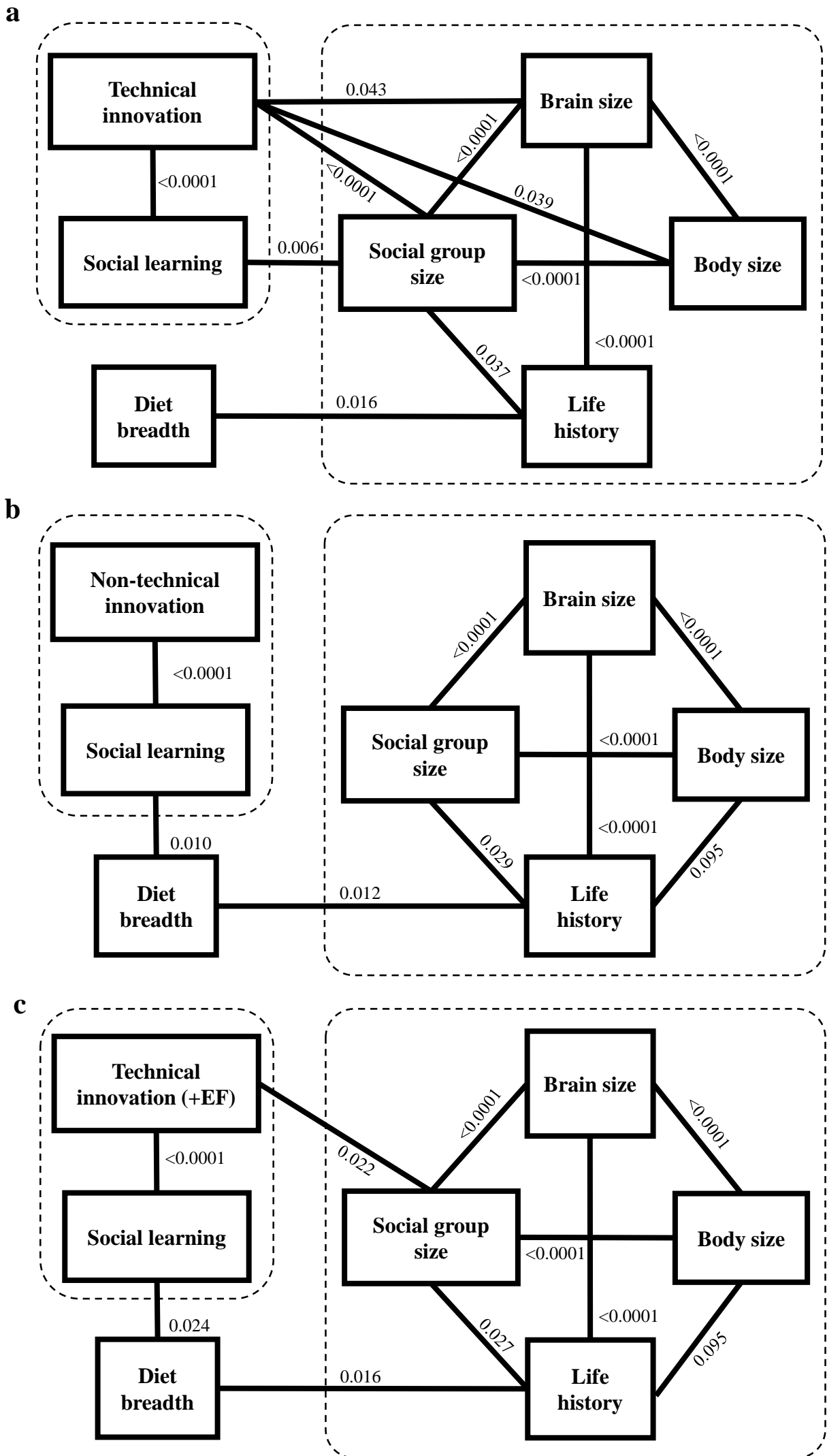
Supplementary material

The dataset to be uploaded to Dryad is included here for reference (NavarreteESM.xls). The electronic supplementary material (PDF file) details additional analyses (NavarreteESM2.pdf).

For Review Only

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