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The coevolution of innovation and technical intelligence in primates

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

1. Introduction

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

While humans may be exceptional innovators, we are far from the only species that devises novel behaviour patterns. Recent research reveals that many animals will invent new behaviours or modify existing behaviours (e.g. devise more efficient foraging techniques), that such innovation is taxonomically widespread and that there is considerable inter- and intraspecific variation in innovation rates [4].

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Innovation has been hypothesized to be an important influence on the success and evolution of many non-human animals, particularly in populations faced with novel challenges such as anthropogenic change [4–6]. Evidence from comparative and experimental studies supports this contention. For example, comparative studies of birds have linked rates of behavioural innovation with range expansion [7–9], with rates of evolutionary diversification [10,11] and with dietary and habitat generalism [12,13]. Experimental studies have associated novel problem-solving with fitness components such as mating success and offspring survival [14–16].

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

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

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

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

Here, we explore the generality and robustness of Overington *et al.*'s [36] conclusions by investigating whether similar relationships between innovation and brain evolution are observed in non-human primates. We take a broadly similar approach by subdividing our primate innovation dataset into technical innovations and non-technical innovations. We focus particularly on innovations that require tool use as this is a core element of technical intelligence hypotheses [37], one of several hypotheses put forward to explain the evolution of enhanced cognition and brain enlargement [20,38–41]. In a second set of analyses, we examine a broader definition of technical innovation, including both innovative tool use and innovative extractive foraging, reflecting arguments that extractive foraging played a role in primate cognitive evolution [42,43].

Our analyses examine the relationship between technical innovation, non-technical innovation, and both absolute and relative brain size, as well as several factors that have been shown to covary with brain size and/or innovation rate, including body size, life-history variables, social group size,

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diet breadth and rates of social learning. While there is potential utility in examining individual brain components and their relation to behavioural innovation, currently insufficient data are available when innovation is subdivided. Moreover, recent work on the coevolution of different brain areas suggests that many components change in volume together as a network [44,45]. This suggests that a focus on large brain areas or the entire brain may be appropriate, particularly for broad categories of behaviour such as innovation that are plausibly reliant on domain-general capabilities, and involve many cognitive and other processes and many parts of the brain.

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

2. Methods

(a) Brain data

Species means for brain size and body mass were obtained from Isler *et al.* [48]. Isler *et al.* compiled endocranial volumes (ECV) for 3813 museum specimens, at least 88% wild-caught, for 167 primate species. ECV provides a good estimate of brain volume that is easily convertible into brain mass [49]. We complemented the dataset with body mass and brain mass for four additional species: *Callicebus moloch, Cercopithecus talapoin* (from [50]), *Saguinus imperator* and *Callithrix geoffroyi* (from [51]). Brain mass in these species was converted into ECV [49] before being added to the dataset. ECV and body mass were natural log-transformed prior to analysis to normalize distributions. Below, we refer to ECV as 'brain size' and to body mass as 'body size'.

(b) Behavioural data

Behavioural data were drawn from Reader et al. [18]. Reader et al. surveyed over 4000 published articles for examples of innovation, social learning, tool use and extractive foraging in living nonhuman primates, using keywords (e.g. 'novel' or 'traditional') to classify behaviour patterns (e.g. as 'innovation' or 'social learning'). Full details of the database and discussion of its merits, disadvantages, reliability and validity are given in Reader et al. [18] and the papers cited therein. The observation frequencies for each of the four behavioural measures were calculated as the total number of reported examples of each class. Initially, we examined each innovation report and categorized it as a 'technical' innovation (involving tool use) or a 'non-technical' innovation (not involving tool use; data will be archived online in the Dryad depository). We go on to conduct further analyses in which 'technical innovation' is broadened to include both innovative tool use and innovative extractive foraging. We also restricted a subset of analyses to foraging innovations only (strictly, innovations that occur in a foraging context), deploying the classification in Reader & Laland [27]. We used the number of published articles on each species in the Zoological Record (taken from [18]) as a measure of research effort. We corrected the behavioural measures for differences in research effort by including research effort as an independent variable in statistical analyses [52].

(c) Diet breadth, life history and social group size

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

(d) Phylogeny

For the phylogenetic analyses, we used the 10 k Trees project dated consensus tree (v. 3) [55], and matched primate species from the brain dataset and the behavioural dataset with species in the tree, taking into consideration changes in nomenclature (electronic supplementary material).

(e) Data analyses

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

To account for non-independence of species-level data, we used PGLS, with phylogenetic signal (Pagel's λ) estimated by maximumlikelihood (henceforth $\lambda = ML$). Analyses were run in R v. 3.0.2 [56] using the 'caper' [57] and 'phytools' packages [58]. Models explored the relationship between brain size and innovation, treating innovation rates as response variables, and including research effort as a covariate. Analyses that examined the relationship between relative brain size and innovation included body mass. We also ran analyses examining absolute brain size, without body mass as a covariate, to allow comparison of absolute versus relative brain measures of brain size as predictors of cognitive differences, an open question in the field [21].

We ran additional analyses (electronic supplementary material) to take into account the fact that a large number of species in our database had zero recorded innovations. We ran a binomial regression predicting the probability that an innovation is observed in each paper based on research effort

(conducted using the method 'glm' in R [56]). We also present the results of using a zero-inflated Poisson (ZIP) model, which provides an alternative method for controlling for the large number of species with zero recorded innovations [59]. However, the ZIP model may not be suitable when there are a small number of observations for some entries (over 58% of the species had under 20 papers recorded in the Zoological Record survey), meaning that the results of these models should be interpreted with caution. Both the binomial model and the zero-inflated Poisson models also help control for the observed heteroscedasticity in the data (if the number of observations for a species is large, we should expect greater absolute variance in the number of reported innovations). However, binomial and ZIP models that incorporate phylogenetic information are not yet established methodologies. Thus, we used non-phylogenetic methods for these analyses.

Exploratory causal graphs were used to further examine interrelationships between variables. Causal graphs were generated by examining the phylogenetic partial correlation between variables, taking into account the remaining variables (using PGLS). For a set of variables $A = \{A_1, \ldots, A_n\}$, this method assesses the relationship between A_i and A_j by examining the correlation between the residuals of a phylogenetic linear 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 remaining variables. In order to guard against the premature rejection of causal relations between variables, we take the conservative stance of treating the correlation as potentially significant if p < 0.1, in which case an edge between A_i and A_j is added to the causal graph. This method allows us to visualize the significant relationships between variables when taking into account the presence of other variables, similar to other path analysis methods [47,60]. Edges were not oriented (i.e. directed) as we reasoned that biological evolution in this domain frequently encompasses feedback processes between traits [18,61].

Although this method uses the full set of covariates (all A_k) to assess independence, which may reduce statistical power, we find that the results of this procedure are the same as a more complex algorithm [62] that uses only connected variables. Our new method can be seen as an exploratory automation of von Hardenberg & González-Voyer [63], building on Pearl's PC algorithm [64]. For PGLS models within a given causal graph, λ is estimated by maximum-likelihood, in order to account for differing levels of phylogenetic signal across linear models. However, given that previous approaches have assumed a fixed common value for λ for all paths [63], we also analyse graphs with λ fixed at 0 or 1, which represent the extreme values of λ , and thereby provide a strong check as to whether our conclusions are robust to different values of phylogenetic signal. The values on the edge of each graph represent the p-value, i.e. the significance of the relationship between variables when taking into account the influence of only connected variables (see figure 2).

3. Results

Where technical innovation was restricted to tool use, out of the 584 reports of innovation, 45% were classified as technical innovations and 55% as non-technical innovations (figure 1). In the broader categorization of technical innovation that included novel extractive foraging behaviour patterns, 60% were classified as technical innovations and 40% as non-technical innovations.

(a) Comparative phylogenetic analyses for all species

Total innovation rate (i.e. technical and non-technical combined) was found to be positively correlated with absolute



Figure 1. Number of reports of innovation, tool use and extractive foraging in our survey of non-human primates. Out 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'.

but not relative brain size in primates (table 1). That is, there was a significant positive correlation between innovation rate and brain volume, but this relationship was no longer significant when body mass was taken into account.

Technical (i.e. involving tool use) and non-technical innovation rates correlated positively with each other (PGLS: $\lambda =$ 0, r = 0.61, $\beta = 0.49 \pm 0.09$, p < 0.0001). A similar correlation was observed using a broader classification of technical innovation, including innovative extractive foraging (PGLS: $\lambda =$ 0.06, r = 0.53, $\beta = 0.44 \pm 0.10$, p < 0.0001). However, despite this positive correlation, different relationships were observed between brain size and technical versus non-technical innovation rates. Technical innovation rate was significantly correlated with absolute but not relative brain size, and we observed a stronger relationship with brain size than that observed for total innovation rate. Similar results were found for technical innovation including extractive foraging (table 1). In contrast, non-technical innovation rate was not significantly correlated with either absolute brain size or relative brain size (table 1). The model including brain size as a predictor of technical innovation, with research effort as a covariate, showed a higher correlation coefficient (r = 0.13) than the model predicting non-technical innovation (r =0.07), with a similar pattern observed using the broader classification of technical innovation including extractive foraging (r = 0.14 versus r = 0.08).

(b) Controlling for zero-inflation

To address the concern that our PGLS results were biased by the large number of primate species with no innovations (zero-inflation), we conducted ZIP and binomial analyses. ZIP models on our 167-species sample confirmed that zero scores on all measures of innovation were more likely in those species where research effort was low (electronic supplementary material, table S1). We found that the number of innovations observed correlated significantly with research effort, body mass and relative brain size using all innovation classifications. In contrast, absolute brain size correlated with Downloaded from https://royalsocietypublishing.org/ on 07 October 2022

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 (top of each pair of rows), and absolute brain size, by not including body mass as a cofactor (lower of each pair of rows), but mass results are thus marked not applicable (n.a.) for these rows). All models were strongly significant ($\rho < 0.001$). Significant relationships between innovation rate and body mass or brain size are in italics.

			model		research	effort	body mass		brain size	
		brain measure	۲	_	β	d	β	d	β	d
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	n.a.	n.a.	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	n.a.	n.a.	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	n.a.	n.a.	0.06	0.16
	technical innovation with extractive foraging	relative	0.71	0.52	0.24	< 0.0001	00.0	1.00	0.28	0.27
		absolute	0.71	0.52	0.24	< 0.0001	n.a.	n.a.	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	n.a.	n.a.	0.06	0.11
innovators (48 species)	innovation	relative	0	0.79	0.58	< 0.0001		0.11	0.98	0.015
		absolute	0	0.78	0.56	< 0.0001	n.a.	n.a.	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	n.a.	n.a.	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	n.a.	n.a.	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	n.a.	n.a.	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	n.a.	n.a.	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	n.a.	n.a.	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	n.a.	n.a.	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	n.a.	n.a.	0.10	0.23

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5 S only two innovation measures, total innovation rate and technical innovation including extractive foraging. Technical innovation was more strongly related to brain size than was non-technical innovation, using both absolute and relative brain size measures and for all classifications of technical innovation (see block A, table S1 in electronic supplementary material). Comparison of Akaike information criterion (AIC) values between models with and without body size found better support for models that included body size (i.e. relative brain size models).

We also ran a set of analyses using a binomial model, which predicted the likelihood that a given paper in the dataset contained an innovation. Binomial models for all species showed that all innovation rates (including total innovations, technical innovations and non-technical innovations) exhibited strong positive correlations with both absolute and relative brain size (p < 0.0001, electronic supplementary material, table S2). Technical innovation was more strongly related to both absolute and relative brain size than was non-technical innovation. These results are consistent with the results of the ZIP model, and again, comparison of AIC values between models with and without body size found better support for models that included body size.

(c) Innovators only analyses

Confirmation of zero inflation in the full species dataset provides further justification for repeating the analysis using the reduced dataset of innovators (table 1). Among our sample of innovators (48 species), we found strong correlations between total innovation rate and both absolute and relative brain size. Technical innovation also exhibited strong correlations with both absolute and relative brain size, and these relationships were stronger than those for total innovations. Non-technical innovation correlated significantly with absolute brain size only, and this correlation was weaker than the one observed between technical innovations and absolute brain size. Brain size was a better predictor of technical innovation than a predictor of non-technical innovation (technical innovation: r = 0.14; non-technical innovation: r = 0.10; technical innovation with extractive foraging: r = 0.26, non-technical innovation without extractive foraging: r = 0.05). Using the binomial models, we again observed strong and significant correlations between all innovation rates and absolute and relative brain size (see electronic supplementary material, table S2), and stronger relationships were observed between technical innovation rates and brain size measures than between non-technical innovation rates and brain size.

(d) Comparisons with Overington *et al.*: foraging innovations

To facilitate a closer comparison with Overington *et al.* [36], extractive foraging innovations were included in technical innovation, and PGLS analyses were restricted to foraging innovations only. This reduced the available pool of innovations considerably, and because of the aforementioned problems with zero-innovation scores, the 167-species analysis was not appropriate. In the innovators only sample, technical innovation correlated significantly with both absolute and relative brain size, but non-technical innovation did not correlate with either (table 1). In the ZIP and binomial models, technical innovation was again more strongly correlated with brain size

measures than was non-technical innovation (electronic supplementary material, tables S1 and S2).

(e) Causal graphs

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

Technical innovation rate shared direct edges with brain size in the best-supported graphs ($\lambda = ML$: p = 0.043, figure 2*a*; $\lambda = 0$: p = 0.014, $\lambda = 1$: p = 0.009, see electronic supplementary material, figure S1), which indicates that these two variables are directly correlated even when the other variables are taken into account. Technical innovation rate also was directly related to social learning rate (p < 0.0001), body size (p = 0.039) and social group size (p < 0.0001). PGLS analyses 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, p = 0.050; social learning: $\lambda = 0$, r = 0.77, p < 0.0001; electronic supplementary material, table S3). However, the relationship between technical innovation and social group size was not statistically significant in the PGLS model ($\lambda =$ 0.91, r = 0.02, p = 0.88). 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, social group size: p < 0.0001; $\lambda = 1$: social learning rate: p < 0.0001, body size: p = 0.007, social group size: p < 0.0070.0001, see electronic supplementary material, figure S1a).

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

Technical innovation rate including extractive foraging shared direct edges with social learning rate (p < 0.0001) and social group size (p = 0.020) in the graphs with $\lambda = ML$ (figure 2*c*), as well as in the graphs with $\lambda = 0$ and $\lambda = 1$ (electronic supplementary material, figure S1*c*), but the direct relationship with brain size was lost (p > 0.1). PGLS analyses showed that the correlation of this measure of technical innovation with social learning was positive ($\lambda = 0, r = 0.76, p < 0.0001$), but the relationship with social group size was not significant ($\lambda = 0.728, r = 0.11, p = 0.17$).

4. Discussion

The innovativeness of a species, defined as the frequency with which novel behaviour patterns are generated (controlling for research effort), covaries with diverse measures of absolute and relative brain size in both birds and primates [18,22]. In birds, brain size covaries more strongly with technical than with non-technical innovation [36], suggesting a potentially important distinction between these types of novel behaviour. Our findings in non-human primates were

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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) give very a similar picture to figure 2*b*. Dotted boxes indicate tightly covarying suites of variables.

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broadly consistent with those of Overington *et al.* [36]. Phylogenetic analyses comprising all primate innovations found that absolute (but not relative) brain size correlated positively and strongly with both technical innovation and total innovations but showed a non-significant relationship with non-technical innovation. However, PGLS analyses do not account for the zero-inflated distribution of innovation counts across species. When this is controlled for, either by deploying zero-inflated Poisson or binomial models, or by reducing the sample to 'innovator' species, we find that total innovation measures covary significantly with absolute and relative brain size, and that technical innovation always exhibits a stronger relationship with brain size than non-technical innovation.

Exploratory causal graph analyses painted a similar picture, where technical innovation shared a direct edge with brain size (figure 2*a*), whereas the number of non-technical innovations did not. Rather, non-technical innovation was linked to brain size via social learning, diet and life-history variables (figure 2*b*). Technical innovation also shared very strong direct edges with social learning, body size and social group size. However, when we add extractive foraging to technical innovation, the direct relationship with brain size was lost (figure 2*c*). This implies that tool use, more so than extractive foraging, may be the relevant factor underlying the direct relationship between technical innovation and brain size.

This direct connection between technical innovation and brain size provides support for 'technical intelligence' hypotheses [37] in suggesting that in some primate lineages the ability to invent novel technical behaviours, specifically those involving tools, may have favoured encephalization, more than the ability to generate novel behaviours per se. Overington et al. [36] restrict their analyses to foraging innovations alone, and use a somewhat broader definition of technical innovations, with technical innovations referring to novel foraging techniques, not just tool use. Our analyses tell a similar story to those of Overington et al. As in birds, the ability to gain access to difficult-to-extract, but potentially nutrientrich, resources through tool use and technical skill may have conferred adaptive advantages, leading to selection for brain regions and circuitry that underlie technical flexibility and proficiency in some primate lineages. This pattern holds when our PGLS analyses were restricted to foraging innovations.

We also observed strong connections in causal graph analyses between primate technical innovation and both social learning and social group size (although the group size-technical innovation link was not significant in a PGLS analysis), suggesting coevolution of elements of social, technical and ecological intelligence, as has been previously argued [65]. Those primates that score highly for innovation and tool use (e.g. the great apes, capuchins, macaques) are also renowned for their social learning [18,65], and there is now extensive experimental evidence demonstrating that primates can acquire many tool-using methods through social learning [61]. Indeed, a robust finding of both our causal graph analyses and our previous work [18,19] is that innovation and social learning evolve together, a conclusion that holds here for both technical and non-technical innovation.

The direct connections between technical innovation and social group size, as well as between social learning and social group size, conflict with previous analyses that found no relation between social group size and total innovation rate or social learning rate [18,66]. This could reflect the effect of examining technical innovations alone, additional power in the current analyses or sample, or the effect of the additional variables incorporated in the present analyses. Theoretical work, however, suggests that the observed relationships of group size with reported technical innovation rates may be no artefact. A wide variety of theoretical studies now link the size of cultural repertoires with social group size, as larger populations provide a more stable repository for the retention of innovations than do smaller groups, as well as more potential innovators [67-70]. These links between technical innovation and both social learning incidence and social group size are, of course, consistent with several social intelligence hypotheses [20,38-41], which supports the suggestion that these explanations are not mutually exclusive [18,71]. The consistently observed edge in our path analyses linking social group size and brain size supports the established finding that social intelligence is an important driver of brain evolution [20,38-41].

Our causal graph analyses linked non-technical innovation to measures of diet breadth via social learning, a finding that evokes ecological intelligence explanations, in which primate intelligence is favoured by the challenge of locating and extracting diverse and constantly changing foods [42,43,72,73]. However, as Overington *et al.* [36] reported for birds, while larger-brained, innovative primate species may be more likely to incorporate novel foods into their diets, and while this ability may be ecologically important, our findings imply that the relationship between innovativeness and brain size in primates is more likely to be primarily driven by technical innovations.

Although the absence of an edge between non-technical innovation and brain size in the best-supported causal graph ostensibly rules out a direct coevolutionary relationship between these variables, it does not preclude a more diffuse coevolutionary interaction. What the causal graph analysis implies is that if there is a causal influence of non-technical innovation on brain evolution it occurs through changes in social learning, diet and life history. One plausible interpretation of these findings is that through social transmission many primates learn to exploit novel foods, and the resources so gleaned both aid survival and fuel brain growth. Cultural drive explanations [5,20,35,41,74] are relevant here, as they propose that selection for innovativeness and/or efficient social learning drove the evolution of encephalization in primates. However, given that most primate species in our sample exhibited zero innovations, we emphasize that any causal role for innovation, be it technical or non-technical, in driving encephalization is likely to be only part of the story, and restricted to a subset of primate lineages.

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

Given the fact that both brains and innovations can perform many functions, a complete analysis would require numerous interacting variables to be investigated. Moreover, it remains an open question as to whether innovation is a driving causal factor in our evolutionary analyses, or whether the innovations observed in our survey are simply the byproducts of broader psychological processes. Reports of technical innovation are relatively sparsely distributed across the primates, and close relatives often differ considerably in innovation rates. This could reflect the difficulty in gathering a comprehensive sample of primate innovation, but also points to technical innovation being just a part of a larger story. Even focused on the restricted set of variables considered in our analyses, the emergent picture is one in which there are multiple drivers of the evolution of the primate brain and intelligence that feed back on each other in complex, nonlinear ways. It would seem that innovativeness in primates, like intelligence and cognition more generally, is not to be explained by a single prime mover, but rather by a complex of factors that encompass technical, social and ecological intelligence.

Data accessibility. The datasets supporting this article are available via the Dryad repository: doi:10.5061/dryad.dk10k.

Authors' contributions. A.F.N. and S.M.R. compiled the data; A.F.N., A.W. and S.E.S. analysed the data; A.F.N., S.M.R. and K.N.L. took the lead in writing the article, with contributions from A.W. and S.E.S. All authors gave final approval for publication.

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