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**TITLE: Coevolution of cultural intelligence, extended life history, sociality and brain size in primates**

Short title: 'Cultural' primates are more social and long-lived

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Explanations for primate brain expansion and the evolution of human cognition and culture remain contentious in spite of extensive research. Further, while multiple comparative analyses have investigated variation in brain size across primate species, very few have addressed why primates vary in how much they utilize social learning. Here, we evaluate the hypothesis that the enhanced reliance on socially transmitted behavior observed in some primates has co-evolved with enlarged brains, complex sociality and extended lifespans. Using recently developed phylogenetic comparative methods, we show that across primate species, a measure of social learning proclivity increases with absolute and relative brain volume, longevity (specifically reproductive lifespan), and social group size, correcting for research effort. We also confirm relationships of absolute and relative brain volume with longevity (both juvenile period and reproductive lifespan) and social group size, though longevity is generally a stronger predictor. Relationships between social learning, brain volume and longevity remain when controlling for maternal investment, and are therefore not simply explained as a by-product of the generally slower life history expected for larger-brained species. Our findings suggest that both brain expansion and high reliance on culturally transmitted behavior co-evolved with sociality and extended lifespan in primates. This coevolution is consistent with the hypothesis that the evolution of large brains, sociality and long lifespans has promoted reliance on culture, with reliance on culture in turn driving further increases in brain volume, cognitive abilities and lifespans in some primate lineages.

### **Significance statement**

Some primate species, particularly humans, have large brains, long lives, complex social relationships, and advanced cognitive and cultural capabilities, but how and why these evolved remains debated. Here we use up-to-date phylogenetic comparative statistical methods applied to a large primate dataset to examine whether the enhanced reliance on culturally transmitted behavior observed in some primates has co-evolved together with enlarged brains, sociality and extended lifespans. Our analyses confirm that these traits did indeed coevolve in primates, and point towards causal scenarios underlying their association. Our findings suggest that large brains, sociality and longer lifespans drove increases in cultural capacity, which in turn may have driven further increases in brain size, cognitive abilities and lifespan in some primate lineages.

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Brain expansion is unquestionably a distinctive feature of primate, and especially human, evolution. This is the case whether the brain is measured in absolute terms, as relative to body size, or as size of the neocortex relative to the rest of the brain (1), and irrespective of whether it is better characterized by variation in a single size dimension (2) or mosaic evolution of component parts (3). The striking variation in brain size in non-human primates, across three orders of magnitude (4), has long demanded an evolutionary explanation (5). While the cognitive implications of cross-species variation in whole brain size remain contentious and require further investigation (5–7), evolutionary increases in overall brain size in primates reflect neuro-anatomical changes that are plausibly linked to increases in general cognitive abilities. For instance, larger primate brains have more neurons in absolute terms (8–11), with coordinated expansion particularly in the neocortex and cerebellum (12), potentially supporting a greater diversity of cognitive functions (7, 10). In support of this idea, overall brain size increases with broad measures of cognitive ability in primates, including performance in laboratory tests of learning and cognition across primate genera (13), and performance in experimental measures of behavioral inhibition across primate species (14).

At ~1500g (15), human brains are at least three times heavier than any other primate species (1). However, humans are also extreme in their long lifespan, social complexity, cognition and cultural capabilities (16, 17), raising questions about whether large brains, long lives, complex cognition and advanced cultural capabilities evolved independently, or coevolved through directly reinforcing processes. Enlarged brains, enhanced cognition and highly developed social learning abilities co-occur not only in primate species but also in some cetaceans and birds (18–22), raising the

possibility of a key role for social learning and culture in brain evolution and intelligence in multiple, independent animal lineages (23–27).

Across primates, support for multiple, non-exclusive hypotheses for enlarged brain (particularly neocortex) size has been identified in comparative studies, emphasizing the roles of social complexity (e.g. group size, (28, 29)), ecological intelligence (e.g. dietary complexity, (30, 31)), technical intelligence (e.g. tool use, technical innovation, (21, 25, 32)), and behavioral complexity (e.g. innovativeness, social learning, tactical deception, (21, 25, 33)). Further, several comparative studies have found that larger brained primates have slower life history strategies, including longer juvenile periods and overall lifespans (e.g.(29)). While mutually reinforcing evolutionary processes have been proposed to account for this association (16), recent comparative analyses suggest that lifespan increases with brain size in mammals rather due to developmental costs - i.e. it requires a longer period of maternal investment to support offspring with greater natal and post-natal brain growth, requiring a slower life history strategy of which longer lifespan is a by-product (34). Primates, however, are potentially distinct from most mammalian taxa in their unusually large, neuron-dense brains (8–11) and in the extensive occurrence of socially transmitted behavior exhibited by some lineages (e.g.(35–37)). Whether the association between extended life history and enlarged brain size is best explained by a cognitive or developmental mechanism, in primates specifically, remains to be explored. Further, despite many previous comparative analyses of brain size and relevant predictors in primates, comparative analyses have not yet directly explored the evolutionary relationships between brain expansion, cultural complexity, sociality and longevity in analyses that include all of these variables, with control for relevant potential confounding variables.

Here we conduct the first direct test of the widely held view that encephalization, sociality, longevity and reliance on culture have coevolved (16, 23–27, 32, 38), in a comparative analysis of primate species. We use a quantitative behavioral measure of reliance on culture, specifically, the number of unique reports of (i.e. richness) of social learning per species from a sample of relevant published literature (21, 39) (henceforth referred to simply as ‘social learning’, see Supplementary Information for further details on this measure). We use Bayesian phylogenetic mixed models to investigate a cluster of related hypotheses concerned with the evolutionary relationships between social learning, brain volume, group size and lifespan. Below, we specify and test four predictions, each of which are independent, yet if all supported would imply support for a cluster of related, and mutually consistent, ideas concerning the factors underlying the evolution of brain, cognition and culture.

#### **Prediction 1: social learning increases with absolute and relative brain volume**

This expectation follows from the hypotheses that (i) high levels of knowledge and skill are required for primates to exploit high-quality, difficult-to-access dietary resources, with these skills primarily acquired through social learning (16, 23–27, 32, 38, 40), and (ii) the energy so acquired is critical to developing and running a large brain (16, 27). Previous comparative analyses have identified positive associations of social learning with the absolute and relative sizes of brain components, primarily the neocortex (21, 25). Here, we extend these analyses to overall brain size measured as endocranial volume (ECV), allowing for much larger (at least threefold) sample sizes, far more representative of the diversity in brain size across primate species (41).

## **Prediction 2: social learning increases with longevity**

This expectation follows from the hypotheses that (i) extended life history, particularly a longer lifespan and period of juvenile dependence, facilitates the acquisition, exploitation and social transmission of life skills (16, 23, 40), and (ii) cultural knowledge promotes survival and long lives (25–27) by acting as a ‘cognitive buffer’, enhancing survival in challenging environmental conditions through behavioral responses (42, 43). Complex skills frequently take time to learn, and hence longer lifespans potentially provide more time for relevant experience to accrue, more time for adults to benefit from knowledge acquired earlier in life, and more time for parents to pass on relevant skills to offspring (16, 23, 26, 27, 40). If an extended juvenile period in particular is critical for the acquisition of adaptive socially transmitted behavior (16), we expect that juvenile period has a strong association with social learning richness. However, costly investment in learning socially transmitted skills may only pay off in later life across a long reproductive lifespan (16), therefore, we may expect the association between social learning and longevity to be driven more strongly by increases in reproductive lifespan. If there is a specific relationship of social learning with longevity, not confounded by relationships of either with absolute or relative brain size, we should still find this association even when controlling for brain volume and body mass. Furthermore, if reliance on socially transmitted behavior is related to longevity via a ‘cognitive buffer’ mechanism rather than as a by-product of a relationship between social learning, brain volume and slower life history traits due to developmental constraints, this relationship should remain when controlling for the potentially confounding effect of maternal investment (measured as the sum of gestation and lactation periods) (34).



**Prediction 3: social learning increases with group size**

This expectation follows from several theoretical and empirical analyses showing that large social groups support greater amounts of adaptive cultural knowledge (e.g. (44–47)), and broader hypotheses that stable social grouping supports the evolution of reliance on social learning (e.g.(20)). If the relationship of social learning to group size is not confounded by associations of either trait with absolute brain volume, relative brain volume or longevity, this prediction should hold when controlling for brain volume, body mass and longevity measures.

**Prediction 4: Absolute and relative brain volume increases with longevity**

Across mammals, a relationship between adult brain mass and longevity is not supported when controlling for maternal investment, suggesting that developmental constraints associated with investing in large-brained offspring underpin this association (34). However, if in primates, associations of longevity with absolute and relative brain volume remain when maternal investment is included in analyses, the relationship between brain volume and lifespan is not confounded with maternal investment and is thus potentially indicative of a cognitive, rather than solely developmental, mechanism whereby greater cognitive flexibility facilitates survival, in primates specifically even if not in mammals more generally. Additionally, if longevity is related to brain volume independently of any potentially confounding effect of social group size, these associations should remain intact when group size is included in statistical models.

## Results

### Prediction 1: Social learning and brain volume

As predicted, social learning richness increases with both absolute ( $<1\%$   $\beta$  coefficients in the posterior distribution crossing zero,  $N=150$ , Supplementary Table S1(i)) and relative brain volume ( $3\%$   $\beta$  crossing zero,  $N=150$ , Supplementary Table S1(ii)).

### Prediction 2: Social learning and longevity

As predicted, social learning richness increases with longevity ( $<1\%$   $\beta$  crossing zero,  $N=117$ , Supplementary Table S2A(i), **Figure 1a**). We find no evidence that social learning increases with juvenile period length, however ( $58\%$   $\beta$  crossing zero,  $N=101$ , Supplementary Table S2B(i)), rather, social learning increases with reproductive lifespan specifically ( $0\%$   $\beta$  crossing zero,  $N=92$ , Supplementary Table S2C(i), **Figure 1a**). Relationships between social learning and longevity, and between social learning and reproductive lifespan, remain intact when maternal investment (summed gestation and lactation time) is included as an additional predictor ( $2\%$ ,  $<1\%$   $\beta$  crossing zero,  $N=87$ ,  $N=82$ , Supplementary Tables S2A (ii), S2C(ii) respectively), while maternal investment itself does not predict social learning in these models ( $\geq 35\%$   $\beta$  crossing zero, Supplementary Tables S2A(ii), S2C(ii)). Relationships between social learning and longevity or reproductive lifespan are also not confounded by those between social learning and absolute or relative brain volume, as they remain when either brain volume or both brain volume and body mass are included as additional predictors ( $<1\%$   $\beta$  crossing zero,  $N=111$ ,  $N=89$ , Supplementary Tables S2A (iii, iv), S2C (iii, iv)).

### Prediction 3: Social learning and group size

As predicted, we find a positive association between group size and social learning ( $<1\%$   $\beta$  crossing zero,  $N=167$ , Supplementary Table S3(i), **Figure 1a**). This association is independent of the relationship between social learning and longevity or reproductive lifespan, as the association remains when either of these life history traits are included ( $4\%$   $\beta$  crossing zero,  $5\%$   $\beta$  crossing zero,  $N=111$ ,  $N=89$ , Supplementary Tables S3(ii.a, ii.b) respectively). The relationship between group size and social learning is also not confounded by the association of either trait with absolute or relative brain volume, as it remains when either brain volume or both brain volume and body mass are included as additional predictors ( $<4\%$   $\beta$  crossing zero,  $N=140$ , Supplementary Tables S3(iii, iv)).

### Prediction 4: Predictors of brain volume

We confirm the expected positive association of absolute brain volume with social group size ( $3\%$   $\beta$  crossing zero,  $N=151$ , Supplementary Table S4(i), **Figure 1b**). Absolute brain volume also increases with longevity, juvenile period length and reproductive lifespan ( $<1\%$   $\beta$  crossing zero,  $N=112$ ,  $N=98$ ,  $N=90$ , Supplementary Tables S4(ii.a, ii.b, ii.c), **Figure 1b**). Relationships between absolute brain volume and longevity, juvenile period and reproductive lifespan remain intact when maternal investment is included in the model, which itself also increases with brain volume (all  $<1\%$   $\beta$  crossing zero,  $N=84$ ,  $N=86$ ,  $N=79$ , Supplementary Tables S4(iii.a, iii.b, iii.c)). Relationships between longevity, juvenile period and reproductive lifespan with absolute brain volume are independent of the association of brain volume and group size, remaining intact when group size is included as an additional predictor (all  $<1\%$   $\beta$  crossing zero,  $N=106$ ,  $N=95$ ,  $N=87$ , Supplementary Tables S4(iv.a, iv.b, iv.c), while group

size is a relatively weak predictor when included with longevity or reproductive lifespan ( $>6\%$   $\beta$  crossing zero, Supplementary Tables S4(iv.a, iv.c).

Similarly, relative brain volume increases with social group size (4%  $\beta$  crossing zero,  $N=151$ , Supplementary Table S5(i), **Figure 1c**). Relative brain volume also increases with longevity, juvenile period and reproductive lifespan ( $<1\%$   $\beta$  crossing zero,  $N=112$ ,  $N=98$ ,  $N=90$ , Supplementary Tables S5(ii.a, ii.b, ii.c), **Figure 1c**). Again, associations between relative brain volume and all three life history measures remain intact when controlling for maternal investment, which itself also increases with relative brain volume (all  $<1\%$   $\beta$  crossing zero,  $N=84$ ,  $N=86$ ,  $N=79$ , Supplementary Tables S5(iii.a, iii.b, iii.c)). The relationship between relative brain volume and life history length is not confounded by social group size, as all three measures remain intact when group size is added to the model ( $<1\%$   $\beta$  crossing zero,  $N=106$ ,  $N=95$ ,  $N=87$ , Supplementary Table S5(iv.a, iv.b, iv.c)). When included with longevity or reproductive lifespan, however, group size is not strongly supported as a predictor of relative brain volume ( $>12\%$   $\beta$  crossing zero, Supplementary Table S5 (iv.a, iv.c)).

Parameters from all statistical models are reported in full in Supplementary Results Tables. All results reported in the main text refer to models including great apes, but none of our main results are qualitatively affected by removing these species ( $N=4$ ) from analyses (Supplementary Results Tables). Variation in social learning, longevity, group size and brain volume data across primate genera is illustrated in **Figure 2**.

## Discussion

We investigated the widely held view that cultural intelligence, extended life history and brain size have coevolved in nonhuman primates (16, 23–27). Using Bayesian phylogenetic generalized linear mixed models, we found a positive relationship between reliance on culture (as measured by reported richness of social learning, corrected for research effort) and measures of both absolute and relative brain volume. Earlier studies had established positive relationships between primate social learning and both absolute and ratio measures of the size of the ‘executive brain’ (combined neocortex and striatum volume) (25), and that social learning, as a component of a composite measure of general cognitive ability, increases with absolute and ratio measures of neocortex size and with executive brain ratio (21). Here, we find that these associations generalize further to overall brain size measured as endocranial volume, across a substantially larger (>3x) sample of primate species. While its occurrence in insects demonstrates that large brains, in absolute terms, are not a prerequisite for social learning (48), enlarged brain size may support more efficient, high-fidelity, or more diverse forms of social transmission (25), due to increases in, for instance, cross-modal integration of perceptual and motor information and the general computational power and flexibility required to implement sophisticated learning strategies (40, 49). Evolutionary expansion in the primate brain is also driven by visual specialization (5, 50, 51) and coordinated expansion of the neocortex and cerebellum with likely corresponding increases in fine visuo-motor control, which may underpin the ability to replicate complex behavioral sequences inherent to high-fidelity social learning (5, 12). In turn, more effective social learning potentially allows individuals to garner high-quality dietary resources that can be invested in brain growth (16). Hence, though the neural mechanisms underpinning social learning largely remain to be

established (6, 52) it remains highly plausible that evolutionary increases in overall brain size are causally associated with elevated social learning capabilities.

Our prediction of a positive relationship between social learning and longevity was also confirmed. There is good reason to expect such a relationship. Longer lifespans provide species reliant on culture more time to learn novel skills, more time to ‘cash in’ on those skills once learned, and more time to pass them on to their offspring (16, 23, 40). Additionally, longer lifespans may confer greater opportunity for behavioral innovations, providing the raw material for social transmission, as longer lifespans are positively associated with greater propensity to innovate in birds (53) and in primates ((32), albeit indirectly). Culturally acquired knowledge is typically adaptive and may often promote growth and survival, of both the learner and their dependent young, and thereby extend life spans (25–27) via a ‘cognitive buffer’ effect whereby social learning allows individuals to adapt behaviorally to challenging environments (42, 43). These benefits may be sufficient to compensate for negative fitness consequences associated with reliance on social learning, such as increased risk of social transmission of parasites (39). While hypotheses for the co-evolution of lifespan and culture propose that increases in both juvenile period and of overall lifespan are related to reliance on culturally-transmitted knowledge (e.g. (16)), here we find that the association between social learning and longevity is driven by an increased reproductive lifespan, rather than an extended period of juvenile dependence. Our findings, therefore, suggest that an extended reproductive lifespan, during which enhanced fitness benefits of earlier costly investment in learning skills for survival can be reaped, primarily drives the association between social learning and lifespan that we identify here. It remains possible that a link between extended juvenile periods and social learning capabilities will be identified

in future studies using novel social learning measures, such as those based on experimental tests. Nonetheless, the current result may point towards an evolutionary explanation. Transgenerational social learning requires not only time for acquisition of skills by juveniles but also time for performance of such behavior by adults, which likely trades off against parental investment. Therefore, extension of the reproductive lifespan may be critical to compensate for the costs of producing offspring highly dependent on social learning for survival. Our finding that the relationship between longevity and social learning remains when measures of maternal investment are included in analyses supports these functional arguments, and argues against an interpretation solely in terms of developmental constraints, in primates at least. Hence, in primates specifically, the combination of social learning with large brains may provide a “cognitive buffer” against environmental unpredictability, improving survival and permitting long lives (see below). Primates may contrast with most mammalian lineages in this regard due to the unusually extensive reliance on culturally transmitted behavior seen in certain lineages (e.g. (35–37)), perhaps necessary for social learning to sufficiently buffer individuals against environmental risks.

We also predicted a positive relationship between social learning and group size, on the expectation that large, stable social groups support greater amounts of adaptive cultural knowledge and facilitate a greater reliance on social learning (20, 44, 45). Whilst this hypothesis is well-established in theoretical models (e.g. (44, 45)) and has found recent empirical support in human historical (46) and experimental (47) studies, previous comparative phylogenetic analyses have failed to find this relationship across primate species (21, 25). The fact that we find a positive association here most likely reflects the greater power of our analyses compared to earlier studies, due to the

availability of a larger group size database (54) and phylogenetic comparative methods that adjust phylogenetic signal according to the traits included in the model, contrasting with the older independent contrasts method which effectively assumes a maximum level of phylogenetic signal and can therefore be overly conservative (55). The relationship between social learning and group size remains when longevity, brain volume and body mass are included, and hence appears not to be simply a by-product of the relationship between group size and absolute or relative brain volume, or confounded by life history traits.

Both large social groups and extended longevity (including increases in juvenile period, reproductive and total lifespan), are associated with enlarged brain volume, whether measured in absolute terms or relative to body mass. Group size has proven a robust predictor of measures of brain size, particularly relative neocortex size (29, 56, 57), and it remains an important predictor of both absolute and relative whole brain volume, as well as social learning, in our analyses. Thus, our findings support previous studies claiming an important role for social intelligence in primate brain evolution (e.g. (29, 56–58)). However, when included together with longevity, longevity is independently related to brain volume, while group size becomes a fairly weak predictor. This result may be significant, as the association of brain volume and longevity is usually not regarded as directly causally relevant in brain evolution (e.g. (29)). Further, a recently published comparative analysis suggests that dietary factors, rather than sociality, are the primary drivers of increased relative brain size in primates (31). It remains to be seen whether these findings generalize to measures of neocortex volume, arguably more relevant to social intelligence (29, 56–58). Nonetheless, together, these results reinforce an emerging consensus that sociality is not the sole driver of primate brain evolution, but rather is embedded in a nexus of evolutionary



conditions that favor brain expansion including dietary, ecological, life history and behavioral factors (12, 16, 21, 25, 29, 32).

Across mammals more broadly, the relationship between adult brain mass and longevity is accounted for by patterns of maternal investment, and is generally interpreted as a manifestation of developmental costs of producing larger-brained offspring, rather than necessarily due to any cognitive or behavioral mechanism (34). Here, however, we find that the associations of longevity with absolute and relative brain volume remain when controlling for maternal investment. Hence, in primates, compared to mammals in general (34), variation in adult brain size across species cannot be fully accounted for by patterns of maternal investment, and the relationship between brain size and lifespan is potentially indicative of a cognitive buffering (42, 43), rather than solely developmental, mechanism through which cultural intelligence facilitates survival. This contrast can perhaps be explained by divergent scaling relationships between brain volume and neuron number (presumably a more relevant correlate of cognitive capacity (7, 10, 12)) in primates compared with other mammalian lineages. Unlike non-primate mammalian lineages such as rodents, in which neuron size increases and neuron density decreases with increased brain volume, in primates the number of neurons increases approximately isometrically with brain volume (8–11). Therefore, in primates, larger brains may confer stronger benefits in terms of increased cognitive function and behavioral flexibility compared with other mammalian lineages. Overall, together with the strong relationship between social learning and longevity, these findings are consistent with the hypotheses that cultural knowledge facilitates survival, and that extended longevity facilitates the acquisition, exploitation and social transmission of life skills (16, 23, 25–27, 40).

Our finding that longevity is a strong, and potentially causally significant,

387 predictor of both brain volume and social learning richness is evocative of the argument  
388 that intelligence and life-history length have co-evolved in humans because our  
389 intellectual abilities allowed us to exploit high-quality, but difficult-to-access, food  
390 resources, with the nutrients gleaned 'paying' for brain growth, and with increased  
391 longevity favored because it allowed more time to cash in on complex, and difficult to  
392 master, foraging skills, with fitness benefits that pay off later in life (16). High levels of  
393 knowledge, skill, coordination and strength are required to exploit the high-quality  
394 dietary resources consumed by humans and other apes. Consistently with this idea, the  
395 most common use of social learning in primates appears to be in acquiring foraging  
396 skills, as ~50% of reports of social learning in a prior compilation occurred within the  
397 context of foraging (25, 59). Complex tool use and extractive foraging abilities require  
398 time to acquire, but in larger-brained animals, an extended learning phase, during  
399 which productivity is low, can be compensated for by higher productivity during the  
400 adult period, provided there is an intergenerational flow of both food and knowledge  
401 from old to young (60). Our results are therefore broadly consistent with a cultural  
402 intelligence explanation (23–27) manifested in particular primate lineages showing  
403 high reliance on social learning, in which selection for efficient social learning has  
404 allowed energy gains in diet, which in turn fueled brain growth, and generated selection  
405 for extended longevity. Previous comparative phylogenetic analyses have found social  
406 learning to co-vary positively with rates of behavioral innovation and tool use in  
407 primates (21, 25). Additionally, the best-supported graphs in exploratory phylogenetic  
408 path analyses link technical innovation directly to brain size and social learning, and  
409 non-technical innovation indirectly to brain volume via diet and life-history measures  
410 (32). Together with the current study, this body of findings is consistent with the  
411 hypothesis that cultural intelligence, as manifested by a cluster of behavioral traits,

including social learning, innovation and tool use, may have been a significant driver of primate brain evolution. However, we highlight two notes of caution in particular. First, the majority of primates exhibit comparatively little social learning (**Figure 2**) (at least, as reflected in our database), which implies that any selection for cultural intelligence has operated primarily in a small number of large-brained primate lineages. Second, our social learning measure is largely based on observational reports, not controlled experimental tests, while social learning is challenging to identify from observation alone (21, 25). However, this approach provides a more naturalistic comparative measure of social learning in comparison to those based on experimental tests, representing a far broader range of primate behavioral diversity necessary for large-scale comparative investigations (21, 25, 32, 39, 61). Further, results based on patterns of observational accounts of social learning across species should be valuable in informing and directing future, larger scale comparative experimental investigations of variation in social learning abilities across species (21, 39, 62).

One comprehensive way to interpret these findings is to recognize multiple waves of selection for enlarged brains and enhanced cognition in primates. In addition to selection for the cognitive skills required for complex social lives (29) and dietary niches (31) characteristic of some primate taxa, our results imply a likely later bout of selection for cultural intelligence amongst a restricted number of large-brained primate lineages. The latter notably includes the great apes, but also other independent lineages such as capuchins and baboons (**Figure 2**), as our results are not contingent on the inclusion of great apes (Supplementary Results Tables). Plausibly, complex sociality and foraging may have led to the evolution of large-brained primate lineages, some of which passed a critical threshold in reliance on socially learned behaviors, leading to mutually reinforcing selection for increased brain size, cognitive abilities and reliance on social

learning and innovation, mediated by conferred increases in longevity and diet quality. The twin challenges of complex socio-ecological niches and reliance on culture may therefore best account for the evolution of large brains, advanced cognition and extended lifespans in primates. However, our analyses do not allow the direction of causality to be inferred, and other interpretations, for instance, in which large brains evolved for other reasons, subsequently allowing for gains in social and cultural complexity, are equally supported by the findings presented here.

Our results do, however, strongly suggest a strong co-evolutionary relationship between cultural intelligence, brain size, sociality, and life-history length in primates. While we have focused here on nonhuman primates, broader comparative data support the idea that enlarged brain size, general cognitive abilities and reliance on culture may have co-evolved in other long-lived, highly social taxa, including some birds (e.g. corvids, parrots) and cetaceans (e.g. toothed whales) (18–20, 22). These associations may be mutually reinforcing (24), with positive feedback loops reaching their zenith in humans, who are extreme in their encephalization, intelligence, culture and lifespan (23, 63).

## **Methods**

### *Data compilation:*

All data used in analyses were obtained from existing published datasets, referenced in full below, with additional details in Supplementary Methods.

Endocranial volume (ECV, in cubic centimeters) and body mass (in grams) data were obtained from (4). Since ECV reflects the interior volume of the cranial cavity,

including not only the volume of the brain, but also the volume of protective structures of the brain, such as the meninges (4), and does not allow for separate estimates of the volumes of individual brain components, it is a relatively crude brain measure (6). Nonetheless, ECV is strongly and near-isometrically related to brain mass in primates (4), which is itself related approximately isometrically to neuron number (8–11). Moreover, brain volume estimates from ECV (hereafter ‘brain volume’) are available for around three times more primate species (N=184 species, see Supplementary Methods) than for volumes of individual brain structures (neocortex, cerebellum etc; typically ~60 species (e.g.(64)), allowing for analyses far more representative of the range of interspecific variation in primate brain size (4). Further, because size estimates from brain tissue can be influenced by variation in environmental effects such as the age and life experience of the individual, along with variation in preservation techniques (6), ECV may be a more consistent measure of species-typical brain size than those derived from direct measurements of volume or mass (4).

Data on social learning richness and a measure of research effort were obtained from (21) via the DataDryad digital repository (65) (see Supplementary Methods for full details on the social learning measure, illustrative examples and discussion of its reliability). Briefly, social learning richness is the number of reports of unique social learning behaviors per primate species, primarily from a literature sample of >4000 articles from primate behavior journals (from 1925-2000) (21). Instances of social learning were identified using keywords (e.g. ‘social learning’, ‘cultural transmission’, ‘traditional’) to minimize subjectivity in the collation of reports from the literature (21, 25). While identifying social learning from literature reports of non-human primate behavior is inherently challenging, this approach allows for a quantitative behavioral

measure of social learning across a large sample of diverse primate species, supporting far larger scale comparative analyses than would be possible using data from controlled experiments alone (21, 25, 32, 39, 61). Experimental approaches to measuring social learning across species are associated with their own particular challenges, especially in comparability and ecological validity of behavioral tests, and limited statistical power due to smaller sample sizes (21, 25, 62). We account for broad-scale species-differences in research effort, here estimated using the number of papers published in the *Zoological Record* (between 1993-2001, total 7288 articles) (21) (see Supplementary Methods for further information).

Data on social group size and life history traits (gestation length, weaning age, age of sexual maturity and maximum longevity) were obtained from the PanTheria dataset (54). As a measure of maternal investment, we summed gestation length and weaning age (following (34)). Reproductive lifespan was calculated as age of sexual maturity subtracted from maximum longevity. Comparative datasets were matched to a dated consensus phylogeny for 301 primate species (10kTrees version 3, using GenBank taxonomy, (66)). Taxonomic mis-matches were resolved using the 10kTrees Translation table and the IUCN Red List website (67).

#### *Statistical analyses:*

To test predictions, we ran a series of statistical models in which the outcome variables were always either brain volume or social learning, fitting independent variables that correspond to specific predicted associations, along with appropriate potentially confounding variables. Accounting for the effects of multiple variables is

509 essential in comparative studies of brain evolution, due to a large number of potential  
510 correlates (6). We analyzed brain volume both in absolute terms, and relative to body  
511 mass, by variably including body mass as an additional predictor variable. Where social  
512 learning was the outcome variable, research effort was always included as a predictor  
513 to account for its effect on the number of records of social learning in the primate  
514 behavioral literature (21, 25). We also controlled for body mass in models in which life  
515 history traits predicted social learning as the outcome variable, due to the well-  
516 established association of larger adult body size with slower life histories (e.g. (68)). For  
517 models including longevity, we re-ran analyses including maternal investment as an  
518 additional predictor to account for its potentially confounding effect on brain volume  
519 and longevity (34). Namely, if associations of brain volume and/or social learning with  
520 longevity are confounded with maternal investment, we expect to find that when  
521 included together with longevity, only maternal investment is a strong predictor of  
522 brain volume and/or social learning (as in (34)). Models including longevity as a  
523 predictor were also re-run using either juvenile period length (age of sexual maturity)  
524 or reproductive lifespan (longevity minus juvenile period), to investigate whether any  
525 identified relationships with longevity were driven by increases in juvenile period  
526 length, reproductive lifespan or both. To investigate whether group size and longevity  
527 predicted brain volume and social learning independently of each other, we ran  
528 additional models in which both group size and longevity were included as predictors.  
529 We re-ran all analyses without great apes, a potentially influential group due to their  
530 high social learning richness and large brains (**Figure 2**), and due to potential  
531 researcher biases in towards identifying social learning in apes compared with  
532 monkeys (see Supplementary Methods). We found that none of our key findings are

affected, demonstrating that our results are robust to removal of potential outliers and to possible biases associated with this group (Supplementary Results Tables).

We used Bayesian phylogenetic generalized linear mixed models to analyze data, which allow for control for phylogenetic non-independence and for modelling non-Gaussian response variables, using the R package MCMCglmm (69). Where brain volume was the response variable, Gaussian models were used with all variables log-10 transformed, diffuse normal priors for the fixed effects with a mean of 0 and a large variance ( $10^{10}$ ), and inverse-Wishart priors for the phylogenetic and residual variance (with  $V=1$ ,  $v=0.002$ ). Where social learning was the response variable, Gaussian models were not appropriate due to the highly skewed distribution of this variable, and we therefore used Poisson models, with all predictor variables log-10 transformed and non-transformed response variables. Poisson models used the same priors for the fixed effects and residual variance as for the Gaussian models, with a parameter-expanded prior ( $V = 1$ ,  $v = 1$ ,  $\alpha\mu = 0$ , and  $\alpha V = 25^2$ ) for the phylogenetic random effect (69, 70). Though a large proportion of the species included in analyses had zero records of social learning, these species are still informative due to the inclusion of research effort in all models (see Supplementary Methods). Further, preliminary analyses established that non-zero inflated Poisson models were appropriate for our data (see Supplementary Methods).

MCMC analyses were run with a sufficient number of iterations and thinning to return effective sample sizes of  $>1000$  for all parameters (see Supplementary Methods). Chain convergence and adequate performance were confirmed by visual inspection of trace plots and checking effective sample sizes. From each model, we report the mean  $h^2$



(a measure of phylogenetic signal equivalent to Pagel's  $\lambda$  (71)), and mean  $\beta$  coefficient estimate from posterior distributions. To assess the strength of evidence for fixed effects, we use the % of posterior  $\beta$  coefficient estimates crossing zero in the direction opposite to predictions (as in (39, 72, 73), for example). Posterior distributions shifted substantially away from zero in a positive or negative direction indicate support for positive or negative associations, respectively, between fixed effects and outcome variables. Conversely, posterior distributions centered on zero or overlapping substantially with zero indicate a lack of evidence for any relationship between the fixed effects and outcome variables. Here, all associations are predicted to be positive in direction. As a measure of model fit, we use a pseudo- $R^2$ , estimated as the squared Pearson's correlation between fitted values and observed data (74). No analysis reported a variance inflation factor (VIF) above 5, demonstrating that multi-collinearity was not a concern in our analyses (see Supplementary Methods).

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## **Author contributions**

S.E.S. and K.N.L. designed the research; S.E.S. compiled data and performed statistical analyses; K.N.L. and S.E.S. wrote the article; S.M.R. and A.F.N. advised on the research and contributed to writing throughout the preparation of the manuscript.

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## FIGURE LEGENDS

**Figure 1:** Posterior distributions of  $\beta$  coefficients for the effects of longevity, juvenile period and group size on a) social learning richness, b) absolute brain volume and c) relative brain volume (i.e. brain volume accounting for body mass). Here, we present effects from the simplest models including only either longevity, juvenile period or group size as independent variables, together with research effort and body mass for the social learning model, and body mass for the relative brain model. However, these results are not affected by the inclusion of additional potential confounding variables (see Methods, Results and Supplementary Information). Percentages indicate the percentage of posterior estimates that cross zero in the opposite of the predicted direction for each effect. Distributions shifted substantially away from zero indicate evidence for effects of predictor variables in the corresponding direction, while those centered close to zero indicate little or no evidence for effects of predictor variables.

**Figure 2:** Summary of raw data on social learning, absolute brain volume, group size and longevity for 52 primate genera, using the phylogeny from 10ktrees (66). For illustration purposes only, all data are summarized as genus-level means, standardized with minimum 0 and maximum 1. Again for illustration purposes only, social learning is displayed as a proportion of research effort, while in statistical analyses, social learning is controlled for research effort by including research effort as an independent variable. Images show a) bearded capuchin (*Cebus libidinosus*), b) chimpanzees (*Pan troglodytes*) and c) guinea baboons (*Papio papio*), illustrating lineages that represent convergent co-evolution of high social learning abilities, large brain volumes, complex social relationships and extended lifespans. Image attributions are as follows: a) Bart van Dorp, CC BY 2.0,

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