

# Coevolution of cultural intelligence, extended life history, sociality, and brain size in primates

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**Explanations for primate brain expansion and the evolution of human cognition and culture remain contentious despite extensive research. While multiple comparative analyses have investigated variation in brain size across primate species, very few have addressed why primates vary in how much they use social learning. Here, we evaluate the hypothesis that the enhanced reliance on socially transmitted behavior observed in some primates has coevolved 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, although longevity is generally the 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 coevolved 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.**

cultural evolution | social learning | brain evolution | primates | phylogenetic comparative analysis

**B**rain expansion is unquestionably a distinctive feature of primate, and especially human, evolution. Primate brain expansion is evident regardless of whether the brain is measured in absolute terms, in relation to body size, or as the 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 nonhuman primates, across three orders of magnitude (4), has long demanded an evolutionary explanation (5). Although 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 neuroanatomical 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 ~1,500 g (15), human brains are at least three times heavier than those of 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, nonexclusive 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 and technical innovation) (21, 25, 32), and behavioral complexity (e.g., innovativeness, social learning, and tactical deception) (21, 25, 33). Further, several comparative studies have found that larger brained primates have slower life histories, including longer juvenile periods and overall lifespans (e.g., ref. 29). Although 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 instead due to developmental costs: i.e., it requires a longer period of maternal investment to support offspring with greater natal and postnatal 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 in some lineages (e.g., refs. 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 potentially confounding variables.

Here, in a comparative analysis of primate species, we directly test the widely held view that encephalization, sociality, longevity, and reliance on culture have coevolved (16, 23–27, 32, 38). We use a quantitative behavioral measure of reliance on culture: specifically, the number of unique reports (i.e., richness) of social learning per species from a sample of relevant published literature (21, 39) (henceforth referred to simply as “social learning”)

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(see *SI Appendix* 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 is independent; however, if all are supported, it would imply support for a cluster of related, and mutually consistent, ideas concerning the factors underlying evolutionary expansions of brains, 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 (4).

### **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 (41, 42). Complex skills frequently take time to learn; therefore, 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 pay off in later life only 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., refs. 43–46) and broader hypotheses that stable social grouping supports the evolution of reliance on social learning (e.g., ref. 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**

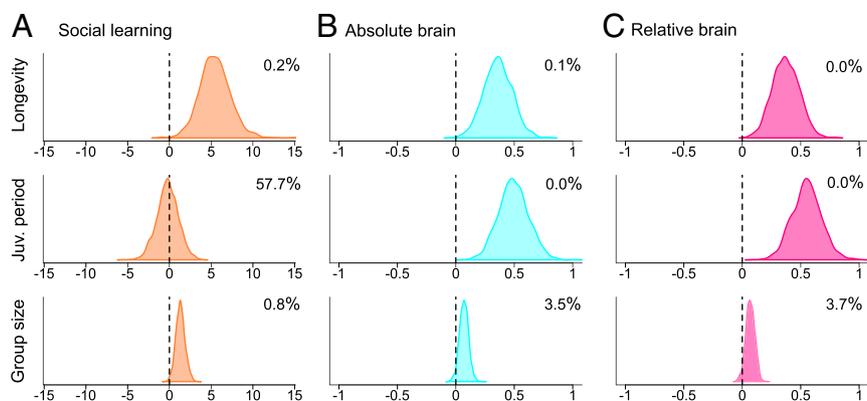
Across mammals, a relationship between adult brain mass and longevity is not supported when controlling for maternal investment, suggesting that developmental constraints associated with investing in large-brained offspring underpin this association (34). However, if associations of longevity with absolute and relative brain volume remain when maternal investment is included in analyses of primate species, the relationship between brain volume and lifespan is not confounded with maternal investment, thus potentially indicative of a cognitive, rather than solely developmental, mechanism underpinning this relationship in primates specifically, even if not across 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 brain volume (<1%  $\beta$  coefficients in the posterior distribution crossing zero,  $n = 150$ ) (*SI Appendix, Table S1i*) and relative brain volume (3%  $\beta$  crossing zero,  $n = 150$ ) (*SI Appendix, Table S1ii*).

**Prediction 2: Social Learning and Longevity.** As predicted, social learning richness increases with longevity (<1%  $\beta$  crossing zero,  $n = 117$ ) (*SI Appendix, Table S2 A, i* and Fig. 1A). We found no evidence that social learning increases with juvenile period length, however (58%  $\beta$  crossing zero,  $n = 101$ ) (*SI Appendix, Table S2 B, i* and Fig. 1A). Rather, social learning increases with reproductive lifespan specifically (0%  $\beta$  crossing zero,  $n = 92$ ) (*SI Appendix, Table S2 C, i*). 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,  $n = 87$ ,  $n = 82$ , respectively) (*SI Appendix, Table S2 A, ii* and *C, ii*) whereas maternal investment itself does not predict social learning in these models ( $\geq 35\%$   $\beta$  crossing zero) (*SI Appendix, Table S2 A, ii* and *C, 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,  $n = 111$ ,  $n = 89$ ) (*SI Appendix, Table S2 A, iii* and *iv* and *C, iii* and *iv*). However, brain volume itself does not predict social learning when included alongside longevity measures (>22%  $\beta$  crossing zero) (*SI Appendix, Table S2 A, iii* and *iv* and *C, iii* and *iv*).

**Prediction 3: Social Learning and Group Size.** As predicted, we found a positive association between group size and social learning (<1%  $\beta$  crossing zero,  $n = 167$ ) (*SI Appendix, Table S3i* and Fig. 1A). This association is independent of the relationship between social learning and longevity or reproductive lifespan, as it remains when either of these life history traits is included (4%  $\beta$  crossing zero, 5%  $\beta$  crossing zero,  $n = 111$ ,  $n = 89$ ) (*SI Appendix, Table S3 ii, A* and *B*). The relationship between group size and social learning is also not confounded by the association of either trait with absolute or relative brain volume, because it remains when either brain volume or both brain volume and body mass are included as additional predictors (<4%  $\beta$  crossing zero,  $n = 140$ ) (*SI Appendix, Table S3 iii* and *iv*). Both absolute and relative brain volume have, however, a weaker effect on social learning when group size is included as an additional predictor (2%, 7%  $\beta$  crossing zero) (*SI Appendix, Table S3 iii* and *iv*) compared with models without group size (<1%, 3%  $\beta$  crossing zero) (*SI Appendix, Table S1 i* and *ii*).



**Fig. 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 strongly affected by the inclusion of additional potentially confounding variables (*Methods, Results, and SI Appendix*). Percentages indicate the percentage of posterior estimates that cross zero in the opposite to the predicted direction for each effect. Distributions shifted substantially away from zero indicate evidence for effects of predictor variables in the corresponding direction whereas those centered close to zero indicate little or no evidence for effects of predictor variables.

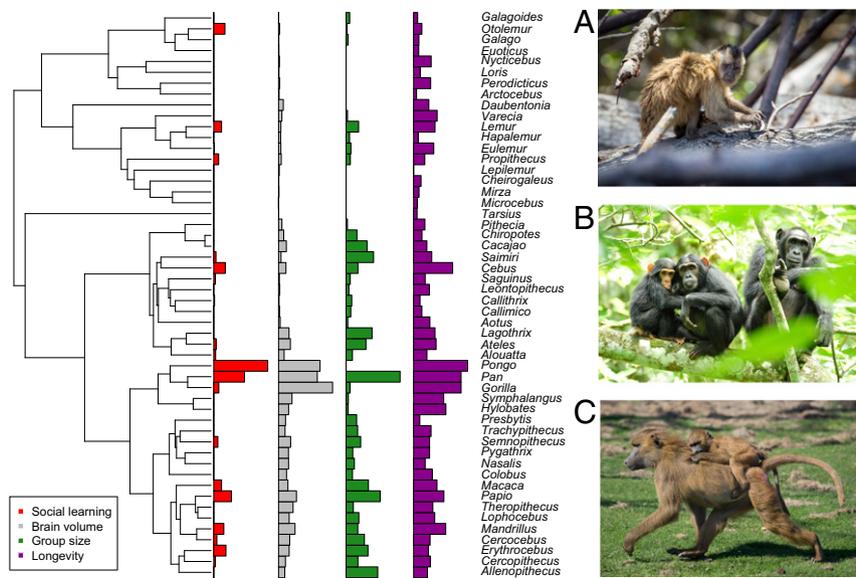
**Prediction 4: Predictors of Brain Volume.** We confirmed the expected positive association of absolute brain volume with social group size (3%  $\beta$  crossing zero,  $n = 151$ ) (*SI Appendix, Table S4i* and Fig. 1B). Absolute brain volume also increases with longevity, juvenile period length, and reproductive lifespan (<1%  $\beta$  crossing zero,  $n = 112$ ,  $n = 98$ ,  $n = 90$ ) (*SI Appendix, Table S4ii, A, B, and C* and Fig. 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,  $n = 84$ ,  $n = 86$ ,  $n = 79$ ) (*SI Appendix, Table S4iii, A, B, and 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,  $n = 106$ ,  $n = 95$ ,  $n = 87$ ) (*SI Appendix, Table S4iv, A, B, and C*) whereas group size is a relatively weak predictor when included with longevity or reproductive lifespan (>6%  $\beta$  crossing zero) (*SI Appendix, Table S4iv, A and C*).

Similarly, relative brain volume increases with social group size (4%  $\beta$  crossing zero,  $n = 151$ ) (*SI Appendix, Table S5i* and Fig. 1C). Relative brain volume also increases with longevity, juvenile period, and reproductive lifespan (<1%  $\beta$  crossing zero,  $n = 112$ ,  $n = 98$ ,  $n = 90$ ) (*SI Appendix, Table S5ii, A, B, and C* and Fig. 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,  $n = 84$ ,  $n = 86$ ,  $n = 79$ ) (*SI Appendix, Table S5iii, A, B, and C*). The relationship between relative brain volume and life history length is not confounded by social group size because all three measures remain intact when group size is added to the model (<1%  $\beta$  crossing zero,  $n = 106$ ,  $n = 95$ ,  $n = 87$ ) (*SI Appendix, Table S5iv, A, B, and 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) (*SI Appendix, Table S5iv, A and C*).

Parameters from all statistical models are reported in full in *SI Appendix, Tables S1–S5*. 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 (*SI Appendix, Tables S1–S5*). Variation in social learning, longevity, group size, and brain volume data across primate genera is illustrated in Fig. 2.

## Discussion

We investigated the widely held view that cultural intelligence, extended life history, sociality, 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 found that these associations generalize further to overall brain size measured as endocranial volume, across a substantially larger (>3 $\times$ ) sample of primate species. Although its occurrence in insects demonstrates that large brains, in absolute terms, are not a prerequisite for social learning (47), evolutionary expansions in 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, 48). Evolutionary expansion of the primate brain is driven substantially by visual specialization (5, 49, 50) 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). Therefore, while the cognitive mechanisms underpinning social learning largely remain to be established (51), it remains highly plausible that evolutionary increases in overall brain size are associated with elevated social learning capabilities. However, our finding that brain volume does not predict social learning when accounting for longevity, together with strong links between social learning and longevity, and longevity and brain size, suggests that the association of social learning and brain volume may be indirect, mediated via increased longevity. Results support a similar picture for relationships between social learning, group size, and brain volume. While we cannot rule out the possibility that the reduced sample size and likely corresponding reduction in power with the inclusion of additional variables



**Fig. 2.** Summary of raw data on social learning, absolute brain volume, group size, and longevity for 52 primate genera, using the consensus phylogeny from 10krees (65). For illustration purposes only, all data are summarized as genus-level means, standardized with minimum 0 and maximum 1. Also for illustration purposes only, social learning is displayed as a proportion of research effort whereas, 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 coevolution of high social learning abilities, large brain volumes, complex social relationships, and long lifespans. (A) Courtesy of Flickr/Bart van Dorp, (B) courtesy of Flickr/USAID in Africa, and (C) courtesy of Flickr/William Warby.

accounts for the loss of a direct relationship between social learning and brain size, these results are consistent with a previous exploratory phylogenetic path analysis showing that social learning and brain volume are related indirectly via links with dietary, social, or life history traits (32).

The positive relationship between social learning and longevity we identify supports the idea that 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, because longer lifespans are positively associated with greater propensity to innovate in birds (52) and in primates (ref. 32, albeit indirectly). Culturally acquired knowledge is typically adaptive and may often promote growth and survival of both learners and their dependent young, and thereby extend lifespans (25–27) via a cognitive buffer effect whereby social learning allows individuals to adapt behaviorally to challenging environments (41, 42). 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). Although hypotheses for the coevolution of lifespan and culture propose that increases in both juvenile period and overall lifespan are related to reliance on culturally transmitted knowledge (e.g., ref. 16), here, we found that the association between social learning and longevity is driven by an increased reproductive lifespan, rather than an extended period of juvenile dependence. 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, our current findings 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. 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. Therefore, in primates, the combination of social learning with large brains may provide a cognitive buffer against environmental unpredictability, improving survival and permitting long lives. 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., refs. 35–37), perhaps necessary for social learning to buffer individuals sufficiently against environmental risks.

Our finding of a positive relationship between social learning and group size supports the expectation that large, stable social groups support greater amounts of adaptive cultural knowledge and facilitate a greater reliance on social learning (20). Although this hypothesis is well-established in theoretical models (e.g., refs. 43, 44) and has found recent empirical support in human historical (45) and experimental (46) studies, previous comparative phylogenetic analyses have failed to find this relationship across primate species (21, 25). The fact that we found a positive association here most likely reflects the greater power of our analyses compared with earlier studies, due to the availability of a larger group size database (53) and phylogenetic comparative methods that adjust phylogenetic signal according to the traits included in the model (*SI Appendix, Methods*), contrasting with the older independent contrasts method, which effectively assumes a maximum level of phylogenetic signal and can therefore be overly conservative (54). The relationship between social learning and group size remains when longevity, brain volume, and body mass are included and therefore seems 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 and 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, 55, 56), 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, 55–57). However, when included together with longevity, longevity is independently related to brain volume whereas group size becomes a fairly weak predictor. This result may be significant because the association of brain volume and longevity is usually not regarded as directly causally relevant in brain evolution (e.g., ref. 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, 55–57). 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 found that the associations of longevity with absolute and relative brain volume remain when controlling for maternal investment. Therefore, in primates, compared with 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 (41, 42), 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 (potentially a more relevant correlate of cognitive capacity) (7, 10, 12) in primates compared with other mammalian lineages. Unlike nonprimate 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, predictor of both brain volume and social learning richness is evocative of the argument that intelligence and life-history length have coevolved in humans because our intellectual abilities allowed us to exploit high-quality, but difficult-to-access, food resources, with the nutrients gleaned “paying” for brain growth, and with increased longevity favored because it allowed more time to cash in on complex, and difficult to master, foraging skills, with fitness benefits that pay off later in life (16). High levels of knowledge, skill, coordination, and strength are required to exploit the high-quality dietary resources consumed by humans and other apes. Consistent with this idea, the most common use of social learning in primates seems to be in acquiring foraging skills, as ~50% of reports of social learning in a prior compilation occurred within the context of foraging (25, 58). Complex tool use and extractive foraging abilities require time to acquire, but, in larger brained animals, an extended learning phase, during which productivity is low, can be

compensated for by higher productivity during the adult period, provided there is an intergenerational flow of both food and knowledge from old to young (59). Our results are therefore broadly consistent with a cultural intelligence explanation (23–27) manifested in particular primate lineages showing high reliance on social learning, in which selection for efficient social learning has allowed energy gains in diet, which in turn fueled brain growth, and generated selection for extended longevity. Previous comparative phylogenetic analyses have found social learning to covary positively with rates of behavioral innovation and tool use in primates (21, 25). Additionally, the best supported graphs in exploratory phylogenetic path analyses link technical innovation directly to brain size and social learning and non-technical innovation indirectly to brain volume via diet and life-history measures (32). Together with the current study, this body of findings is consistent with the 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 (Fig. 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, whereas 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 with those based on experimental tests, representing a far broader range of primate behavioral diversity, necessary for large-scale comparative investigations (21, 25, 32, 39, 60). 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, 61).

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 among a restricted number of large-brained primate lineages. The latter notably include the great apes, but also other independent lineages such as capuchins and baboons (Fig. 2), as our results are not contingent on the inclusion of great apes. 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 socioecological 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 coevolutionary relationship among cultural intelligence, brain size, sociality, and life-history length in primates. Although we have focused here on nonhuman primates, broader comparative trends support the idea that enlarged brain size, general cognitive abilities, and reliance on culture may have coevolved in other long-lived, highly social lineages, including some birds (e.g., corvids and parrots) and 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, 62).

## Methods

**Data Compilation.** All data used in analyses were obtained from existing published datasets, referenced in full below, with additional details in *SI Appendix, Methods*.

Endocranial volume (ECV, in cubic centimeters) and body mass (in grams) data were obtained from ref. 4. Because 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) (*SI Appendix, Methods*) than for volumes of individual brain structures (neocortex, cerebellum, etc.; typically ~60 species) (e.g., ref. 63), 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 ref. 21 via the DataDryad digital repository (64) (see *SI Appendix, 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 >4,000 articles from primate behavior journals (from 1925 to 2000) (21). Instances of social learning were identified using keywords (e.g., “social learning,” “cultural transmission,” and “traditional”) to minimize subjectivity in the collation of reports from the literature (21, 25). Although identifying social learning from literature reports of nonhuman 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, 60). 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, 61). We account for broad-scale species differences in research effort, here estimated using the number of papers published in the *Zoological Record* (between 1993 and 2001, total 7,288 articles) (21) (see *SI Appendix, 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 (53). As a measure of maternal investment, we summed gestation length and weaning age (following ref. 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) (65). Taxonomic mismatches were resolved using the 10kTrees Translation table and the International Union for Conservation of Nature (IUCN) Red List website (66).

**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 essential in comparative studies of brain evolution, due to multiple potential correlates (29). We analyzed brain volume both in absolute terms, and relative to body mass, by variably including body mass as an additional predictor variable. Where social learning was the outcome variable, research effort was always included as a predictor to account for its effect on the number of records of social learning in the primate behavioral literature (21, 25). We also

controlled for body mass in models in which life history traits predicted social learning as the outcome variable, due to the well-established association of larger adult body size with slower life histories (e.g., ref. 67). For models including longevity, we reran analyses including maternal investment as an additional predictor to account for its potentially confounding effect on brain volume and longevity (34). Namely, if associations of brain volume and/or social learning with longevity are confounded with maternal investment, we expect to find that, when included together with longevity, only maternal investment is a strong predictor of brain volume and/or social learning (as in ref. 34). Models including longevity as a predictor were also rerun using either juvenile period length (age of sexual maturity) or reproductive lifespan (longevity minus juvenile period), to investigate whether any identified relationships with longevity were driven by increases in juvenile period length, reproductive lifespan, or both. To investigate whether group size and longevity predicted brain volume and social learning independently of each other, we ran additional models in which both group size and longevity were included as predictors. We reran all analyses without great apes, a potentially influential group due to their high social learning richness and large brains (Fig. 2), and due to potential researcher biases toward identifying social learning in apes compared with monkeys (*SI Appendix, Methods*). We found that none of our key findings were affected, demonstrating that our results are robust to removal of potential outliers and to possible biases associated with this group (*SI Appendix, Tables S1–S5*).

To analyze data, we used Bayesian phylogenetic generalized linear mixed models, which allow for control for phylogenetic nonindependence and for modeling non-Gaussian response variables, using the R package MCMCglmm (68). 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  $V = 1$ ,  $\nu = 0.002$ ). Where social learning was the response variable, Gaussian models were not appropriate due to the highly skewed distribution of this variable; we therefore used Poisson models, with all predictor variables log-10 transformed and with nontransformed 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 ( $V = 1$ ,  $\nu = 1$ ,  $\alpha\mu = 0$ , and  $\alpha V = 25^2$ ) for the phylogenetic random effect (68, 69). Although 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 (*SI Appendix, Methods*). Further, preliminary analyses established that Poisson models without a zero-inflation term were appropriate for our data (*SI Appendix, Methods*).

Markov chain Monte Carlo (MCMC) analyses were run with a sufficient number of iterations and thinning to return effective sample sizes of >1,000 for all parameters (*SI Appendix, 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  $\lambda$ ) (70) and mean  $\beta$  coefficient estimate from posterior distributions. To assess the strength of evidence for fixed effects, we use the percentage of posterior  $\beta$  coefficient estimates crossing zero in the direction opposite to predictions (as in refs. 39, 71, and 72, 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 used a pseudo  $R^2$ , estimated as the squared Pearson's correlation between fitted values and observed data (73). No analysis reported a variance inflation factor (VIF) above 5, demonstrating that multicollinearity was not a concern in our analyses (*SI Appendix, Methods*).

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