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Primate mosaic brain evolution reflects selection on sensory and cognitive specialization

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The mammalian brain is composed of numerous functionally distinct structures that vary in size within and between clades, reflecting selection for sensory and cognitive specialization. Primates represent a particularly interesting case in which to examine mosaic brain evolution since they exhibit marked behavioural variation, spanning most social structures, diets and activity periods observed across mammals. Although studies have consistently demonstrated a trade-off between visual and olfactory specialization in primates, studies of some regions (for example, the neocortex) have produced conflicting results. Here, we analyse the socioecological factors influencing the relative size of 33 brain regions, using updated statistical techniques and data from more species and individuals than previous studies. Our results confirm that group-living species and those with high-quality diets have expanded olfactory or visual systems, depending on whether they are nocturnal or diurnal. Conversely, regions associated with spatial memory are expanded in solitary species and those with low-quality diets, suggesting a trade-off between visual processing and spatial memory. Contrary to previous work, we show that diet quality predicts relative neocortex size at least as well as, if not better than, social complexity. Overall, our results demonstrate that primate brain structure is largely driven by selection on sensory and cognitive specializations that develop in response to divergent socioecological niches.

The mammalian brain consists of numerous functionally distinct structures, many of which vary greatly in size both within and between clades[1]. This neuroanatomical variation reflects both neurodevelopmental/functional constraints on size changes and selection for ecologically relevant cognitive and sensory specialization[1]. Accordingly, while different regions tend to scale against overall brain size with different allometric slopes[2], many species exhibit region-specific deviations from such allometric scaling (that is, relative region size). Such differences in relative region size are likely to reflect adaptive evolution since they necessitate genetically driven departures from otherwise constrained neurodevelopmental schedules[1]. This idea is generally referred to as the mosaic brain hypothesis[3], which posits that the relative sizes of individual brain areas reflect selection on specific sensory and cognitive functions.

Consistent with the mosaic brain hypothesis, differences in the relative sizes of specific regions have been linked to both intra- and interspecific differences in behaviour and cognition. For example, taxi drivers have larger hippocampi than non-taxi drivers[4], and sex differences in rodent ranging patterns correlate with differences in hippocampus size[5]. Across species, food-caching birds have relatively large hippocampi[6], nocturnal birds and mammals have relatively large olfactory bulbs[7,8] and song control nuclei are expanded in bird species with larger song repertoires[9]. It seems to be species differences in relative region size, not absolute size, that reflect differences in behavioural specialization (for example food-caching birds have relatively, but not absolutely, larger hippocampi[6]). Although conducting comparative analyses of neuroanatomy across orders may be inappropriate due to between-group differences in neuron density and processing power per unit of neural tissue[10], differences in relative region size among species in the same order are likely to reflect variation in the importance of specific cognitive capabilities.

Primates represent a particularly interesting group in which to examine mosaic brain evolution since members of this order exhibit an impressive amount of behavioural variation, spanning almost all social structures, diets and activity periods observed across mammals[11]. This behavioural variation is likely to be reflected by differences in brain structure since these behaviours may pose different cognitive and sensory demands. In particular, researchers have proposed that frugivory may require greater spatial memory and sensory information processing than folivory[8,12–14], that more complex social systems may require cognitive skills such as transitive inference and/or enhanced processing of social signals[15,16], and that diurnality and nocturnality may place greater demands on visual and olfactory brain areas, respectively[8]. Numerous studies have therefore examined the impacts of socioecological factors on the internal structure of primate brains[8,15–20].

Comparative analyses linking relative region size to diet quality, social complexity and/or activity period have not been undertaken for many brain areas that are important for species-specific behaviours. Examples include the hypothalamus, which is involved in circadian rhythm regulation and feeding motivation[21], and the striatum, which is involved in motor control and assessing the reward value of social decisions[22]. Past work on some regions, such as the neocortex, has produced highly conflicting results. Specifically, while some studies have linked a larger neocortex to larger group sizes[15,17,18], possibly reflecting greater needs for social information processing, one study suggested that the neocortex is largest in pair-living species, perhaps to facilitate coordination and/or deception[16]. Further complicating matters, some of these studies suggest that diurnal or frugivorous species also have larger neocortices[17,18]. Although multiple factors could certainly influence the sizes of individual brain areas, most existing work has examined the impact of one sociological factor at a time. Additional methodological issues may also explain these inconsistencies, including the use of

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different scaling variables (for example, rest of brain volume (ROB) versus medulla size), phylogenies that have become outdated, and/or residuals as response variables[23].

While previous investigations of some brain areas combined with socioecological factors have been undertaken, there has not yet been a comprehensive, simultaneous analysis of the factors influencing regional size variation across the entire primate brain. Furthermore, new neuroanatomical data and statistical methods have recently become available. Almost all previous work has relied primarily on the same neuroanatomical dataset (from Stephan and colleagues[24]), leading to low and idiosyncratic species and individual sample sizes, which may coincidentally favour particular hypotheses[25]. Here, we conduct a comparative analysis of 33 brain areas using larger species sample sizes ($n = 17–58$ per region) with values obtained from more individuals ($n = 1–44$ per species per region) than previous studies. We also use up-to-date phylogenetic methods, which allow us to more effectively examine discrete variables and account for phylogenetic uncertainty. We aimed to investigate the relationship between socioecological variables and the relative sizes of functionally distinct brain regions to determine whether and how primate brain structure has been influenced by selection on specific sensory and cognitive functions.

Results

For each brain region, we: (1) modelled region volume as a function of ROB volume, suborder, social complexity (either social system (SS) or mean group size (GS)), diet quality (either diet category (D) or diet quality index (DQI)) and activity period; and (2) constructed 15 reduced models that omit different combinations of predictor variables. We compared reduced models with each other and with the full (including all predictors) model using the Bayesian information criterion (BIC). Continuous variables were log-transformed before analysis to reduce skew. The different proxy measures for diet quality were found to be essentially interchangeable (Supplementary Fig. 1) and produced very similar results across analyses. We employed phylogenetic least squares (PGLS) regression and incorporated phylogenetic uncertainty by using two recent phylogenies[26,27]. Model details (for example, species sample sizes; PGLS coefficient estimates and P values; Type III analysis of variance (ANOVA) P values) are reported for all equivalent best-fit models (that is, difference in BIC (dBIC) < 2; Supplementary Tables 13–28, 37–40). We also confirmed coefficient estimates for the absolute best-fit models (that is, dBIC = 0) using fully Bayesian phylogenetic regression analyses in BayesTraits[28] that incorporated the Bayesian posterior distribution of trees for one of the phylogenies[26] (Supplementary Tables 29–32). Here, we present results in detail from models using the 10kTrees consensus tree[26] because this set provides the largest species sample size (see Methods for details; remaining results can be found in the Supplementary Tables). Specifically, we present the cumulative model weights (that is, the sum of relative model weights) for the best-fit models (dBIC < 2) that include the relevant predictor variable (Tables 1–4). Details on functional categorizations of brain regions can be found in the Methods. The results presented below are generally consistent across phylogenies and statistical methods (Supplementary Tables 1–40).

Sensory processing areas. Olfactory structures are larger in strepsirrhines (main and accessory olfactory bulbs (MOB, AOB); piriform lobe; palaeocortex), species with higher-quality diets (MOB; AOB; weak evidence for the piriform lobe), nocturnal species (MOB; AOB; palaeocortex) and species with larger group sizes (AOB; weak evidence for the palaeocortex) (Table 1). Specifically, group-living species exhibit expanded AOBs relative to pair-living species. Visual structures are expanded in haplorhines (primary visual cortex grey matter (V1 GM); weak evidence for the optic tract), diurnal/

Table 1 | Results for sensory processing (visual, olfactory, gustatory) areas

Model structure	D + SS	D + GS	DQI + SS	DQI + GS
Suborder				
Strepsirrhines > haplorhines				
AOB	**0.63**	**0.96**	**0.63**	**0.71**
MOB	0.43	0.43	0.35	0.45
Palaeocortex	**0.63**	**0.66**	**0.83**	**0.66**
Piriform lobe	**0.72**	**0.84**	**0.76**	**0.78**
Haplorhines > strepsirrhines				
Optic tract	0.12	NA	0.14	NA
V1 GM	0.14	0.13	0.15	0.07
Diurnal > cathemeral				
AOB	**0.63**	**0.96**	**0.63**	**0.71**
LGN	**0.59**	**0.63**	**0.57**	**0.54**
Mesencephalon	**0.66**	**0.71**	**0.54**	**0.60**
Activity pattern				
Diurnal > nocturnal				
LGN	**0.59**	**0.63**	**0.57**	**0.54**
Dysgranular insula	NA	NA	0.17	0.15
Mesencephalon	**0.66**	**0.71**	**0.54**	**0.60**
Optic tract	0.44	**0.58**	0.32	0.49
V1 GM	0.43	0.17	0.26	0.17
Cathemeral > nocturnal				
Optic tract	0.44	**0.58**	0.32	0.49
Nocturnal > cathemeral				
AOB	**0.63**	**0.96**	**0.63**	**0.71**
Nocturnal > diurnal				
AOB	**0.63**	**0.96**	**0.63**	**0.71**
MOB	NA	0.15	NA	0.29
Palaeocortex	0.26	0.36	**0.62**	0.43
Diet quality				
Frugivores > folivores				
AOB	**0.63**	**0.66**	-	-
MOB	0.32	0.34	-	-
Piriform lobe	NA	0.19	-	-
V1 GM	**0.61**	NA	-	-
Omnivores > folivores				
Piriform lobe	NA	0.19	-	-
V1 GM	0.61	NA	-	-
Frugivores > omnivores				
Dysgranular insula	0.22	0.19	-	-
Insula GM	**0.61**	**0.54**	-	-
DQI ↑				
V1 GM	-	-	**0.54**	0.35
DQI ↓				
Palaeocortex	-	-	0.24	0.15
Social complexity				
Group-living > pair-living				
AOB	**0.63**	-	0.44	-

Continued

Table 1 | Results for sensory processing (visual, olfactory, gustatory) areas (continued)

Model structure	D + SS	D + GS	DQI + SS	DQI + GS
Group-living > solitary				
Optic tract	0.47	-	0.49	-
V1 GM	0.40	-	0.23	-
Pair-living > solitary				
Optic tract	0.47	-	0.49	-
Palaeocortex	NA	-	0.23	-
V1 GM	0.40	-	0.22	-
Group size ↑				
AOB	-	0.44	-	0.33
LGN	-	0.29	-	0.27
V1 GM	-	**0.66**	-	**0.60**
Group size ↓				
Piriform lobe	-	0.25	-	0.24
Mesencephalon	-	**0.71**	-	**0.60**

Values represent the cumulative model weights for the best-fit models (dBIC < 2) that include the relevant predictor variable. If a region is not included under a predictor/comparison, that predictor/comparison was not included in any best-fit models for the region. Specific comparisons (for example, diurnal > nocturnal) were included on the basis of coefficient estimates and *P* values (see Supplementary Information). Bold font indicates higher (>0.5) cumulative model weights. NA indicates that a predictor was not included in any best-fit models for the given model composition. The model was structured as follows: region (log) ~ rest of brain (log) + suborder + activity period + … *, where additional model terms (*) could include the following: D + SS, diet category + social system; D + GS, diet category + group size (log); DQ + SS, diet quality (log) + social system; DQ + GS, diet quality (log) + group size (log).

Table 2 | Results for the telencephalon and neocortex

Model structure	D + SS	D + GS	DQI + SS	DQI + GS
Suborder				
Haplorhines > strepsirrhines				
Telencephalon	0.20	NA	0.13	NA
Neocortex GM + WM	**0.70**	**0.73**	**0.65**	**0.67**
Neocortex GM	**0.53**	0.39	0.44	0.33
Diet quality				
Frugivores > folivores				
Telencephalon	**0.61**	0.35	-	-
Neocortex GM + WM	0.37	0.24	-	-
Neocortex GM	0.42	0.31	-	-
Omnivores > folivores				
Telencephalon	**0.61**	0.35	-	-
Neocortex GM + WM	0.37	0.24	-	-
DQI ↑				
Telencephalon	-	-	0.43	0.28
Neocortex GM + WM	-	-	**0.65**	**0.67**
Neocortex GM	-	-	**0.72**	**0.55**
Social complexity				
Group-living > pair-living				
Telencephalon	**0.61**	-	NA	-
Group-living > solitary				
Telencephalon	0.61	-	NA	-
Group size ↑				
Telencephalon	-	**0.75**	-	**0.76**
Neocortex GM + WM	-	**0.73**	-	**0.67**
Neocortex GM	-	0.09	-	NA

GM, grey matter; WM, white matter. See Table 1 footnote.

cathemeral species (V1 GM; optic tract; lateral geniculate nucleus of the thalamus (LGN); mesencephalon), species with higher-quality diets (V1 GM) and species with larger group sizes (V1 GM; optic tract; weak evidence for the LGN). Areas associated with taste processing are expanded in frugivores relative to omnivores (insular GM; weak evidence for its dysgranular subregion). Exceptions to these overall patterns include reductions of the midbrain and piriform lobe in species with larger group sizes and weak evidence for a reduction of the palaeocortex with increasing diet quality. In addition, the AOB is expanded in diurnal relative to cathemeral species.

To examine whether species with larger groups and higher-quality diets exhibit expansion of olfactory or visual structures depending on whether they are nocturnal or diurnal, respectively, we ran models for these areas that included either nocturnal or diurnal/cathemeral species only. We did not include interaction terms in our models because some of the models presented here already push the limits of parameterization due to data availability[29]. In these cases, we modelled region volume as a function of ROB volume, social complexity (either social system or mean group size) and diet quality (either diet category or DQI). We found that olfactory structures (MOB) are larger in nocturnal species with high-quality diets, while visual structures (V1 GM; LGN) are larger in diurnal species with larger group sizes and high-quality diets (Supplementary Tables 25–28).

Telencephalon and neocortex. Given that the neocortex represents the majority of the telencephalon, we discuss these areas together. These areas are larger in haplorhines (neocortical GM; neocortical grey and white matter (GM + WM); weak evidence for telencephalon), species with higher-quality diets (telencephalon; neocortex GM + WM; neocortex GM) and species with larger group sizes (telencephalon; neocortex GM + WM; weak evidence for neocortex GM). Overall, diet quality has at least as strong an effect, if not more, on relative neocortex size as diet quality measures are always included in at least one best-fit model for the neocortex, while social system is never included and group size is not consistently included (Table 2).

Spatial cognition. Regions associated with spatial cognition are expanded in strepsirrhines (schizocortex; hippocampus; septum), diurnal/cathemeral species (weak evidence for the schizocortex), species with lower-quality diets (schizocortex; hippocampus; septum) and species with smaller group sizes (schizocortex; hippocampus) (Table 3).

Other brain areas. Subcortical regions, the cerebellum and the brainstem are expanded in strepsirrhines (striatum; pallidum; hypothalamus; thalamus; subthalamic nucleus; epithalamus; cerebellum; medulla; trigeminal motor (Vmo); hypoglossal (XII) brainstem nuclei) (Table 4). Some of these areas are also expanded in diurnal/cathemeral species (pallidum; hypothalamus; subthalamic nucleus; weak evidence for the thalamus) and species with smaller group sizes (amygdala; diencephalon; hypothalamus; thalamus; subthalamic nucleus; epithalamus; cerebellum; medulla; Vmo; facial (VII) brainstem nuclei; XII). Diet quality is positively associated with the relative size of the subthalamic nucleus and negatively associated with the relative size of the cerebellum, hypothalamus, epithalamus, medulla and Vmo.

Table 3 | Results for spatial cognition areas

Model structure	D + SS	D + GS	DQI + SS	DQI + GS
Suborder				
Strepsirrhines > haplorhines				
Hippocampus	0.20	0.15	0.44	0.43
Schizocortex	**0.52**	**0.51**	**0.76**	**0.60**
Septum	**0.84**	**0.69**	**0.69**	**0.72**
Activity pattern				
Diurnal > nocturnal				
Schizocortex	NA	NA	0.41	NA
Cathemeral > nocturnal				
Schizocortex	NA	NA	0.41	NA
Diet quality				
Folivores > omnivores				
Hippocampus	0.17	0.14	-	-
Schizocortex	**0.74**	0.17	-	-
Frugivores > omnivores				
Schizocortex	**0.74**	0.17	-	-
DQI ↓				
Hippocampus	-	-	**0.75**	**0.79**
Schizocortex	-	-	**0.76**	**0.85**
Septum	-	-	**0.69**	**0.72**
Social complexity				
Pair-living > group-living				
Schizocortex	**0.74**	-	**0.76**	-
Solitary > group-living				
Schizocortex	**0.74**	-	**0.76**	-
Solitary > pair-living				
Schizocortex	**0.74**	-	**0.76**	-
Group size ↓				
Hippocampus	-	**0.13**	-	**0.37**
Schizocortex	-	**0.85**	-	**0.85**

See Table 1 footnote.

Discussion

The results presented here reinforce a mosaic view of primate brain evolution[3], as species differences in the relative sizes of individual brain components reflect selection for sensory and cognitive abilities relevant to their specific environments (Figs. 1 and 2). Broadly, our results confirm that ecology influences whether similar cognitive processes, including both social and foraging cognition, occur in visual or olfactory domains[20]. While olfactory areas are relatively large in nocturnal strepsirrhines, expansion of visual areas occurred in diurnal species; however, within each of these groups, olfactory and visual structures are enlarged in both frugivores/omnivores and group-living species (Table 1; Supplementary Tables 25–28). Furthermore, our results confirm previous suggestions that enhanced visual processing in haplorhines and species with high-quality diets may account for their expanded neocortical areas and relatively large brains[19] (Table 2). This is contrary to some previous work, which suggested that neocortical expansion was primarily driven by greater social complexity[15,16]. Diurnality may also place higher demands on motor areas and regions associated with endocrine system control (Table 4). Finally, our results suggest that spatial cognition regions are reduced in haplorhines, species with high-quality diets and group-living species (Table 3), a pattern essentially opposite to that exhibited by visual information processing areas. This may reflect a trade-off between sensory perception and spatial memory within the domains of foraging and social cognition, mediated by the distance and accessibility of food/conspecifics.

Strepsirrhines and haplorhines diverged relatively early in primate evolution, producing largely nocturnal and diurnal forms, respectively[30]. This instigated an evolutionary trade-off between olfactory and visual system specialization. Accordingly, diurnal primates not only have larger, more convergent orbits, increased visual acuity and (in many cases) trichromatic vision, but also have reduced olfactory abilities (for example, loss of the vomeronasal system)[30]. In addition, the relative sizes of olfactory and visual brain areas are negatively correlated across species[8]. These differences suggest that nocturnal and diurnal species face different sensory barriers to foraging and sociality, the neural correlates of which are reflected in our results. More specifically, this study confirms previous findings[8,20] that brain olfactory structures are larger in nocturnal strepsirrhines, reflecting greater sensitivity for processing olfactory cues in species living in low-light environments. Unlike in previous studies, our main results do not suggest that solitary species have expanded AOBs, which has been suggested to reflect improved pheromone detection in spatially dispersed individuals[20]; however, some of our supplementary results do confirm this finding (for example, see Supplementary Tables 7 and 19). Consistent with earlier results, we found that that group-living species exhibit relatively larger AOBs than pair-living species[20,31], which is likely to be related to chemosignal-mediated inter- and/or intrasexual competition. In many group-living species, males compete with each other over access to females. If dominance relationships change frequently between reproductively active males, this may necessitate persistent olfactory signalling and reassessment among males[32]. In addition, when females experience overlapping fertile phases in polygynandrous systems, it may be advantageous for males to detect female fertility using olfactory signalling. Since monogamous species have relatively low levels of male–male competition and males do not need to choose between simultaneously cycling females, selection on chemosignal perception may be reduced, resulting in their relatively small AOBs. Finally, we found that both OBs are expanded in frugivores, confirming previous work linking frugivory to brain olfactory structure expansion in primates[8,20]. These results probably reflect the fact that that frugivores, especially nocturnal frugivores, rely on olfaction to detect and discriminate among fruits according to ripeness and toxicity[33].

By contrast, diurnality is associated with larger visual brain structures, including V1 GM, the optic tract and the LGN. Previous work linking V1 and diurnality[8] used a measure that included both grey matter and underlying white matter (from Stephan and colleagues[24]), the latter of which was measured using arbitrarily defined borders, therefore potentially introducing inaccuracy[34]. Our work provides further support for this relationship since we included only grey matter measurements. Although previous work did not report an expansion of the LGN in diurnal primates[8], others did find more LGN parvocellular neurons, associated with the analysis of fine detail with colour, in diurnal species[19]. In addition to these classic visual structures, we found that diurnal species are characterized by expanded mesencephalons (that is, midbrains). This area contains the superior colliculus, which responds to visual stimuli and mediates eye movements. The midbrain may therefore be larger in diurnal species since they require greater capacity to control responses to light and other visual stimuli. Our results also suggest that diurnality may place increased demands on other systems, including those involved in visually guided motor control[35] and the endocrine system.

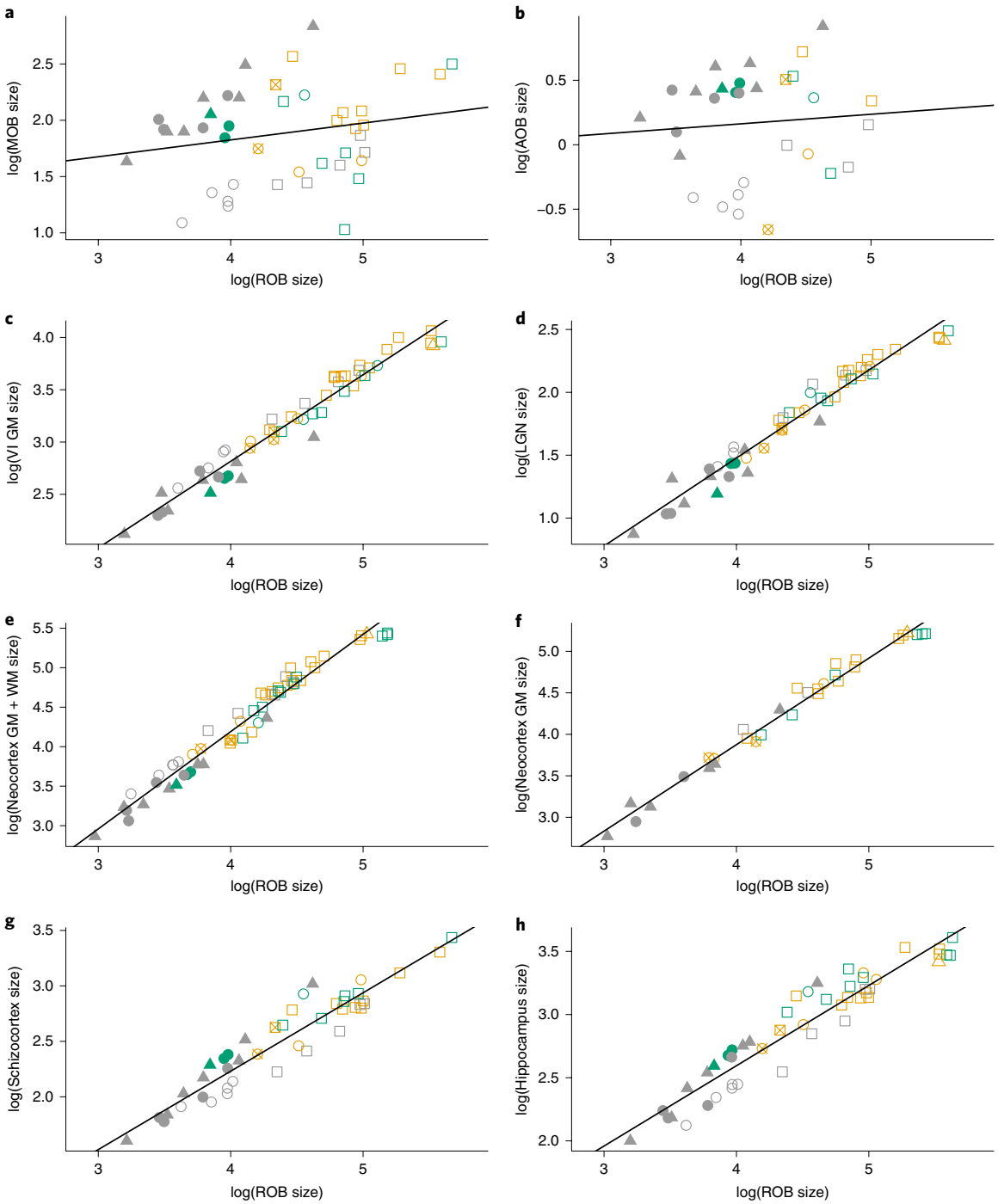

Fig. 1 | Relative region size differs between primate species due to variation in diets, social systems and activity patterns. a–h, Linear regression models of region size on ROB volume for MOB (**a**), AOB (**b**), V1 GM (**c**), LGN (**d**), neocortex GM + WM (**e**), neocortex GM (**f**), schizocortex (**g**) and hippocampus (**h**). Activity patterns are indicated by symbol fill: diurnal (open), cathemeral (cross), nocturnal (filled). Diet is indicated by the colours of symbols: folivore, green; frugivore, orange; omnivore, grey. Social systems are shown by the shapes of symbols: group-living, square; pair-living, circle; solitary, triangle.

Visual structures are further expanded in group-living species, reflecting the fact that complex social systems in diurnal species are facilitated by social communication via visual signalling. Specifically, visual signalling is likely to have replaced many functions of olfactory signalling in diurnal haplorhines, leading to the emergence of multiple social signal types[36,37]. Visual areas, in addition to the neocortex, are also enlarged in species with higher-quality diets, confirming previous work using smaller sample sizes[8,18,19]. Diurnal frugivores and omnivores may rely more heavily on vision than folivores as they must assess fruit ripeness and/or locate and track their prey. This hypothesis is supported by studies demonstrating a positive relationship between frugivory and LGN parvocellular neuron number[19]. Given that visual areas make up approximately half of the primate neocortex, visual specializations likely explain why species with high-quality diets also have larger neocortices[19]. Furthermore, given that the neocortex (including both grey and white matter) scales hyperallometrically with brain size, this relationship is consistent with findings that frugivorous and omnivorous primate

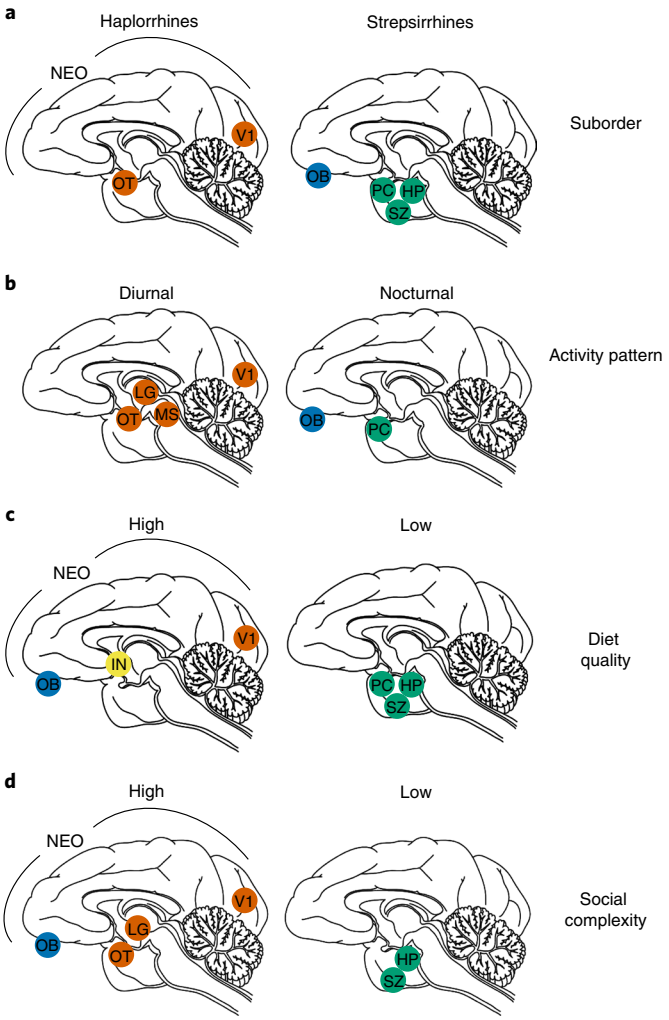

Fig. 2 | The relative sizes of specific brain regions increase across primate species according to suborder and socioecology. a–d, Regions that increase according to suborder (**a**), activity pattern (**b**), diet quality (**c**) and social complexity (**d**). The labelled regions are those that increase in relative size according to the category illustrated. Most are not visible from the views shown because the structure is internal, and circles represent the approximate location of the region relative to the medial surface. Functional categories are indicated by the colours of circles: visual, orange; olfactory, blue; gustatory, yellow; spatial cognition, green. HP, hippocampus; MS, mesencephalon (midbrain); NEO, neocortex; OB, olfactory bulbs; OT, optic tract; PC, palaeocortex; SZ, schizocortex. Credit: brain outlines, K. Chiou.

species have relatively larger brains than folivores[12,13,38]. In fact, previous work has shown that primates with relatively large brains also have expanded visual areas[19].

However, our results contradict some previous work that suggested that species differences in relative neocortex sizes are primarily driven by differences in social complexity rather than diet quality[15–17]. Specifically, researchers have posited that neocortex size places an upper limit on group size by constraining the number of relationships an individual is able to remember, maintain and/or monitor, or the number of social strategies the individual can employ[39]. Accordingly, expanded neocortices would be favoured if and when cohesive social groups are critical for solving certain ecological problems[15]. Other researchers have suggested that larger neocortices allow individuals to employ strategies that may aid in pair-living, such as coordination or deception[16]. However, our

Table 4 | Results for other brain areas

Model structure	D + SS	D + GS	DQI + SS	DQI + GS
Suborder				
Strepsirrhines > haplorhines				
Striatum	0.27	0.24	NA	NA
Striatum (including NAcc)	0.48	0.40	0.41	0.35
Pallidum	0.36	0.37	0.31	0.39
Hypothalamus	**0.66**	**0.74**	**0.59**	**0.73**
Thalamus	NA	0.19	0.13	0.10
Subthalamus	0.36	0.48	0.31	0.37
Subthalamic nucleus	NA	0.39	0.14	**0.77**
Epithalamus	0.30	0.18	0.18	0.12
Cerebellum	0.31	0.24	0.25	0.17
Medulla	0.33	0.24	0.45	0.36
Vmo	0.25	NA	0.18	0.16
XII	0.35	0.21	NA	NA
Activity pattern				
Diurnal > nocturnal				
Pallidum	0.35	**0.51**	0.32	**0.51**
Hypothalamus	**0.53**	**0.74**	0.37	**0.73**
Thalamus	NA	0.22	NA	NA
Subthalamus	0.20	**0.61**	0.30	0.48
Subthalamic nucleus	NA	0.46	NA	**0.77**
Cathemeral > nocturnal				
Pallidum	0.35	**0.51**	0.32	**0.51**
Subthalamus	0.20	**0.61**	0.30	0.48
Subthalamic nucleus	NA	0.46	NA	**0.77**
Diet quality				
Folivores > omnivores				
Medulla	**0.68**	0.42	-	-
Vmo	0.20	NA	-	-
Folivores > frugivores				
Hypothalamus	0.16	NA	-	-
Medulla	**0.68**	0.42	-	-
DQI ↓				
Hypothalamus	-	-	**0.59**	0.29
Epithalamus	-	-	0.22	0.12
Medulla	-	-	**0.85**	**0.69**
Vmo	-	-	0.36	0.29
Cerebellum	-	-	0.37	0.30
Omnivores > folivores				
Subthalamic nucleus	NA	0.07	-	-
DQI ↑				
Pallidum	-	-	NA	0.11
Subthalamus	-	-	NA	0.11
Subthalamic nucleus	-	-	NA	**0.77**
Social complexity				
Pair-living > solitary				
Thalamus	0.22	-	0.17	-

Continued

Table 4 | Results for other brain areas (continued)

Model structure	D + SS	D + GS	DQI + SS	DQI + GS
Pair-living > group-living				
Hypothalamus	0.36	-	NA	-
Solitary > group-living				
Hypothalamus	0.36	-	NA	-
Group size ↓				
Amygdala	-	0.27	-	0.27
Diencephalon	-	0.31	-	0.39
Hypothalamus	-	0.41	-	0.30
Thalamus	-	0.38	-	0.14
Subthalamus	-	0.13	-	NA
Subthalamic nucleus	-	0.49	-	**0.77**
Epithalamus	-	0.25	-	0.20
Cerebellum	-	NA	-	0.20
Medulla	-	0.34	-	NA
Vmo	-	0.47	-	0.26
VII	-	0.32	-	NA
XII	-	**0.78**	-	**0.52**

NAcc, nucleus accumbens. See Table 1 footnote.

results suggest that diet quality predicts relative neocortex size at least as well as, if not better than, social complexity (Table 2). This is consistent with our previous work showing that relative brain sizes across primates are best predicted by diet rather than sociality[38], and may likewise reflect the fact that seemingly complex social behaviours in primates may be governed by a simple set of associative rules rather than cognitively complex, flexible problem-solving skills[40]. Furthermore, other brain regions play critical roles in complex cognitive processes, including social cognition (for example, the cerebellum[41]). Similarly, researchers have hypothesized that insula size may be related to social complexity, since it is involved in interoceptive representation and, therefore, some aspects of social awareness[42]. However, no relationship has been found between relative insula size and group size[43] or social system; instead, we find that the insula is expanded in frugivores. This may reflect the insula's role in multimodal sensory processing and sweet taste signal reward perception[44], and suggests that this region may play a role in the evolution of high-sugar diets.

Spatial cognition areas are enlarged in strepsirrhines, species with low-quality diets and solitary species, and this pattern is basically the reverse of that observed for visual perception areas. This may reflect a trade-off between sensory perception and spatial memory, depending on the distance to or accessibility of food and conspecifics. More specifically, species that are often in close proximity to food and conspecifics and/or that forage opportunistically may require more elaborate sensory systems to frequently recognize and distinguish between these resources, while species that are isolated from or must travel to find food and conspecifics may face greater demands on spatial memory to locate them. For example, we find that omnivores possess relatively small spatial cognition areas compared with folivores. This confirms previous work on the primate hippocampus[45] and adds the schizocortex, a region that is functionally connected to the hippocampus and facilitates spatial memory. These results are likely to reflect high population densities of the insect species that are opportunistically hunted by the insectivores in our study, which often rely heavily on visual and/or auditory cues to locate their fast-moving prey[45,46]. Furthermore, the folivores that seem to be driving this result (for example, among pair-living species, *Avahi* and *Indri*) selectively forage on young leaves and flowers, which are relatively small, dispersed food sources[47,48]. Spatial cognition areas are also expanded in solitary-living species. Given that individuals in these species are dispersed in space, they probably rely heavily on spatial memory to locate potential mates. Studies also suggest that nocturnal, solitary primates may plan their routes to out-of-sight food targets[49] and that they may use detailed mental representation rather than route-based network maps[50].

Finally, we find that folivores have relatively large medullas compared with omnivores. Given that folivores have bodies that are relatively large for their brains, and that the medulla regulates basic functions of the autonomic nervous system, their expanded medullas may be a function of body size. This finding has implications for comparative neuroanatomy, as it suggests that studies using the medulla as a scaling variable[20] may be confounded by species differences in diet, body size and, therefore, relative medulla size.

Overall, this study shows that primate brains are a canonical example of mosaic brain evolution[3]. As a clade, their comparative neuroanatomy suggests that selection has acted on specific perceptual, spatial and cognitive abilities, each of which allow these species to deal with the challenges created by their physical and social environments. Nocturnal and diurnal species rely on different sensory systems to facilitate frugivory and group living, and species with dispersed mates or food sources exhibit expanded spatial brain areas. The primate order is highly diverse, with different clades invading new ecological niches with new activity patterns and diets, in turn leading to new spatio-temporal distributions and social organizations. Primate evolution is a splendid example of the key role of sensory interaction in driving species diversity and adaptation, with neuroanatomy and sensory anatomy reflecting the cognitive and sensory specializations that develop in response to divergent socio-ecological niches.

Methods

Data collection and compilation. We compiled total brain and brain region volumes (for 33 regions total) from published literature sources (Supplementary Data 1; Supplementary Appendix). Species sample sizes range across regions from 17 to 58 species, and individual sample sizes range from 1 to 44 per species per region, depending on data availability. The final value used for each measure and species represents a weighted average of the values provided across studies, which include both region volume and total brain volume, weighted according to the study sample size (Supplementary Data 1). The details of specimen preparation and measurement methodology differed across collections and can be found in the original sources, although a brief summary for each is provided below (more information can also be found in the Supplementary Appendix).

Many of the regional measurements included in this study were obtained from Stephan et al.[24,51,52]. These brain specimens were fixed with either Bouin's fluid or 10% formalin, embedded in paraffin and sectioned between 10 and 25 mm; a series of equidistant sections was stained for Nissl substance with cresyl violet. Frahm et al.[34] provided V1 grey and white matter measurements from the same collection. Bauernfield et al.[43] provided insula and insular subdivision measurements from Nissl-stained coronal sections from the Stephan collection, in addition to the Great Ape Aging Project, the Welker collection and the UCSD. Sherwood et al.[53] provided medulla and brainstem subdivision volumes using histological sections from the Stephan and Zilles collections. Brains from the latter were fixed by with either 4% formalin or Bodian's solution, embedded in paraffin and sectioned with a microtome at 20 mm, and an equidistant series of sections was stained for Nissl substance. Volumes were measured in ImageJ. Neocortex, LGN and V1 GM volumes from histological sections from the Comparative Mammalian Brain Collection at the University of Wisconsin–Madison were from refs. [54,55]. Measurements were taken using the Amira software package. Barger et al.[56,57] provided amygdala, hippocampus and striatum volumes from histological sections. Brains were fixed with 4% formalin solution, embedded in paraffin and sectioned in the coronal plane at 20 mm, and every 10th to 16th section was Nissl stained. Volumes were measured using SteroInvestigator software. Stimpson et al.[58] provided amygdala measurements from histological sections. Brains were immersed in 10% formalin before being transferred to 0.1 M PBS with 0.1% sodium azide. Temporal lobe blocks (including the amygdala) were immersed in buffered sucrose solutions up to 30%, embedded in tissue freezing medium, frozen in a slurry of dry ice and isopentane and sectioned in the coronal plane at 40 mm. Zilles & Rehkamper[59] provided medulla, cerebellum, mesencephalon, diencephalon, telencephalon, striatum, hippocampus, palaeocortex, amygdala, septum and neocortex volumes for orangutans (*Pongo pygmaeus*). One whole

specimen had been fixed in 70% alcohol before the authors extracted the brain, embedded it in paraffin, cut it into 20 mm serial sections and Nissl stained every 20th section. The other brain was a museum specimen that had been fixed in various fluids before the authors embedded it in paraffin, cut it into several sections and stained it using a silver staining technique. Structure volumes were analysed using a computer-controlled image analyser (Micro-Videomat 2). De Sousa et al.[60] provided V1 and LGN measurements from histological sections and post-mortem magnetic resonance imaging (MRI) scans of brains from the Stephan, Zilles, Yakovlev-Haleem and Welker collections, the Great Ape Aging Project and the Mount Sinai School of Medicine. Volumes were measured in ImageJ or using in-house software. Macleod et al.[61] provided cerebellum volumes from both histological sections from the Stephan and Zilles collections and in vivo MRI scans from the Yerkes Regional Primate Research Center. Cerebellum and neocortex measurements obtained from Rilling and Insel[62,63] are based on in vivo MRI scans of anesthetized individuals from Yerkes. Sherwood et al.[64] and Barks et al.[65] provided neocortex, hippocampus, striatum, thalamus, cerebellum, amygdala and insula measures for multiple gorilla species (*Gorilla gorilla gorilla*, *G. g. graueri* and *G. beringei*) from post-mortem MRI scans. Scans were processed using either EasyVision or Brainvox image analysis software. When individual specimen IDs were provided, measurements taken on the same individual and brain region across multiple studies were removed (see Supplementary Appendix and the Brain Region Data and Brain Region Data Notes tabs in Supplementary Data 1). We did not include neuroanatomical data from Semendeferi and Damasio[66] or Navarrete and colleagues[67] since these are not comparable with the other datasets included here. Specifically, although Semendeferi and Damasio[66] presents whole brain volumes, this measure excludes the medulla, the pons and most of the midbrain. Navarrete et al.[67] explicitly compare their data to others[24,51,52,59] and note several regions for which there are marked, statistically significant differences in average brain region volumes (for example, the hippocampus is up to 60% smaller in their dataset). On investigation of these data, we found further inconsistencies with earlier data, which may be based on differences in the regional boundaries used for measurement. Since regional boundary information is not available, even after contacting the authors, we are not using these data at this time—please see the authors' published erratum[68].

Activity periods were collected for each species from published literature sources[69–72] using a three-category scheme: diurnal, cathemeral and nocturnal (Supplementary Data 1: 'Activity Period' tab). We repeated analyses to account for uncertainty surrounding the origin of the *Aotus* specimens (see Supplementary Appendix). Although many subspecies are nocturnal, this genus may exhibit an "incomplete adaptation to a nocturnal niche"[72] since subspecies that are devoid of diurnal predators and sympatric species that compete for resources are cathemeral (for example, *A. azarai*)[72]. Perhaps this is not surprising given that, relative to the Palaeocene origin of diurnal haplorhines[30], this genus very recently began to transition from a diurnal ancestor (that is, 10–13 Myr ago)[72]. Accordingly, we present in detail analyses conducted with *Aotus* coded as cathemeral (analyses with *Aotus* coded as nocturnal are available in the Supplementary Tables). DQIs were collected from Sailer et al.[73] and Leonard and Robertson[74]. These data were supplemented with data from other primary sources[75–93] (DQI Data tab in Supplementary Data 1). In all cases, the DQI was calculated using the formula from Sailer et al.: $DQI = 1s + 2r + 3.5a$ (where s is the percentage of plant structural parts, r the percentage of plant reproductive parts and a the percentage of animal prey in the diet), which was derived using the negative relationship between diet quality and body size across primate species[73]. We collected dietary categories from a previously published dataset[38] and used a three-category scheme of folivore, frugivore and omnivore (Supplementary Data 1: 'Diet Data' tab). Species designated as frugivore/folivores in the source dataset were assigned as frugivores in this study. Social system data were collected from Shultz et al.[94] and DeCasien et al.[38] using a three-category scheme representing the three fundamental types of social organization[95]: solitary, pair-living and group-living (Social System Data tab in Supplementary Data 1). Species designated in those sources as polygynous or polygynandrous were placed in the group-living category. Species that forage solitarily but sleep in stable pairs were placed in the pair-living category since these have been suggested to represent stable community structures[94,96–100], indicating that they are probably subject to similar selective pressures on cognition as pair-living species (Social System Data tab in Supplementary Data 1). For other species that exhibit multiple social system types, designations were taken from DeCasien et al.[38], which assigned species social systems after consolidating categorizations recorded in published literature sources. We repeated analyses with *Pongo* classified as either group-living or solitary, since orangutans forage solitarily but have extended stable social groups[94]; classifying *Pongo* as group-living provides a relatively better model fit in reconstructions of primate social system evolution[94]; and solitary living may have emerged relatively recently in *Pongo*, as longer and more severe periods of low food availability (due to the onset of the El Niño/Southern Oscillation around 3–5 Myr ago) may have forced females to disperse more widely, preventing males from effectively guarding a harem of females[101]. Accordingly, we present in detail analyses conducted with *Pongo* coded as solitary (analyses with *Pongo* coded as group-living are available in the Supplementary Materials). Mean group sizes were collected from DeCasien et al.[38] (which included an average of 4.7 mean group size data points per species to analyse possible effects of intraspecies variation). For four species not included in DeCasien et al.[38], mean group sizes were taken from additional primary and secondary sources[11,102–104] (Group Size Data tab Supplementary Data 1).

Statistical analyses. All statistical analyses were carried out in R (v. 3.5.1). Humans (*Homo sapiens*) were excluded from all analyses since we are an outlier with regard to brain size and exhibit social and dietary behaviours that are difficult to classify comparably to other primates. Accordingly, excluding humans or presenting results with humans omitted is common practice in comparative studies of neuroanatomy.

For each brain region, we: (1) modelled region volume as a function of ROB volume (total brain volume minus the volume of the region of interest), suborder (Strepsirrhini or Haplorrhini), social complexity (either social system or group size), diet quality (either diet category or DQI) and activity period; and (2) constructed 15 reduced models that omit different combinations of predictor variables (except ROB volume, which is included in all models). The different combinations of proxy variables and coding systems for *Pongo*'s social system and *Aotus*' activity pattern (see 'Data collection and compilation') resulted in 12 sets of 16 models, each comprising of 1 full and 15 reduced models. We compared reduced models with each other and with the full (including all predictors) model using the BIC; dBIC values between 2 and 6 indicate moderate evidence that the model with the lower BIC provides a relatively better model fit, while values greater than 6 indicate strong evidence for improved fit[105]. We used BIC, rather than the Akaike information criterion because the former uses a more conservative penalty for additional terms[105,106]. Consequently, BIC is more likely to suggest the most parsimonious model. Models were not further compared with each other using null hypothesis significance testing (NHST) methods since mixing analysis paradigms is advised against, as the information theoretic approach used here (that is, BIC) already provides relative model weights (which may be more informative than NHST model comparisons)[106,107]. To accommodate frequentist perspectives, model details (that is, PGLS model coefficients and P values; corrected P values for three-level variables = 0.05/3 = 0.0167) and ANOVA results (F values and P values) are provided in the Supplementary Materials.

We incorporated ROB volume in all models to explicitly examine species differences in relative region size and to control for allometry. Suborder was included as a potential predictor since previous work has identified grade shifts in the relative size of certain brain regions (for example, neocortex[3]). All continuous variables were log-transformed before analysis to reduce skew. Interaction terms were not included for the sake of interpretability and to prevent overparameterization[108]. Across the 12 full models constructed using different combinations of proxy variables, variance inflation factors (VIFs) averaged 1.6 and were under 4 for almost all models, indicating generally low levels of multicollinearity. Some models of the insular subregions had VIFs between 4 and 10; however, this still represents a generally accepted level of multicollinearity (though different researchers may consider different VIF thresholds to be acceptable)[109].

To test whether larger groups and higher-quality diets are associated with expanded olfactory and visual structures in nocturnal and diurnal species, respectively, we ran models of these areas (olfactory: MOB, AOB; visual: V1 GM, LGN, optic tract) for nocturnal and diurnal/cathemeral species separately. In these cases, we modelled region volume as a function of ROB volume, social complexity (either social system or mean group size) and diet quality (either diet category or DQI). Models were not run if only one diet category or social system was present in a subgroup. Although no simple, universally accepted rule exists regarding the ratio of sample size to the number of predictors, a commonly used rule states that the number of cases should be at least ten times the number of estimated terms[29]. Owing to data availability, some of the models presented push the limits of parameterization, so we did not add interaction terms to these models.

Species represent non-independent cases since they may share traits due to phylogenetic inertia, so we used PGLS regression models[110–112]. The advantages of using PGLS over independent contrasts include the fact that PGLS can use discrete explanatory variables more effectively since it assumes that the errors, rather than the explanatory variables, are multivariate normally distributed[113,114]. We used the topologies and branch lengths from the GenBank taxonomy consensus tree provided on the 10kTrees website (v. 3)[26]. To account for phylogenetic uncertainty, we repeated the analyses for the four models presented here in detail using the molecular phylogeny from Perelman and colleagues[27]. For each model, we allowed the phylogenetic scaling factor (λ) to take the value of its maximum likelihood[23]. Results from models incorporating the 10kTrees phylogeny are presented here in detail because this set provides the largest species sample size. Results from all other models are provided in the Supplementary Tables.

In some of the analyses, maximum-likelihood estimations of λ produced by the PGLS models resulted in a value of zero. Given that the log-likelihood plots of λ are very flat in these cases (see Supplementary Fig. 2, for example), it is doubtful that these traits should be modelled using ordinary least squares regression (equivalent to $\lambda = 0$) and that this simply reflects relatively low species sample sizes[23]. Accordingly, these models were run using a value of λ obtained by calculating the 95% confidence interval for λ, extracting 100 equally spaced values of λ within this interval and averaging these values with each value weighted according to its likelihood[38]. If the upper confidence interval value was not defined, then a λ of 1 was used as the maximum value.

We also considered the influence of uncertainty in phylogenetic relationships by using 1,000 different trees from the 10kTrees dataset, which were created using Bayesian phylogenetic methods and sampled in proportion to their probability[26]. Specifically, fully Bayesian regression analyses were run for the absolute best-fit models (that is, dBIC = 0) for each region using the Continuous program in BayesTraits v. 2.0 (ref. [28]). These analyses were limited to one run for each of the four models presented here in detail due to time and processing constraints. This allowed us to confirm coefficient estimates from consensus tree analyses. Discrete variables were dummy coded before analysis (for example, suborder = 0 (strepsirrhines) or 1 (haplorhine); activity pattern = 0 (nocturnal) or 1 (diurnal or cathemeral); diet category: diet1 = 0 (folivore or omnivore) or 1 (frugivore), diet2 = 0 (folivore or frugivore) or 1 (omnivore))[115]. Markov chain Monte Carlo (MCMC) analyses provided posterior distributions of PGLS regression models (regression coefficients and scaling parameters). The analysis sampled the tree block of 1,000 trees in proportion to their posterior probability to account for phylogenetic uncertainty, and λ was sampled during the MCMC regression analysis. Uniform, uninformative priors were used as these reflect the assumption that all values of the parameters within the program's available range (−100 to 100) are equally likely a priori[28], and this analysis was run for 6,000,000 iterations, sampling every 200 iterations, with a burn-in of 200,000. MCMC diagnostics were run using the R package coda[116]. Specifically, we ensured proper mixing occurred by visually inspecting all trace and density plots. We examined autocorrelation plots to confirm reduced correlation between successive samples and confirmed that the effective sample sizes for all variables were greater than 1,000. Finally, we ran each chain twice and confirmed convergence using the Gelman–Rubin statistic, with all models required to have a potential scaling reduction factor below 1.1[117]. We report the posterior means of the variables included in each model and the probability that each explanatory parameter value has the same sign (positive or negative) as the mean estimate (p_{MCMC}).

Functional categorizations. Sensory processing areas: The primary visual cortex receives input from the retinas via the optic tract and LGN. The OBs receive input from olfactory receptor cells and project to the palaeocortex (that is, prepiriform cortex, retrobullar cortex) and piriform cortex. The mesencephalon (midbrain) includes the tectum (which contains the inferior and superior colliculi) and the tegmentum. It is discussed along with visual brain areas since the superior colliculus receives inputs from visual areas (for example, the retinas, visual cortex and frontal eye fields), influencing both visual perception and eye movements[118]. The anterior insula is involved in processing gustatory information[44].

Telencephalon and neocortex: The telencephalon includes the cerebral cortex, corpus striatum, olfactory system and associated white matter. The cerebral cortex, excluding the allocortex (palaeocortex, archicortex and mesocortex), constitutes the neocortex[118]. Given that the neocortex represents the majority of the telencephalon, these areas are discussed together.

Spatial cognition areas: The hippocampus plays an integral role memory formation, particularly for tasks that require combining information from multiple sources, as in spatial navigation[119]. The schizocortex includes the entorhinal, perirhinal, presubicular and parasubicular cortices, which receive input from and project to the hippocampus[118]. Here, the septum includes the septum pelliculum, septum verum, diagonal band of Broca, bed nuclei of anterior commissure and stria terminalis. The diagonal band of Broca carries septohippocampal projection cells, which modulate hippocampal function[120].

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The authors declare that all data supporting the findings of this study are available in the paper and its Supplementary Information.

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Author contributions

A.R.D. designed the project and performed the analyses with input from J.P.H. A.R.D. compiled the data. Both authors wrote the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Study description	For each brain region, we: 1) modelled region volume as a function of rest of brain volume, suborder, social complexity (either social system or mean group size), diet quality (either diet category or diet quality index), and activity period; and 2) constructed 15 reduced models which omit different combinations of predictor variables. We compared reduced models to each other and to the full (including all predictors) model using the Bayesian Information Criterion (BIC). Continuous variables were log-transformed prior to analysis to reduce skew. The different proxy measures for diet quality were found to be essentially interchangeable, and produced very similar results across analyses. We employed phylogenetic least squares (PGLS) regression and incorporated phylogenetic uncertainty by using two recent phylogenies. Model details (e.g. species sample sizes; PGLS coefficient estimates and p-values; Type III ANOVA p-values) are reported for all equivalent best fit models (i.e. dBIC<2) in the Supplementary Material. We also confirmed coefficient estimates for best fit models (i.e. dBIC=0) using fully Bayesian phylogenetic regression analyses in BayesTraits which incorporated Bayesian posterior distribution of trees for one of the phylogenies. In the main manuscript, we present results in detail from models using the 10kTrees consensus tree because this set provides the largest species sample size. Specifically, we present the cumulative model weights (i.e. the sum of relative model weights) for the best fit models (dBIC<2) that include the relevant predictor variable.
Research sample	We compiled total brain and brain region volumes (for 33 regions total) from published literature sources (Supplementary Data 1; Supplementary Materials: Appendix). Activity periods were collected for each species from published literature sources using a three category scheme, including diurnal, cathemeral, and nocturnal (Supplementary Data: "Activity Period" tab). Diet quality indices (DQI) were collected from Sailer et al. and Leonard & Robertson. This was supplemented with data from other primary sources (Supplementary Data 1: "DQI Data" tab). In all cases, the DQI was calculated using Sailer et al.'s formula: DQI = 1s + 2r + 3.5a (s = % plant structural parts; r = % plant reproductive parts; a = % animal prey in the diet), which was derived using the negative relationship between diet quality and body size across primate species. We collected dietary categories from a previously published dataset38 and used a three category scheme of folivore, frugivore, and omnivore (Supplementary Data 1: "Diet Data" tab). Social system data were collected from Shultz et al. and DeCasien et al. using a three category scheme representing the three fundamental types of social organization94, which includes solitary, pair-living, and group-living (Supplementary Data 1: "Social System Data" tab). Mean group sizes were collected from DeCasien et al. (which included an average of 4.7 mean group size data points per species in order to analyze possible effects of within species variation). For four species not included in DeCasien et al., mean group sizes were taken from additional primary and secondary sources (Supplementary Data: "Group Size Data" tab).
Sampling strategy	Sample sizes were determined by data availability.
Data collection	A.R.D. collected the data. We compiled total brain and brain region volumes (for 33 regions total) from published literature sources (Supplementary Data 1; Supplementary Materials: Appendix). Activity periods were collected for each species from published literature sources using a three category scheme, including diurnal, cathemeral, and nocturnal (Supplementary Data: "Activity Period" tab). Diet quality indices (DQI) were collected from Sailer et al. and Leonard & Robertson. This was supplemented with data from other primary sources (Supplementary Data 1: "DQI Data" tab). In all cases, the DQI was calculated using Sailer et al.'s formula: DQI = 1s + 2r + 3.5a (s = % plant structural parts; r = % plant reproductive parts; a = % animal prey in the diet), which was derived using the negative relationship between diet quality and body size across primate species. We collected dietary categories from a previously published dataset38 and used a three category scheme of folivore, frugivore, and omnivore (Supplementary Data 1: "Diet Data" tab). Social system data were collected from Shultz et al. and DeCasien et al. using a three category scheme representing the three fundamental types of social organization94, which includes solitary, pair-living, and group-living (Supplementary Data 1: "Social System Data" tab). Mean group sizes were collected from DeCasien et al. (which included an average of 4.7 mean group size data points per species in order to analyze possible effects of within species variation). For four species not included in DeCasien et al., mean group sizes were taken from additional primary and secondary sources (Supplementary Data: "Group Size Data" tab).
Timing and spatial scale	Data collection occurred throughout 2017 and early 2018.
Data exclusions	Humans (Homo sapiens) were excluded from all analyses since we are an outlier with regard to brain size and exhibit social and dietary behaviors that are difficult to classify comparably to other primates. Accordingly, excluding humans or presenting results with humans omitted is common practice in comparative studies of neuroanatomy.
Reproducibility	One aim of this study is to test the reproducibility of previous studies using updated data and statistical techniques.
Randomization	For each brain region, we: 1) modelled region volume as a function of rest of brain volume (ROB; total brain volume minus the volume of the region of interest), suborder (Strepsirrhini or Haplorhini), social complexity (either social system or group size), diet quality (either diet category or DQI), and activity period; and 2) constructed 15 reduced models which omit different combinations of predictor variables (except ROB, which is included in all models). We compared reduced models to each other and to the full (including all predictors) model using the Bayesian Information Criterion (BIC).
Blinding	Blinding is not relevant for a comparative analysis.

Did the study involve field work? ☐ Yes ☒ No

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☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging