Ecological not social factors explain brain size in cephalopods

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Abstract

Social factors have been argued to be the main selection pressure for the evolution of large brains and complex behavior on the basis of data from mammals and birds. Coleoid cephalopods (octopuses, squid, and cuttlefish) have large brains, complex nervous systems and show signs of intelligent behavior comparable to that of birds, cetaceans, and primates. However, many cephalopods live largely solitary, semelparous, short lives, and many are cannibalistic, leaving little to no opportunity for parental care, complex group dynamics, or social learning. This suggests that the large brains found in cephalopods are not the result of social selection pressures. Here, motivated by the predictions of the "Asocial Brain Hypothesis" formal model, we compare the relationships between brain size and social, ecological, and other factors in cephalopods, predicting that ecological factors should be the primary selection pressure. Consistent with these predictions, we find that benthic (seafloor) habitats—arguably more complex environments than open-ocean (pelagic) habitats—are strongly associated with larger brain sizes, whereas measures of sociality are not, therefore suggesting ecology as a primary selection pressure on brain size in cephalopods. These results align with the "Asocial Brain Hypothesis," which predicts that ecological complexity rather than sociality drives the evolution of large brains in asocial animals. Our findings challenge the long-standing emphasis on social drivers of brain expansion and show that ecological selection pressures can produce complex brains in highly divergent evolutionary lineages, which diverged from vertebrates over 500 million years ago. This result highlights the need for more general frameworks that capture different pathways to large brains and intelligence—both social and asocial—and underscores the power of modeling and comparative approaches to unify disparate findings in the study of brain evolution.

Introduction

The evolution of large brains across the animal kingdom has been a subject of extensive research, with various social, behavioral, developmental, and ecological factors being proposed as key drivers of this energetically costly adaptation[14–17]. Comparative studies have identified a range of predictors for larger brains, including group size, social structure, sexual competition, parental care, length of the juvenile period, predation pressures, diet, locomotion, and sensory capabilities[18–22]. Among these, social factors have become the dominant explanatory predictor, after initial work by Jolly[23] and Humphrey[24] argued for social complexity as a driver for intelligence among primates, and the hypothesis gain support on the basis of data from mammals and birds[1–5]. The social brain hypothesis (SBH) in particular, was developed to explain the evolution of large brains in primates[25], and argues that larger brains evolved to cope with the complex demands of social group living, such as cooperation, deception, and competition[26–28], as well as pair bonding and social cohesion[29,30].

The SBH has been tested among various taxa with nuanced results. Some findings have indicated the quality of social relationships rather than group size. A comparative study of cetaceans, for example, found a quadratic relationship with group size, where the largest-brained species (and those with larger social repertoires) formed mid-sized social groups rather than smaller/loose aggregations or megapods[31]. Similarly, among birds, species with small social groups (5-30 individuals) seem to have larger relative brain sizes than solitary species or those forming large groups[29,32,33]. An analysis of sexual competition and brain size in bats found larger brains among species with monogamous rather than promiscuous females[34]. A study on African cichlid fishes included sex-specific analyses and found that females providing sole parental care had larger brains than those in species with biparental care, with no effect of care type on male brain size[35].

In other taxa, no relationship or even a reverse relationship has been found between social measures and brain size. Among carnivorans, an analysis using fossil data indicated that, contrary to a previous analysis of mammalians[36], sociality was not linked with increased encephalization across clades and this relationship was likely driven solely by canids[37]. A study of a rodent group, African mole-rats, showed larger absolute brain size and neuron numbers among solitary species, with the authors highlighting the entanglement of body size with both brain size and the evolution of group living[38]. Among non-avian reptiles, relative brain size was not correlated with habitat complexity, and in contrast with findings in primates, solitary species had larger brains than social ones[39].

Most of the research effort has been on vertebrates, but social insects are a notable exception with some studies exploring the relationship between sociality and brain size. Due to the nature of labor division in many of these species, sociality could be expected to have an inverse effect on brain size; however, differences in expected cognitive load due to variation in how specialization takes place in a colony– e.g. by age where an individual progresses through all tasks in some groups, changes in how labor is divided as a colony grows in size, and variation in colony size over time and within species– complicate this prediction[40,41]. This very different expression of sociality, as well as the presence of high intraspecific variation in relative brain volume and the contribution of particular cellular mechanisms to behavioral variation apart from volumetric measures of brain size, may explain the inconsistent results for tests of the social brain hypothesis among insect groups[40,41].

Taken together, these disparate findings highlight how expressions of social behavior with differing cognitive demands - e.g. dominance hierarchies in primates, cooperative breeding in birds, and colonial societies of related individuals in insects - across and within different taxa complicate any clear relationship with behavioral complexity, cognition, and brain size. A recent meta-analysis of the Social Intelligence Hypothesis (here encompassing the Machiavellian Intelligence Hypothesis and the SBH) found broad support for a "significant positive relationship between sociality and cognition across interspecific, intraspecific and developmental studies"[42]. The authors note that despite criticisms of measures of brain size and cognitive ability, there was not a significant difference in effect sizes across studies with different measures of cognition, or between studies of primates vs. non-primates. However, they also note that the vast majority of studies have been carried out on primates, other mammals, and birds, and that insects - the only invertebrates in the studies surveyed - were highly underrepresented given the number of taxa. Therefore, it remains unclear the extent to which sociality is linked with cognition outside these heavily-studied taxonomic groups.

Two competing key explanatory variables for the evolution of large brains are ecology, and life history and development. Research on the importance of ecological complexity in driving brain size has focused on the cognitive abilities required for innovation, problem-solving and foraging for difficult-to-extract or high-energy foods and the larger brains that can be supported by ecologies with

more calories and energy availability. In one study testing measures of ecological vs. social variables[43–45], frugivorous diets (requiring spatial memory and extractive foraging and providing higher energy) were a better predictor of larger brains than social group size among primates, while there was no support for the SBH. A comparative study of mammals and birds[43–45] found that while experimental measures of self-control were predicted by absolute brain size, they were not strongly linked with residual brain size or at all with social group size, casting doubt both on the link between sociality and cognition and the validity of residual brain size as a measure of cognition. Another study found that brain size among primates was predicted by manipulation complexity, which was also linked with tool use and extractive foraging[43–45].

The 'cognitive buffer hypothesis' focuses on life history and development, arguing that the behavioral flexibility afforded by large brains will allow organisms to respond to socioecological adversity, with the fitness cost of additional developmental time offset by reduced extrinsic mortality, resulting in overall longer lives and time for reproduction[46]. There has been some support for this hypothesis, with studies of mammals[46–48], birds[46–48], and amphibians[48] showing a coevolutionary relationship between large brains and longer lifespans. However, the causal pathways or even directionality of this relationship is unclear, and a recent analysis of cetaceans showed a negative relationship between brain size and lifespan[49].

This body of research has been largely empirical, yielding disparate and sometimes contradictory relationships between a variety of variables[18,36,47]. One way to unify this disparate body of work is through the use of general theories that formally describe the complex co-evolutionary relationships between all relevant variables.

A unifying model of brain evolution

General theories that formally mathematically or computationally model the causal pathways and coevolutionary relationships can shed light and make clear predictions. One such theory was developed by Muthukrishna et al.[50]. The analytic and computational models (see Figures 1 and 2 below) were developed to incorporate sociality, ecology, and life history into a single framework. The model revealed three regimes for the evolution of large brains. The first set and second set of predictions were for social and highly social animals. The "Cultural Brain Hypothesis", described the social learning path to larger brains, which has been tested with primates[51] and cetaceans[31]. The "Cumulative Cultural Brain Hypothesis", revealed a narrow set of parameters within the social learning path that would lead to an autocatalytic takeoff consistent with the human pathway characterized by an ever-increasing reliance on culture and technology (see also[52]). The final set of predictions, which we label the "Asocial Brain Hypothesis" (ABH), was a regime that applied to asocial animals, and remains untested. The predictions of the as-yet-untested ABH was the motivation for this present research. Here we summarize the models and predictions.

Muthukrishna et al's model had three key assumptions:

1. Larger and more complex brains are more costly than less complex brains because they require more calories, take longer to develop, and have organizational challenges. Therefore, increasing brain size/complexity decreases an organism's fitness; an organism should have the smallest brain possible that allows it to thrive.[1] BUT

[1] For simplicity, we assume that brain size, complexity, and organization (e.g., neuronal density) are captured by a single state variable, which we will refer to as "size".

2. A larger brain correlates with an increased capacity and/or complexity that allows for the storage and management of more adaptive knowledge.[2] AND
3. More adaptive knowledge increases an organism's fitness either by increasing its number of offspring compared to conspecifics and/or by reducing its probability of dying before reproduction. Adaptive knowledge can be acquired asocially, through experience, trial and error, and causal reasoning, or socially, by learning from others.

Muthukrishna et al. formalized the logic of these assumptions using an analytic approach—an adaptive dynamics evolutionary model[53] and a simulation to capture the co-evolutionary dynamics. Figure 1a below shows the variables for the analytic and agent-based simulation models, and the stages of the simulation model. Figure 1b below shows the mathematical relationships between the variables in the analytic and simulation models. The analytic and simulation solutions can be found in Muthukrishna et al.[50].

Variable	Description	Values
b_i	Brain size of individual i	$[0, \infty]$
a_i	Adaptive knowledge of individual i	$[0, b_i]$
s_i	Reliance on social learning (over asocial learning) of individual i	[0,1]
τ	Transmission fidelity	[0,1]
ζ	Asocial learning efficacy	[0,1]
r	Per capita birth rate	≥ 0
d	Per capita death rate	≥ 0
ϕ	Scaling coefficient used to scale relationship between adaptive knowledge and r	≥ 0
β	Scaling constant relating brain size to death rate (similar to κ in simulation)	≥ 0
λ	Death rate mitigation (e.g. richness of ecology) used to scale effect of a_i in reducing d	≥ 0
n	Increase in population size	$[-\infty, \infty]$

Individual variables
b_{ij}: Brain size [0 - ∞]
a_{ij}: Adaptive knowledge [0 - ∞]
s_{ij}: Social learning probability [0 - 1]
v_{ij}: Oblique learning probability [0 - 1]
l_{ij}: Learning bias [-∞ - ∞]

Simulation Constants
ρ: Malthusian growth rate [0.8]
μ: Genetic mutation rate [0.005]
σ_b: Brain deviation [0.05]
σ_a: Adaptive knowledge deviation [0.1]
σ_s: Social learning deviation [0.1]
σ_v: Oblique learning deviation [0.1]
σ_l: Learning bias deviation [0.5]

Stage 1: BIRTH
Assumptions
1. Higher population adaptive knowledge can support a larger population
2. More individual adaptive knowledge leads to more offspring

Variables and parameters
φ: Reproductive skew (mating structure)
k_j: Carrying capacity of deme j
A_j: Mean adaptive knowledge in deme j
N_{jt}: Population in deme j at time t
χ: Scaling coefficient for k_j

See Equations 1 - 4

Stage 2: LEARNING
Variables and parameters
τ: Transmission fidelity
ζ: Asocial learning efficacy
A_j: Mean adaptive knowledge in deme j
N_{jt}: Population in deme j at time t

See Equations 5 - 6

Stage 3: MIGRATION
Variables and parameters
m: migration rate

Stage 4: SELECTION
Assumptions
1. Larger brains are more costly
2. Adaptive knowledge can mitigate the cost of a larger brain

Variables and parameters
c_{max}: Maximum brain cost
κ: Maximum brain empty brain
λ: Death rate mitigation (richness of ecology)

See Equation 7

(a)

[2] Adaptive knowledge could potentially relate to locating food, avoiding predators, securing mates, hunting prey, and so on.

Adaptive Dynamics Analytic Model	
$a_i = s_i \cdot \tau \cdot a_m + (1 - s_i) \cdot \zeta \cdot b_i$	(1)
$\bar{a}(s, b) = s \cdot \tau \cdot a_{max} + (1 - s) \cdot \zeta \cdot b$	(2)
$\bar{a}(s, b) = s \cdot \tau \cdot \nu \cdot b + (1 - s) \cdot \zeta \cdot b$	(2a)
$\frac{dN}{dt} = (r - d) \cdot N$	(3)
$r = \rho\left(1 - \frac{N}{k_0 + k_1 \bar{a}}\right) = \rho\left(1 - \frac{N}{k_0 + k_1(s \cdot \tau \cdot \nu \cdot b + (1 - s) \cdot \zeta \cdot b)}\right)$	(4)
$d = \beta \cdot b^n \cdot e^{-\lambda a / b}$	(5)
$r(N^*) = d(b)$	(6)

Agent-Based Simulation Model	
$k_j = \chi A_j + N_{j_0}$	(1)
$N_{j_{t+1}} = \frac{N_{j_t} e^{\rho}}{1 + \left(\frac{N_{j_t}}{k_j}(e^{\rho} - 1)\right)}$	(2)
$a_{ij}^T = \frac{1}{1 + e^{-\varphi(a_{ij} - A_j)}}$	(3)
$p_{ij} = \frac{a_{ij}^T}{\sum_{i=1}^{N_j} a_{ij}^T}$	(4)
$a_{mj}^T = \frac{1}{1 - e^{-l_{ij}(a_{mj} - A_j)}}$	(5)
$p_{mj} = \frac{a_{mj}^T}{\sum_{i=1}^{N_j} a_{mj}^T}$	(6)

(b)

Figure 1. (a) Variable definitions for the analytic model, with individuals *i* represented by brain size b_i, adaptive knowledge a_i, and reliance on social over asocial learning s_i (b) Variable definitions for the agent-based simulation model. The mathematical relationships between variables for the analytic model (left) and agent-based simulation model (right).

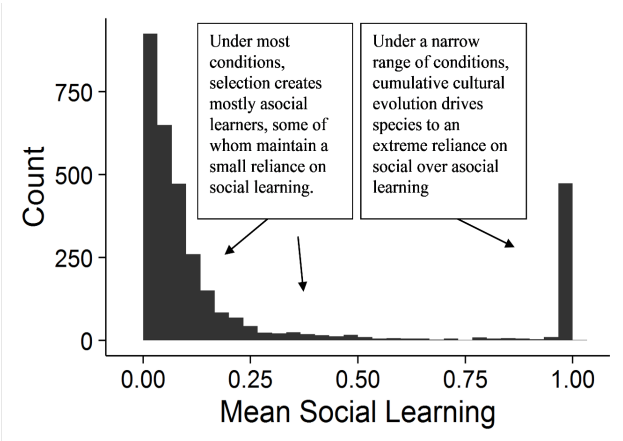


Figure 2. The different equilibrium regimes for reliance on social learning that emerged in the simulation. Most conditions select for individuals primarily reliant on asocial learning (left side), while a small range of conditions may create individuals primarily reliant on social learning (right side). A narrow set of conditions lead to an extreme reliance on social learning (far right). These mechanisms identified by the model that lead to these three regimes are the Asocial Brain Hypothesis, Cultural Brain Hypothesis, and Cumulative Cultural Brain Hypothesis, respectively.

The third unanticipated regime (top left of Figure 2), the "Asocial Brain Hypothesis" (ABH), describes the pathway to big brains through asocial learning (e.g., through individual trial-and-error). According to the ABH, animals on this asocial learning path to larger brains are characterized, among other things, by a weaker, non-existent, or negative relationship between sociality, length of the juvenile period, and brain size. The logic behind this is that larger brains and more knowledge can increase carrying capacity but without reliance on social learning there is less fitness return from the knowledge possessed by a larger group or longer juvenile period to learn from this group. Instead, time is spent on the more inefficient learning by oneself through trial and error in the environment (compared to learning the solutions discovered by other group members). It's therefore worth reaching adulthood quickly for exploitation of knowledge learned and perhaps further asocial learning from the environment. As a result, we expect that the evolution of larger brains in asocial animals to be primarily driven by the complexity and available calories in their ecology.

Cephalopods as a unique comparative case in brain evolution
With a last common ancestor with humans and other vertebrates over 500 million years ago, cephalopods not only have flexible bodies, but also flexible cognition and behavior. For instance, many species of cephalopods exhibit a variety of foraging and predator-avoidance strategies[6]. These strategies, such as camouflage, navigation, mimicry, and tool use can be flexibly adjusted to nearby species or other contextual cues[54,55]. Although they do not display the cohesion and complex sociality of many mammalian and bird species, communicative body patterns are used widely across the squid and cuttlefish in mating contexts, where aggressive visual signaling as well as tactical deception have been observed in a range of species[56–58]. Many species, especially the well-studied *Octopus vulgaris*, display cognitive abilities such as tool use, navigation and problem solving as well as many types of learning[59]. Playful behavior, an otherwise rare occurrence in the animal kingdom, has also been observed in some octopuses[60].

Cephalopods, therefore, represent an independent evolutionary origin of intelligence from that of the vertebrate animals we often view as possessing advanced cognition, such as primates, cetaceans, and birds. At the same time, cephalopods are generally live largely solitary, semelparous, short lives[6–13]. Many are cannibalistic, a barrier to social tolerance let alone sociality[61], including complex group dynamics or social learning.. In our current sample of 79 species where brain data is available, at least incidental cannibalism was observed for 21 species with data largely unavailable for the remainder. A previous review of a broader set of species found cannibalism in 34 species, associated with various factors including population density, body size, stress, and prey availability[61]. Cephalopods also exhibit little to no parental care or pair-bonding, often dying after first reproduction[62–64]. As these characteristics run counter to established theory and empirical findings from other, more social, vertebrate taxa, cephalopods are a promising asocial animal group on which to evaluate prominent hypotheses on the evolutionary drivers of brain size[65–67].

Cephalopods also contrast with cetaceans, the marine group previously tested for the cultural brain hypothesis, through occupying a far broader range of ocean habitats ranging from shallow coastal water, the open ocean, and the sea floor at a wide range of depths[68]. Overall, benthic (seafloor) habitats can be considered more complex than pelagic (open water) habitats as measured by calorie and energy availability and biodiversity. However, these measures depend on factors such as geographic scale, latitude, depth, substrate, and specific organismal lifestyles (e.g. daily vertical migration from the depths to the surface)[69,70]. Additionally, much remains to be discovered about organisms inhabiting the deep sea, open ocean, and other environments[71,72]. To capture the variety of ecological selection pressures these habitats impose, we include several environmental variables including benthic vs pelagic habitats, depth in meters, and latitude (described further in results and methods).

To test the ABH, we systematically surveyed the cephalopod literature to identify and capture a wide variety of qualitative and quantitative data on extant coleoid cephalopod species' brain and body size, physiology, ecology, life-history, sociality and behavior. We read all 3933 papers in the Zoological Record and extracted all available data on 115 variables (see Supplemental Material for full list) for all 79 species for which comparable adult brain size data are available from the year 1866 to July 2020. We also added papers published up to 2024 which contained new brain data. This data revealed large gaps in what we do and do not know about extant coleoid cephalopods. Here we report the results of the 3 variables for which we had full data: Ecology (as measured by benthic vs. pelagic habitat), Depth (minimum and maximum, with minimum more reliable as maximum depth is more difficult to confirm), and sociality (as measured by categorizing species as solitary or gregarious, with an additional category of tolerant/aggregative in sensitivity checks). The availability

of these data allowed us to compare ecology to sociality. The results of other analyses, including those relevant to the theoretical predictions, are less reliable. All other variables with sample sizes are reported in the Supplementary Information (SI).

Results and Discussion

The Asocial Brain Hypothesis predictions were pre-registered as applicable to cephalopods (https://osf.io/nbwsx). Here we present the key results with the most complete data, comparing ecology against sociality, with the full set of results in the SI. All analyses are Bayesian multilevel models with total central nervous system (CNS) volume as the outcome variable with missing covariates imputed during model fitting. Among other robustness and sensitivity checks, where multiple data points were available for the same species, we ran it with the maximum brain size value in the main analysis and with all values in sensitivity checks report in SI - these did not affect the results. Each model also includes as a predictor dorsal mantle length (ML) as a standard measure of cephalopod body size[73]. All continuous variables are logged and standardized (mean 0, standard deviation of 1) and all models incorporate phylogenetic relationships as a correlation matrix to account for evolutionary relatedness between species; for further details on model specification and variable operationalization, see the Methods section. All analysis code and data are openly available at https://github.com/kcbasava/ceph-brain-evolution. The data are also available at cephdata.com and will be posted on Figshare.

For each model, we report the point estimate for the mean of the posterior distribution and the lower and upper bounds of the 95% Credibility Interval (CI) and the result plots report marginal posterior predictions with covariates held at their mean. A headline summary of the results for the main variables is presented in Figure 3 and Table 1. As mantle length is a reliably large and positive predictor of brain size (a posterior mean point estimate of ~0.75 across models on a logged and standardized scale) with a known biological cause, for ease of interpretation, we interpret the coefficients of our predictors benchmarked relative to this estimate as this is plausibly the largest effect size we could observe (i.e., body size should be the strongest predictor of brain size). The relationship between brain size and habitat was two thirds as large as the relationship between brain size and body size; the relationship with minimum depth was a quarter, maximum depth was an eighth, and the relationship with sociality was a third, but in the negative direction.

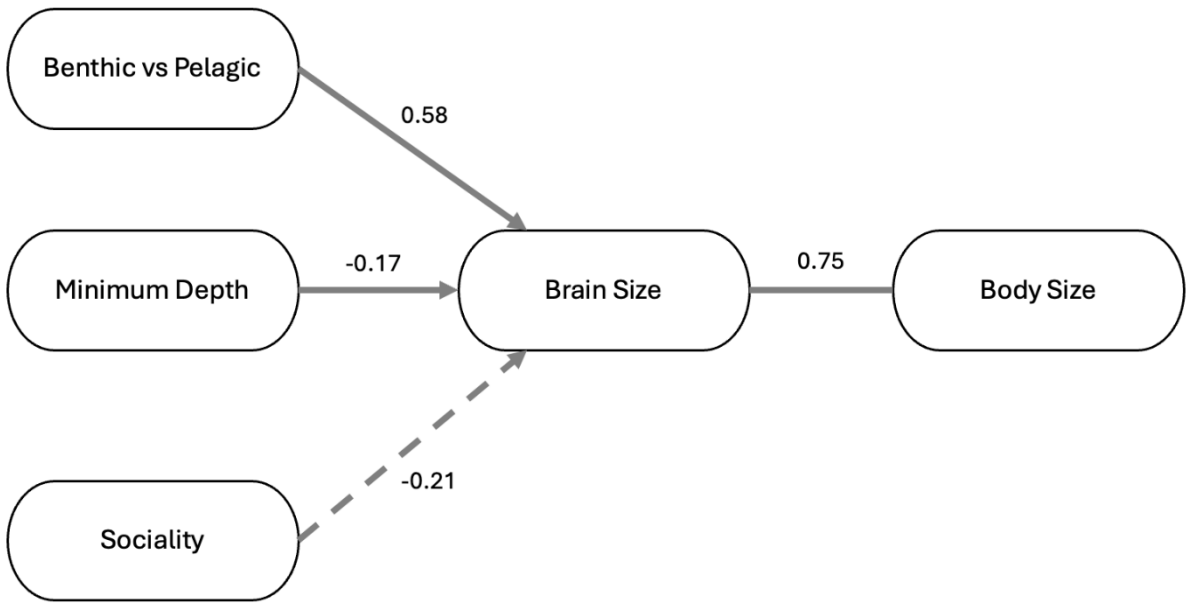


Figure 3. Strongest predictors of brain size found in our analysis. The dashed line from sociality indicates that the credibility interval included 0. Note that these are the main effects with phylogenetic and research effort controls.

Ecological complexity

For asocial learning species such as cephalopods, the ABH predicts a positive relationship between brain size and richer ecologies across all regimes[50]. This prediction emerges in the model because richer ecologies with more calories can support larger brains for both social and asocial learners. Additionally, this relationship is expected to be reinforced by a greater behavioral repertoire leading to more access to calories consistent with ecological explanations for brain evolution.

In our statistical models, ecological complexity was operationalized through: habitat type (benthic, pelagic); minimum and maximum depth in meters and broad categories (shallow, deep, ontogenetic or daily migration); latitude; dietary breadth, measured through the number of taxonomic categories consumed (e.g. crustaceans, gastropods); and number of predators, also measured through the number of taxonomic categories (e.g. other cephalopods, bony fishes).

Habitat type

We ran an analysis considering habitat as a binary variable (benthic vs. pelagic). The effect of benthic habitats on CNS was positive (0.58 [0.08, 1.07]). To test the robustness of this effect - as lifestyles are not always easily divisible into benthic and pelagic - we also considered a three-category measure of habitat (pelagic, benthic, and variable / near bottom / demersal, included under the binary measure as benthic). The results still revealed a positive effect for near bottom/demersal habitat species (0.64 [0.09, 1.20]) and for non-bottom benthic species (0.54 [-0.02, 1.09]). The estimates for pelagic were somewhat negative in both analyses (-0.42/-0.41 [-1.60/-1.56, 0.79/0.77]). We plot these relationships in Figures 4 and 5 below.

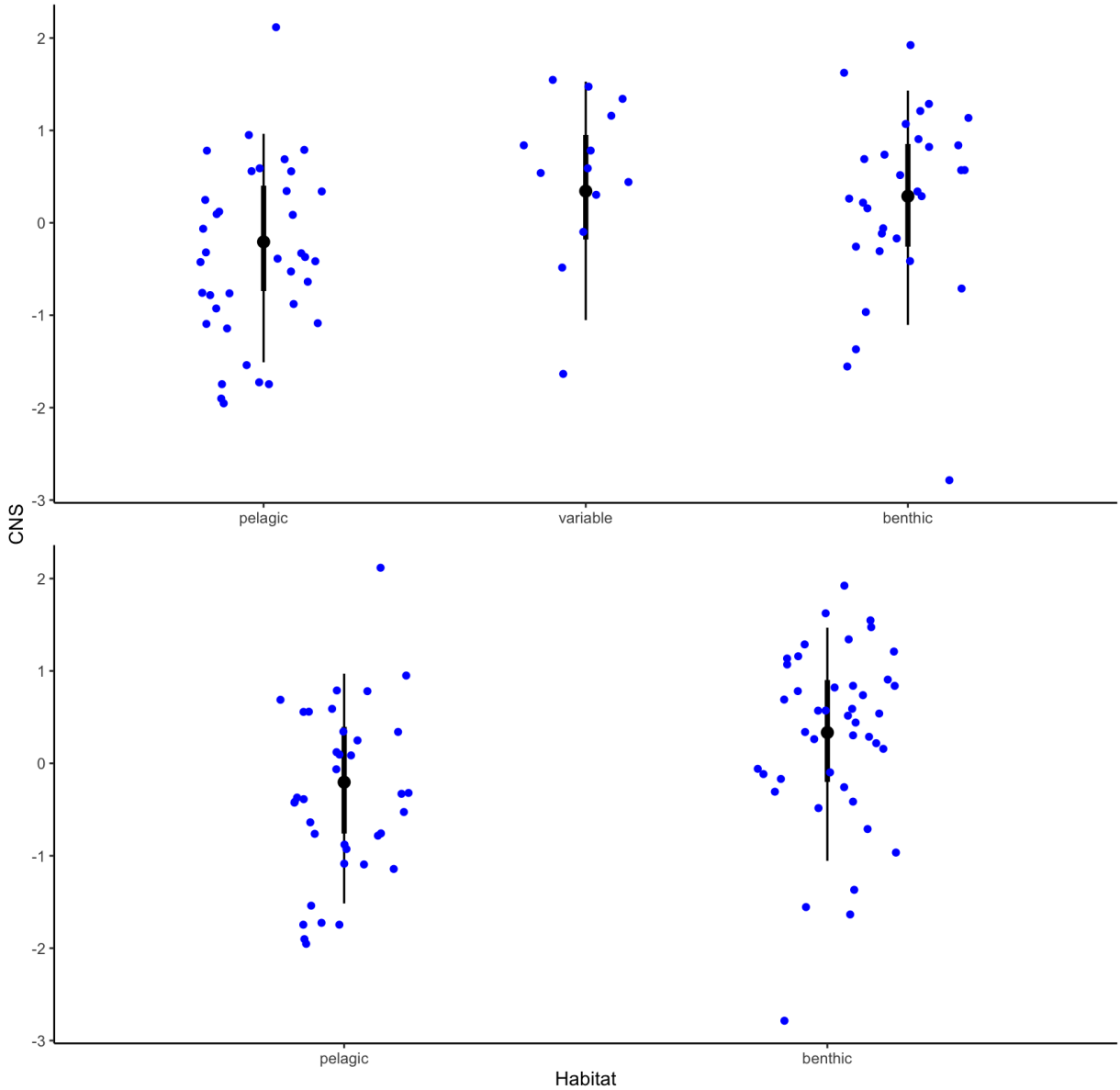


Figure 4. Plot of results from analyses predicting brain size from habitat coded into three or two categorical types. Bars show predicted CNS (medians with highest density continuous intervals) and blue dots observed data for three-category habitat (top) and binary habitat categories (bottom).

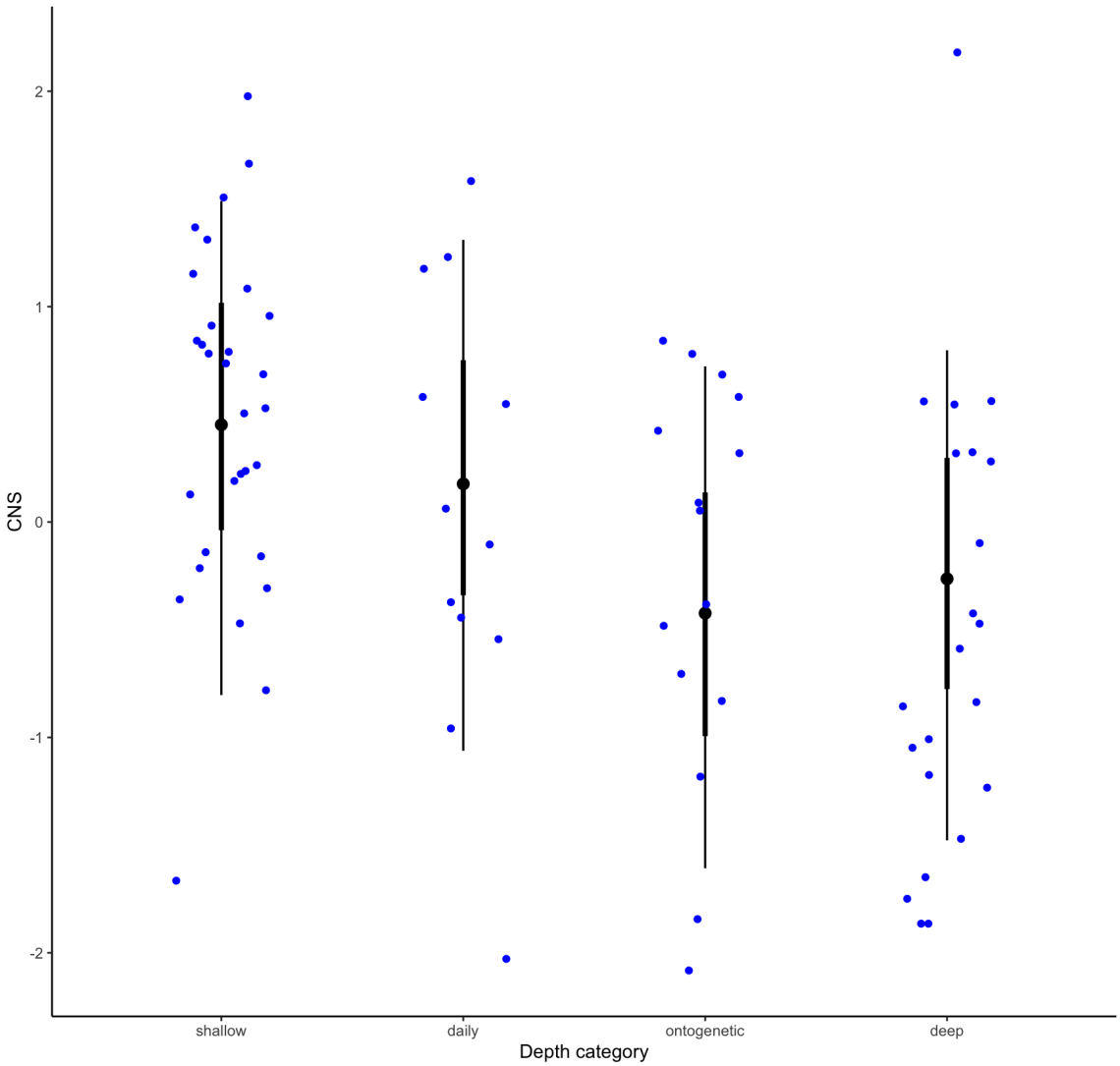


Figure 5. Plot of results from analyses predicting brain size from depth measured in four categories. Bars show predicted CNS (medians with highest density continuous intervals) for different depth categories and blue points observed data. From left to right: shallow water, daily migration, ontogenetic migration, deep water. CNS is logged and standardized.

The results of the analyses conducted with the first version of habitat codes are consistent with the predictions of the ABH with selection for larger brains in more complex habitats. However, this is complicated by some species displaying elements of a pelagic lifestyle in addition to interacting with the benthos. Depth range as a potential proxy for ecological complexity did not positively predict larger brains in our analyses (it did show a negative effect, but this was likely driven by higher maximum depth in species with the largest depth ranges). The distribution of depth ranges in meters for each species in the dataset is shown in Figure S1, colored by habitat and ordered in ascending order of relative brain size (CNS/ML). In particular, the plot illustrates how species with relatively larger brains tend to live in benthic or variable habitats.

The phylogenetic analysis of Lindgren et al.[68] indicated convergent morphological changes in cephalopods with shifts to different oceanic habitats. These included the presence of photophores for bioluminescence in pelagic cephalopods, accessory nidamental glands to protect eggs for species which attach them to substrate, and corneas among benthic taxa for protection from sediment. It is logical that selective pressures of different habitats would likewise influence brain evolution across cephalopod taxa.

Depth

Depth measures in our dataset are somewhat imprecise given that many species have wide and/or variable ranges or engage in vertical migration, and the potential biases in measurement methods (e.g. different capture methods in fisheries studies). Minimum is more reliable since it's easier to measure how shallow a species is than how deep. Minimum recorded depth had a negative effect (-0.17 [-0.28, -0.04]). Maximum recorded depth also had a negative effect (-0.10 [-0.26, 0.04]), though the CI included 0.

Considering depth as a 4-factor categorical variable, categorizing species into shallow water, daily vertical migration, ontogenetic migration (usually descending as they grow from paralarvae/juveniles to adults), and deep sea also indicated lower CNS for ontogenetically migrating species (-0.85 [-1.35, -0.24]) and deep-sea species (-0.70 [-1.21, -0.20]). The estimate for shallow-water species was centered around 0 (0.15 [-1.00, 1.31]) and for daily vertical migration slightly negative (-0.26 [-1.82, 0.82]).

Thus the effect of depth was overall negative, consistent with our predictions, assuming that shallow habitats tend to be more complex than deep-sea ones due to the presence of sunlight and greater energy availability (although this is complicated by numerous factors such as temperature, latitude, and oxygen levels affecting diversification, competition, and predator-prey interactions[74,75]; see SI for further discussion). However, the categorical measure of deep-sea lifestyles and ontogenetic migration to the depths both showed lower estimates of brain size. Overall, further research on specific environmental aspects of different depths, as well as how variables like predation pressures and prey availability differ for cephalopod species inhabiting benthic or pelagic habitats[76] will likely shed more light on ecological selection pressures on brain size.

Sociality

The ABH predicts a weak, non-existing, or negative relationship between brain size and sociality for cephalopods, as asocial learners do not benefit from a larger group in the way social learners do (larger groups have more models to learn from). This prediction is one of the key differences between the SBH and ABH. Consistent with this prediction, whether species were solitary or gregarious was not positively associated with brain size (Figure S2). Sociality instead had a somewhat negative effect (-0.26 [-0.60, 0.17]), although the credibility interval crosses 0. We also ran an analysis using three categories for sociality rather than the binary measure, with an additional 'in-between' code meant to capture species that appear tolerant of or would associate with other individuals close by (coded as solitary in the binary variable). These include some species that have been observed aggregating in the wild or displaying pair bonding behaviors such as *Abdopus* species[77,78] or that appear unusually tolerant of proximity in lab conditions such as *Rossia macrosoma*[79] and *Sepia bandensis*[80]. The results were broadly similar for social species strictly coded (-0.21 [-0.58, 0.21]). Tolerant species had a slightly higher estimate for brain size (0.37 [-0.02, 0.79]), but interpretation of this result is complicated by the small number of species in this category (11 total) and the heterogeneity of characteristics that could classify species as falling between solitary and gregarious.

A supplementary analysis was also run to look at sociality only among the 54 decapodiforme species (squid, bobtail squid, and cuttlefish) in our dataset. The effect remained negative (-0.24 [-0.76, 0.25]), indicating that this effect was not driven only by larger brains among octopuses, which are predominantly solitary. A corresponding analysis among octopodiformes was not possible, as none were coded as gregarious.

Our sociality findings starkly contrast with many of the predictions and findings from mammals and other social vertebrates. Sociality in cephalopods is strongly phylogenetically conserved, with schooling present exclusively (though not universally) among the decapodiformes. Solitary and social species can generally be clearly distinguished; however, there are many aspects of sociality such as group sizes and schooling dynamics in the latter that have not been adequately observed or described in the literature. Cannibalism, common among at least some cephalopods, is another factor that may have obstructed the evolution of richer social lifestyles through inhibiting the possibility of any social trust between conspecifics[61]. Additional field research is needed to draw more fine-grained conclusions about how sociality interacts with cognition and brain size in cephalopods.

Table 1. Summary of the results for our main predictor variables, indicating the strength of the relationship relative to that of body to brain size, the direction of the relationship and consistency/lack thereof with the ABH, and our subjective assessment of the reliability of this relationship. Remaining results using variables with more missing data is reported in the SI.

Variable	Strength of relationship relative to ML:brain relationship	Sign of relationship	Results consistent with ABH	Strength of evidence*	Number of species with data on focal predictor
Benthic (vs. pelagic) habitat	~⅔	positive	yes	strong	79
Depth	¼ (minimum depth) ⅛ (maximum depth)	negative	yes	medium	79
Sociality	~⅓	negative	yes	medium	79

*Informal strength of evidence assessment based on amount of missing data, source data quality, effect size, CI ranges, and accuracy of variable definitions, as discussed in the main text.

Overall conclusions

In summary, our findings are consistent with ecological theories of brain evolution, but not consistent with social theories[25,30], as solitary vs. gregarious lifestyles did not predict larger brain sizes in our dataset. This was the case both across species in all three major groups and within squids and cuttlefish, which do display some levels of social grouping and interspecific interactions. In contrast, habitat in particular emerged as the most reliable predictor of brain size in cephalopods, with shallower-living and benthic species tending to have larger brains. Since shallower and benthic habitats to be relatively more complex than deep sea and pelagic habitats—for instance, pelagic food webs tend to have lower species diversity than do benthic ones, possibly leading to greater specialization among benthic foragers[71,81]—this finding is consistent with the idea that environmental variability selects for greater cognitive capacities and larger brains[82]. Overall, these findings are consistent with hypotheses that have emphasized how large brains may coevolve with the ability for innovative and complex behaviors, allowing animals to survive in variable environments and cope with ecological challenges[68,82].

Limitations and future directions

The main limitation of this analysis is the sparsity of cephalopod data available in the literature, including for species for which brain data is available. Our dataset includes comparative quantitative brain data for 79 species, which amounts to roughly 10% of the total number (around 820) of extant

cephalopod species. To maximize the use of the data we do have, we used a Bayesian multilevel modeling approach so that no data was discarded. Nevertheless, the amount of data does affect the size of the Credibility Intervals we calculate and all analyses, particularly those reported in the SI, should be interpreted with this in mind.

For example, our measure of predator breadth, which is an important aspect of ecology, suffers from missing data, overgeneralization of taxonomic categories, and difficulty with accurate measurements for many species. This contrasts with the full data in habitat type, which is far easier to measure and classify. A far greater amount of lab and field data would be needed to properly test the predictive value of variables like behavioral innovation rate, which has been shown to predict brain size in birds and primates[19,83]. While our results similarly support some aspects of the cognitive buffer hypothesis[84], i.e. selective pressures for cognitive ability from a variable environment, this predicts that large brains will preferentially be selected in longer-lived species[46], which does not apply well to short-lived coleoid cephalopods. Further research will help clarify the aspects of these different environments that serve as selection pressures, and how these interact with variables such as predation pressure and diet that were less conclusive in our analyses.

Another possible limitation is that by constraining our analyses to species with presently available quantitative brain data, we risk a selection bias if these particular 'brain data' species are exceptional in relevant characteristics compared to non-sampled species. For instance, shallow-water species might have been easier for researchers to sample in addition to having larger brains and, in turn, possess more complex behavior due to their shallow-water habitats. Similarly, smaller species might be less likely to be sampled due to their small sizes and have different behavioral repertoires than bigger species. However, we found limited evidence of this bias. The present dataset, which primarily builds on brain data from Wirz[85] and Maddock and Young[64,85,86] (updated by Nixon & Young[64,85,86]), with the inclusion of a few more recent brain analyses (Chung et al.[87,88], Montague et al.[89]), spans a wide variety of species that are diverse in size and habitat and covers a wide range of families across the major lineages (squid, octopuses, and cuttlefish) of the coleoid cephalopod phylogeny. It therefore seems unlikely that brain size directly influences the probability of sampling, which would be the worst case scenario from a selection bias perspective.

A further limitation of the current study was the single measurement of brain and body size for the majority of species, which means that intra-species variability was not taken into account and idiosyncrasies of the individuals that happened to be measured might have affected the validity of our results. To mitigate this, we ran sensitivity checks by including the additional brain and mantle estimates for the 36 species in our dataset with additional (one or two) brain and mantle length measures. The results of these analyses are summarized in the SI and are consistent with the estimates from our main analyses.

Finally, as our analyses used whole brain size as the focal outcome, they did not take into account measures of brain structure, organization, and neuron numbers which have been suggested to relate to variation in behavioral repertoires and complexity in cephalopods and other species[90,91]. Among cephalopods, this includes research on relative lobe size and how these link with ecological factors[64,85,86].

In summary, our findings starkly contrast with the relationship between sociality and brain size among primates and other vertebrate species such as birds. Cephalopods are a unique comparison to these other taxa that have most often been the subject of comparative brain evolution studies[66,92]. In addition to focusing on a previously neglected group in this literature, our study evaluates – and finds broad support for – predictions derived from the ABH model – encouraging further efforts toward

more general theories for the evolution of expanded brains and intelligence that apply across the animal kingdom[50]. Modeling is essential to theory development for the study of complex systems[93], and can help make sense of the variety of empirically discovered relationships reported in the literature. We also hope that this dataset and approach motivates more specific formal theories that capture the evolutionary history and phenotypic constraints of cephalopod physiology and life history as building blocks of a fully general theory and theoretical framework of brain evolution[94].

Methods

Prior to the development of the cephalopod database we present here, the most comprehensive comparative study on cephalopod brain size to date was published as part of a 2007 PhD dissertation by Borelli[95] and in a subsequent journal article by Ponte and colleagues[96]. While an ambitious and useful contribution, this effort had limitations with regard to broader research efforts on comparative brain evolution:

1. The dataset expresses brain size in relative terms (specifically, the size of each brain lobe is computed as a proportion to the whole central nervous system) and does not include absolute brain and body size measurements, which makes these data unsuitable for comparative regression analyses.
2. The dataset does not include social, behavioral, or life-history variables necessary for directly evaluating predictions of the ABH.
3. Due to the nature of available cephalopod phylogenies, Ponte et al.[96] were forced to discard data on more than half of their 78 species when running phylogenetically-controlled analyses.
4. Upon reviewing Borelli's primary brain data sources[64,85,86] and their subsequent use in the literature, we found inconsistencies that ultimately required us to conduct a careful, systematic re-evaluation of all data (refer to Supplementary Information for details).
5. The dataset contains brain measures from the juvenile specimens for a few species. As cephalopod brains are still maturing during the juvenile period[97,98] and possibly during adulthood[99], it is not appropriate to use these for comparative analyses with measures from adult specimens.
6. Considerable advances in empirical work on cephalopods, including additional brain data measurements, have been made since Borelli's pioneering 2007 PhD data collection.

The present study overcomes these limitations. The dataset we present in this paper was developed with three main goals[92]: (1) to assess key hypotheses on the evolutionary drivers of brain size in cephalopods, starting with the Asocial Brain Hypothesis (ABH); (2) more generally, to move toward a theoretical reconciliation of empirical findings from comparative brain size studies in other animal groups; (3) provide a dataset to the cephalopod research community for further analyses and theory-building. Drawing on the predictions of the ABH as well as previous brain evolution literature, here we empirically assess whether measures of ecology, age at sexual maturity (i.e., length of juvenile period), sociality, and behavioral complexity predict brain size in coleoid cephalopods.

Data collection

Brain and body size data were taken mainly from Wirz[85] and Maddock and Young[86], updated by Nixon & Young[64], combined with a few newer species-specific brain data estimates[87–89,100,101]. We used brain size measurements from adult specimens of identifiable species (79 total). Data on behavior, ecology, physiology, and other traits were collated from a systematic review of articles written on each species on Web of Science, taking into account alternate species names. The bulk of the data was captured up until November 2020, which was followed up by a more targeted data collection effort for particular species and variables. We also captured and coded data from major books on cephalopod ecology, physiology, and behavior[62,64,102–105].

Due to a lack of data on pre-adult stages, we coded our variables focusing on adult brain and behavior. We did not distinguish between observations of male or female individuals except in cases of sex-specific variables (e.g. male courtship displays).

Variable operationalization
Brain size was operationalized as the total central nervous system (CNS) volume including optic lobes (in millimeters^3) from the sources listed above. Body size was operationalized as the mantle length from the same specimens in millimeters. In the analyses reported here, we use the maximum recorded total CNS volume and, when available, its associated mantle length size. As sensitivity checks, we re-ran main models with available supplementary CNS data (see https://github.com/kcbasava/ceph-brain-evolution/tree/main/sensitivity-checks).

We operationalized the length of the juvenile period/age of sexual maturity through the oldest age at which a species is not observed to be sexually mature measured in number of days, with lifespan (also in days) included in the models for which this was a predictor. We analyze both the maximum and minimum recorded ages. Sociality was measured as a categorical variable with species coded as solitary (avoiding other conspecifics except for mating), tolerant/aggregative (an in-between category with individuals sometimes observed as congregating outside of reproductive contexts and appearing tolerant of nearby individuals), or gregarious (usual or obligate schooling),. This was coded as a binary variable in the main analyses with 'tolerant' species coded as solitary/0. Sensitivity checks were run with the three-category measure.

Species were characterized as having benthic or pelagic habitats, with benthic defined as animals living on and/or closely interacting with the seafloor and pelagic animals primarily living in the water column. After further review of these variables, it was decided to create a third category for species observed interacting both with the seafloor and swimming in the water column (demersal/in-between) that would otherwise be classified as benthic. Depth was measured through the minimum and maximum depths in meters at which adult individuals of each species had been recorded, as well as a 4-category variable which classified species as living in shallow waters, undergoing daily vertical migration, migrating to the depth as adults (i.e. ontogenetic migration), and living in the deep sea.

Behavioral complexity was measured through (a) combined social behaviors and cognitive measures, (b) number of defense/antipredator behaviors, and (c) number of foraging behaviors, each used as predictor variables (full description in SI). The combined cognition measure was intended to capture behavioral complexity both as measured through lab studies of abilities such as learning, memory, and problem solving, as well as through field observations of interactions with conspecifics in the wild, e.g. with deception in mating contexts and communication abilities, for species which have not been studied in one or the other context.

Researcher effort was accounted for by including variables for (1) number of articles published on Web of Science for the species name (or alternative names) and (2) articles read during coding of the dataset. The former was used as the standard variable for research effort while the latter was used for variables more likely to be biased due to frequency of observation (i.e. count variables including dietary breadth, number of predators, or foraging strategies).

Statistical models
All analyses are Bayesian multilevel linear regression models and were run using the *brms* package in *R* [106], an interface to the probabilistic programming language *Stan* [107]. They generally follow the operationalization of Bayesian multilevel regression models from McElreath[108] as implemented in brms by Kurz[109]. All models included brain size (as total CNS volume) modeled as a function of body size (as mantle length). Other variables were included as derived from adjustment sets from a directed acyclic graph (DAG) depending on the focal predictor. The code describing the DAG, including all variables and hypothesized causal paths, are available in the *R* scripts at

https://github.com/kcbasava/ceph-brain-evolution. All variables except for habitat, categorical measure of depth, and sociality were standardized (mean centered with a standard deviation of 1) and log-transformed prior to analyses. Priors were chosen to be weakly regularizing. A consensus phylogeny created from the results of the phylogenetic software (discussed in detail in the Supplementary Information) was incorporated as a covariance matrix following the implementation in Kurz[110]. Models were fitted according to the following structure:

```
brm(bf(CNS ~ mi(ML) + mi(X1) + X2 + effort + (1 | gr(species, cov = cormat))) +
       bf(X1 | mi() ~ 1 + mi(ML) + X2 + (1 | gr(species, cov = cormat))) +
        bf(ML | mi() ~ 1 + X2 + (1 | gr(species, cov = cormat))),;
       data = d, data2=list(cormat=cormat),
       prior = c(prior(normal (0,1), class = Intercept),
       prior(normal(0, 0.5), class = b)))
```

where CNS is total brain volume, ML is mantle length , effort is research effort, X_1 is a predictor or predictors with missing data defined by the second bf() formula and X_2 is a predictor or predictors without missing data. 'Cormat' represents the correlation matrix for the consensus phylogeny. Models were run for 8000 iterations. As a robustness check accounting for uncertainty in branch lengths, models were also run over a set of 100 phylogenies sampled from the posterior distribution of the phylogenetic inference analysis (described in detail in Supplementary Information) and the results combined using the combine_models() function in *brms*.

Sensitivity checks were run using additional measures of brain data and mantle length for species with measures from multiple individuals to ensure broadly similar results were attained. Sensitivity checks were also run with focal predictors with missing data in the main analyses (age at sexual maturity, predator breadth, diet breadth, hunting repertoire, and defense repertoire) with the missing cases dropped instead of imputed. These analyses did not contradict any of the findings from the imputed analyses (see analyses and supplementary data available at https://github.com/kcbasava/ceph-brain-evolution/tree/main/sensitivity-checks).

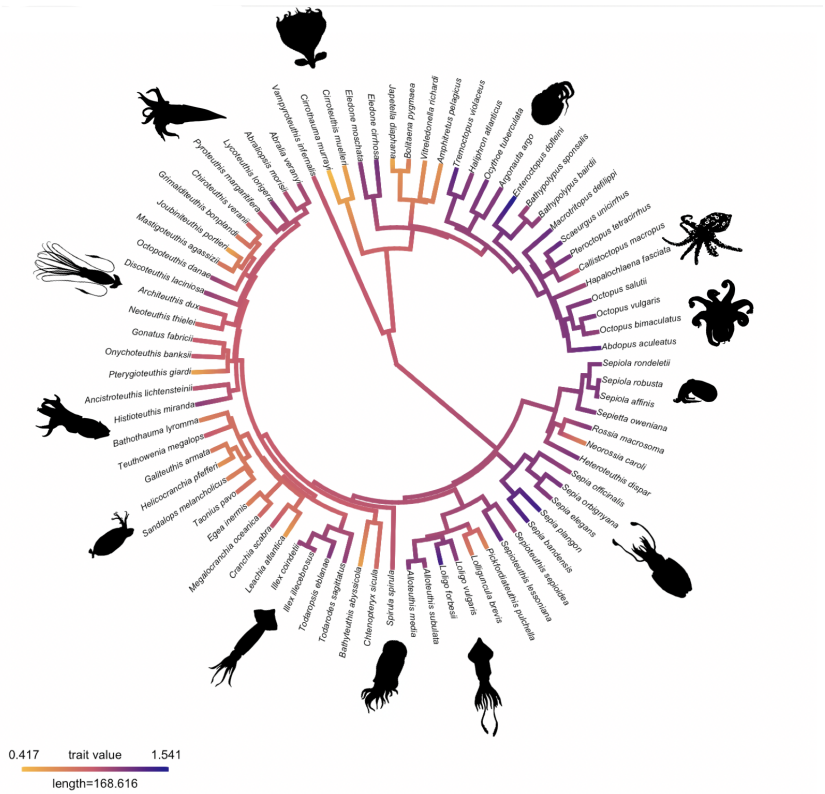
Some variables, e.g. communication and reproductive behaviors or hunting behaviors, were aggregated into a single measure to make use of all available observations for each species. A detailed definition for each variable and operationalization in the analyses are provided in the Supplementary Information. While this helped make use of all available data rather than discarding variables, it is likely this aggregation biased these codes towards heavily studied species even after accounting for researcher effort with the number of articles on the species in Web of Science.

Phylogeny

Although there are available phylogenies of coleoid cephalopod species (e.g. [68,111]), the usual approach to comparative analyses would require matching the species in our dataset to those present on a chosen phylogeny and discarding those not included, which would significantly reduce our sample size. As we did not wish to discard any species with brain data, we decided to create an updated phylogeny for our analyses instead. With assistance from Jan Strugnell, we developed a new phylogeny for all 79 species by combining previously published phylogenetic analyses and additional sequence data on GenBank (described in Methods and in Basava et al.[112]).

In order to make use of all species for which brain measurements were available, we built a composite phylogenetic topology based on results of prior phylogenetic studies and inferred divergence times with the *BEAST2* software[113] using sequence data from GenBank[114]. A detailed account of the methods for building the phylogeny are in the Supplementary Information. As relationships between coleoid species at more detailed levels than the octopodiforme-decapodiforme

split are still uncertain[115,116], we consider our phylogeny to be a rough approximation of a "true" set of evolutionary histories that nonetheless, when properly included in our statistical models, should partly guard against unobserved confounding through shared evolutionary trajectories. An ancestral state reconstruction of relative brain size (logged CNS/ML) using the '*contMap'* function from the package *phytools* in *R*[117] is shown on the consensus phylogeny in Figure 6. Relative brain size is somewhat phylogenetically conserved, with larger measures appearing among the incirrate octopuses and cuttlefish.


Vampyroteuthis infernalis
Cirroteuthis muelleri
Cirrothauma murrayi
Eledone cirrhosa
Eledone moschata
Japetella diaphana
Bolitaena pygmaea
Vitreledonella richardi
Amphitretus pelagicus
Tremoctopus violaceus
Haliphron atlanticus
Octopus tuberculata
Argonauta argo
Enteroctopus dofleini
Bathypolypus sponsalis
Bathypolypus bairdi
Muusoctopus johnsonianus
Muusoctopus longibrachus
Muusoctopus leonis
Muusoctopus rigbyae
Muusoctopus robustus
Muusoctopus sasakii
Muusoctopus profundorum
Muusoctopus hoyle
Muusoctopus ?
Muusoctopus ?
Muusoctopus ?

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