Ecological not social factors explain brain size in cephalopods: we need a new model for the evolution of big brains

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Abstract
Sociality has 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 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, and short lives, leaving little to no opportunity for parental care, complex group dynamics, or social learning. A formal model is needed that takes these factors into consideration. Here we test the formal model of the "Asocial Brain Hypothesis" on cephalopod molluscs. We compiled a database of brain size, ecology, behavior, sociality, and life history from 3933 publications on the 79 species of octopus, squid, and cuttlefish for which comparable brain data is available. We analyze these data using an updated phylogeny and Bayesian multilevel models. In a set of pre-registered statistical analyses derived from the predictions of the "Asocial Brain Hypothesis" formal model, we find a large effect of habitat, suggesting ecology as a primary selection pressure on brain size in cephalopods. We also find evidence of a positive relationship between brain size and number of predator groups and no relationship between brain size and sociality. These results are inconsistent with social explanations for brain evolution but consistent with ecological explanations. They emphasize the need for new theories to explain the evolution of brains more generally, including in the cephalopods, which diverged from vertebrates over 500 million years ago.

Introduction
In this paper, we test the predictions of the Asocial Brain Hypothesis (ABH) with coleoid cephalopods, a well-studied, primarily asocial animal group. In doing so, we hope to motivate better models of brain evolution and a better understanding of asocial animals and invertebrates. Consistent with the ABH, our results suggest that ecological rather than social factors explain the evolution of big cephalopod brains, suggesting that social factors are not the only path to encephalization. These results support the mathematical model[1] from which the ABH is derived, which incorporates ecology, sociality, life history, and asocial and social learning, predicting an encephalization pathway for asocial learners based on ecology, for social learners based on social learning, and an extreme reliance on social learning co-evolving with very large brains consistent with a human pathway. However, this general model of brain evolution or a model like it needs to be expanded to deal with specifics of cephalopod life history and also encompass the evolution of insect brains.

In this paper we first discuss the most well supported current theories of brain evolution, explain the value of formal mathematical modeling for developing and testing unifying models of brain evolution, and why cephalopods offer an important test of these various explanations. The remainder of the paper presents the results, discussion, and methods.

Current theories of brain evolution

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[2–5]. 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[6–10]. Among these, sociality has become the dominant explanatory predictor, after initial work by Jolly[11] and Humphrey[12] argued for social complexity as a driver for intelligence among primates. The social brain hypothesis (SBH), developed to explain the evolution of large brains in primates[13], predicts the evolution of larger brains to cope with the complex demands of social group living, such as cooperation, deception, and competition[14–16], as well as pair bonding and social cohesion[17,18].

The SBH has been tested among various other taxa with mixed levels of support. Some findings have indicated the quality of relationships rather than group size. A comparative study of cetaceans 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[19]. An analysis of sexual competition and brain size in bats found larger brains among species with monogamous rather than promiscuous females[20]. 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[21]. 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[17,22,23].

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[24], sociality was not linked with increased encephalization across clades and this relationship was likely driven solely by canids[25]. 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[26]. 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[27].

Much focus 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[28,29]. 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[28,29].

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"[30]. 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 other 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 available. In one study testing measures of ecological vs. social variables[31–33], 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 social brain hypothesis. A comparative study of mammals and birds[31–33] 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[31–33].

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[34]. There has been some support for this hypothesis, with studies of mammals[34–36], birds[34–36], and amphibians[36] 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[37].

A unifying model of brain evolution

This largely empirical approach has yielded disparate and sometimes contradictory results[6,24,35], highlighting the need for unifying, formally modeled more general theories that model the causal pathways and coevolutionary relationships. One such theory was developed by Muthukrishna et al.[38]. The analytic and computational models (see Figures 1 and 2 below) were developed to incorporate sociality, ecology, and life history into a single framework that made clear predictions. The model predicted three regimes for the evolution of large brains. The first set of predictions, the "Cultural Brain Hypothesis", described the social learning path to larger brains, which has been tested with primates[1] and cetaceans[19]. The second hypothesis, 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[39]). The third set of predictions, which we label the "Asocial Brain Hypothesis" (ABH), was a regime that applied to asocial animals. The ABH, which until now has remained untested, 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, are harder to birth, 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
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[40] 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.

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

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_o: 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)

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

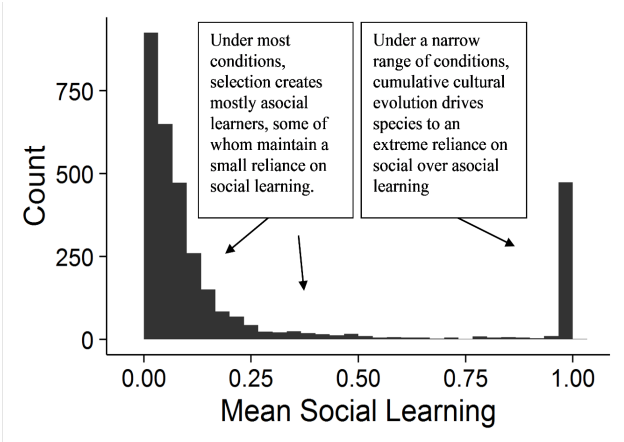
$k_j = \chi A_j + N_{j_0}$	(1)
$N_{j_{t+1}} = \frac{N_{j_t} e^{\rho}}{1 + \left(\frac{N_{j_t}}{k_j}(e^{\rho} - 1)\right)}$	(2)
$a_{ij}^T = \frac{1}{1 + e^{-\varphi(a_{ij} - A_j)}}$	(3)
$p_{ij} = \frac{a_{ij}^T}{\sum_{i=1}^{N_j} a_{ij}^T}$	(4)
$a_{mj}^T = \frac{1}{1 - e^{-l_{ij}(a_{mj} - A_j)}}$	(5)
$p_{mj}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

The analytic and simulation solutions can be found in Muthukrishna et al.[38], however, the model yields 3 distinct regimes, which offer the Asocial Brain Hypothesis, Cultural Brain Hypothesis, and Cumulative Cultural Brain Hypothesis for the evolution of brains through different evolutionary pathways. Muthukrishna et al.'s model was designed to understand the evolution of

brains in social species, but the mathematics revealed another unanticipated pathway via asocial learning, which we call the Asocial Brain Hypothesis. Although the model makes clear directional predictions, it is not ideally suited to capture all the characteristics of asocial species, particularly their juvenile periods and life histories. Thus, although it serves as a reasonable starting point and the basis for our pre-registered predictions, further models specific to the characteristics of cephalopods are required to understand the implications of their specific life history.



(a)

	Evolving characters	Brains $\log(\bar{b})$	Adaptive Knowledge $\log(\bar{a})$	Group Size $\log(\bar{N})$	Social Learning $\log(3+\overline{Ns})$	Juvenile Period $\overline{sv}$
Primarily asocial: bottom	$\log(\bar{b})$	1	0.99 [.98,.99]	0.72 [.67,.75]	0.72 [.68,.76]	0.17 [.09,.25]
	$\log(\bar{a})$	0.78 [.77,.80]	1	0.69 [.65,.74]	0.70 [.66,.74]	0.15 [.06,.23]
	$\log(\bar{N})$	0.42 [.39,.45]	0.55 [.53,.58]	1	0.98 [.98,.98]	0.22 [.14,.30]
	$\log(3+\overline{Ns})$	-0.23 [-.26,-.19]	0.13 [.10,.17]	0.61 [.58,.63]	1	0.22 [.14,.30]
	$\overline{sv}$	-0.53 [-.56,-.51]	-0.34 [-.37,-.30]	-0.21 [-.25,-.18]	0.42 [.39,.45]	1

(b)

Figure 2. (a) 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. (b) The correlations between brain size, adaptive knowledge, group size, social learning, and juvenile period (mean, log scale), with color indicating correlation strength *r* (red = -1, blue = 1). See Muthukrishna et al. for details of how values are calculated. The bottom triangle shows the predicted correlations for the Asocial Brain Hypothesis. The top right shows the predicted correlations for the Cultural Brain Hypothesis.

The third unanticipated regime, 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 weak or non-existent relationship between sociality (e.g., group size), length of the juvenile period, and brain size. This is because a longer juvenile period and delay in reproduction allows more time for learning. When this learning is more efficient, as it is for learning socially from others compared to asocially figuring things out on your own, the payoff to spending more time exploring for the eventual adult payoff is higher. Social learners benefit from being juveniles for longer, learning from and not competing with the adult members of the group

around them. In contrast, if learning by yourself, it's worth reaching adulthood quickly for exploitation of knowledge learned and perhaps further asocial learning. Figure 2c shows the predicted relationship between variables for more social learners (top triangle; e.g. primates and cetaceans) and asocial learners (bottom triangle, e.g. cephalopods).

Cephalopods as an 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[41]. These strategies, such as camouflage, navigation, mimicry, and tool use can be flexibly adjusted to nearby species or other contextual cues[42,43]. 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[44–46]. 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[47]. Playful behavior, an otherwise rare occurrence in the animal kingdom, has also been observed in some octopuses[48].

Cephalopods, then, 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 short-lived and asocial. Many are cannibalistic, a barrier to social tolerance let alone sociality[49]. In our current sample of 79 species, at least incidental cannibalism was observed for 21 species with data largely unavailable for the remainder. A previous review found cannibalism in 34 species, associated with various factors including population density, body size, stress, and prey availability[49]. Cephalopods also exhibit little to no parental care or pair-bonding, often dying after first reproduction[50–52]. As these characteristics run counter to established theory and empirical findings from other, more social, vertebrate taxa, cephalopods are a promising animal group on which to evaluate prominent hypotheses on the evolutionary drivers of brain size[53–55].

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[56]. Overall, benthic habitats can be considered more complex than pelagic 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)[57,58]. Additionally, much remains to be discovered about organisms inhabiting the deep sea, open ocean, and other environments[59,60]. 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.

Although there are available phylogenies of coleoid cephalopod species (e.g. [56,61]), 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.[62]).

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[63] and in a subsequent journal article by Ponte and colleagues[64]. 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.[64] 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[52,65,66] 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[67,68] and possibly during adulthood[69], 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[70]: (1) to assess key hypotheses on the evolutionary drivers of brain size in cephalopods, starting with the 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.

Results and Discussion

The Asocial Brain Hypothesis predictions from Bendixen et al.[70] were pre-registered as applicable to cephalopods (https://osf.io/nbwsx). Here we present the key results for each pre-registered set of hypotheses. 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 checls, where multiple data was available, we ran it with different values - reported in the Supplemental Information - 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[71]. 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. Upon publication, the data will also be made available in easy to browse formats at https://cephdata.com.

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 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). For example, the relationship between habitat and brain size was two thirds as large as the relationship between brain size and body size.

Hypothesis/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
Depth	<⅓ (maximum depth); ¼ (minimum depth)	negative	yes	medium	79
Benthic (vs. pelagic) habitat	~⅔	positive	yes	strong	79
Dietary breadth	~0	-	no	weak	51
Number of predator groups	<¼ (conditional on habitat); otherwise 0	positive (conditional on habitat)	yes (conditional on habitat); otherwise no	weak	64
Sociality	~¼	negative	yes	medium	79
Age of sexual maturity	<¼ (minimum); <¼ (mean); ~⅓ (maximum)	negative (minimum); positive (mean and max)	yes	weak	31
Foraging behaviors repertoire	<¼	negative	no	weak	34
Defensive behaviors repertoire	~0	-	no	weak	43
Cognitive repertoire	~0	-	no	weak	39

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.
*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. "Minimum", "maximum" and "mean" refers to the minimum, maximum and mean of minimum and maximum recorded values.

Ecological complexity

For asocial learning species such as cephalopods, the ABH predicts a positive relationship between brain size and richer ecologies across all regimes[38]. 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: depth in meters and broad categories (shallow, deep, ontogenetic or daily migration); habitat type (benthic, pelagic); 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).

Latitude

Latitude was measured through minimum and maximum recorded ranges of species in degrees. As this variable contains negative values, to calculate mean latitude, 90 was added to all the minimum and maximum latitude variables so that 0 would be furthest south and 180 would be furthest north prior to logging and standardizing it as with the other continuous variables. This was used as an ecological control variable in most of the models testing other predictors.

To specifically test the effects of distance from the equator, the absolute value of the average of the original maximum and minimum latitude measures was used. Distance from the equator did not suggest any effect (-0.03 [-0.16, 0.10]). Latitude range, as one measure of environmental variability, had a slightly negative effect (-0.18 [-0.34, -0.01]).

Dietary breadth and predation pressure

Dietary breadth was not associated with a larger brain size (0.02 [-0.20, 0.25]). The interaction with habitat was weakly negative for pelagic (-0.09 [-0.46, 0.31]) and weakly positive for benthic (0.13 [-0.27, 0.52]).

Number of predator taxa was weakly positive (0.08 [-0.11, 0.27]). When considered in interaction with habitat, this effect was close to 0 among pelagic species (0.04 [-0.18, 0.25]) and somewhat positive among benthic species (0.24 [-0.10, 0.54]). (Figure 3b.)

Dietary breadth in isolation was not a clear predictor of brain size with an estimate centered evenly around 0. For the interaction with habitat, the estimate was positive for benthic species with an effect size around ⅕ that of brain-body size (although with relatively wide CIs). Dietary breadth is a variable with inexact measurement methods (sum of taxonomic categories of prey species, with a large amount of variation in each category) and high potential for missing data even with species observed from stomach contents. We also needed to impute values for nearly a third of species. With more systematically collected observational data, the relative effects of both diet breadth and type on brain size could be examined with more precision. The effect of predator breadth was more reliably positive with the bulk of the posterior distribution being positive, which was also stronger for the interaction with habitat; however, similar to dietary breadth, there was a significant amount of missing data. Like diet and number of defensive and foraging behaviors, this is also a variable dependent on observations in the wild or data from stomach content of predator species, so further field research will provide a more accurate assessment of predation pressure across species and how this variation affects brain sizes.

Depth

Minimum recorded depth had a negative effect (-0.14 [-0.27, -0.01]). The interaction with habitat was mostly negative for pelagic species (-0.13 [-0.30, 0.02]) and did not appear to be present within benthic species (-0.03 [-0.32, 0.25]) (Figure 5a).

Maximum recorded depth also had a negative effect (-0.22 [-0.38, -0.05]). The interaction with habitat was mostly negative within pelagic species (-0.76 [-1.19, -0.31]) and positive among benthic species (0.63 [0.15, 1.10]) (Figure 3a).

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 [-1.346, -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]) (Figure S1).

The effect of depth appeared to be overall negative, with maximum, minimum, and mean depths all having primarily negative posterior distributions. This is generally 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[72,73]. 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). 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[74] will likely shed more light on ecological selection pressures on brain size.

Habitat

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 verify this effect - as lifestyles are not always easily divisible into benthic and pelagic - we also decided to consider a three-category measure of habitat (pelagic, benthic, and 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 benthic species (0.54 [-0.02, 1.09]) (Supplementary Fig. 1). The estimates for pelagic were somewhat negative in both analyses (-0.42/-0.41 [-1.60/-1.56, 0.79/0.77]).

Overall, whether a species occupied a primarily benthic or pelagic habitat was a reliable predictor of brain size with a posterior mean estimate of approximately 0.5 for benthic habitats in focal models, although with relatively wide CIs. For comparison, the point estimate for mantle length - a strong predictor of brain size - is approximately 0.75 across models (Table 2). The habitat variable is complete in our dataset, and it is generally clear from the scientific literature whether species primarily live in the benthos or open water column, although there is ambiguity

with a few species that may primarily live and/or hunt in different habitats and have not been sufficiently observed (e.g. the bobtail squid *Heteroteuthis dispar* and some loliginid squids like *Loligo vulgaris* and *Loligo forbesii*). That said, the effects in our 3-category habitat model taking into account these edge cases and the consistent positive effect of benthic habitat across models indicate that benthic and pelagic lifestyles were a likely selection pressure for brain size in cephalopods.

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 3c, 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.[56] 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.

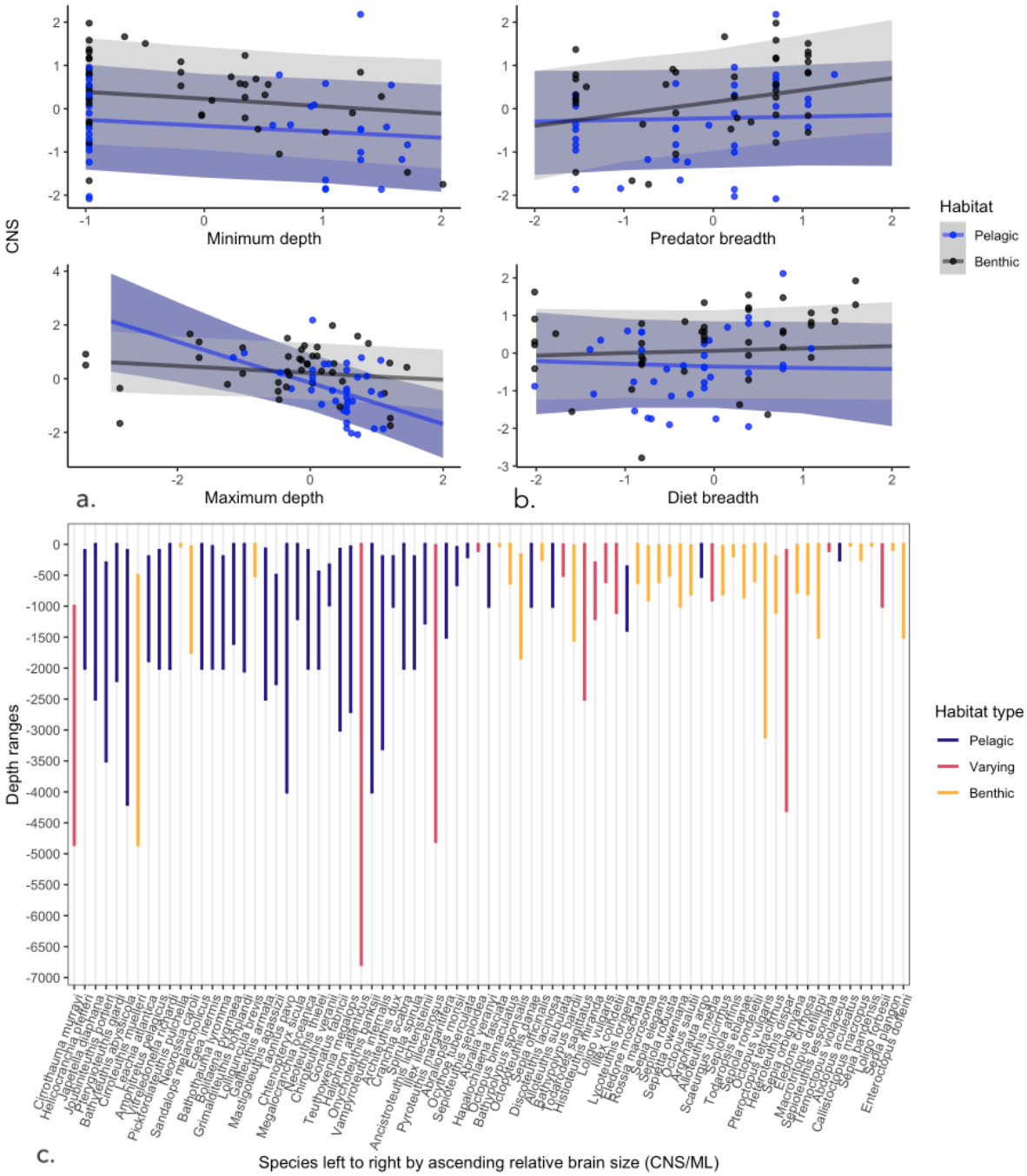


Figure 3. (a) Posterior estimates for CNS predicted by minimum (top) and maximum (bottom) recorded depth among pelagic (blue) and benthic (grey) species. Lines indicate posterior medians and shaded areas highest density continuous intervals. CNS and depth are logged and standardized. (b) Posterior estimates for CNS predicted by predator breadth (top) and dietary breadth (bottom). CNS and depth, predator breadth, and diet breadth are logged and standardized. (c) Depth ranges for species, ordered left to right by ascending brain size (CNS/ML) and colored by habitat type.

Sociality
The ABH predicts a weak or non-existing 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 social brain hypothesis and asocial brain hypothesis. Consistent with this prediction, whether species were solitary or gregarious was not positively associated with brain size (Figure 4a). Sociality instead had a somewhat negative effect (-0.21 [-0.58, 0.17]). 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[75,76] or that appear unusually tolerant of proximity in lab conditions such as *Rossia macrosoma*[77] and *Sepia bandensis*[78]. The results were broadly similar for social species strictly coded (-0.19 [-0.57, 0.21]). Tolerant species had a slightly higher estimate for brain size (0.18 [-0.24, 0.64]), 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 (-0.25 [-0.63, 0.22]), 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 findings of a somewhat negative effect of sociality on brain size is consistent with the ABH and contrasts 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[49]. Additional field research is needed to draw more fine-grained conclusions about how sociality interacts with cognition and brain size in cephalopods.

Age at sexual maturity
The ABH predicts a weak or non-existent relationship between brain size and age of sexual maturity relative to lifespan. This prediction emerges for the cephalopods because asocial learners need to move from exploration to exploitation faster, given that asocial learning is less efficient than social learning. In contrast, for social learning species, the juvenile period is extended and age of sexual maturity is delayed to allow for more time to efficiently learn from other members of the group.

In line with this prediction, we found no consistent relationship between brain size and age of sexual maturity (Fig. 4b). On the one hand, maximum recorded age at sexual maturity had a

positive effect (0.30 [0.04, 0.53]). On the other hand, sensitivity checks were run with mean and minimum recorded age of sexual maturity; mean was also positive but the estimate more centered around 0 (0.18 [-0.07, 0.39]) and minimum negative with 95% CI including 0 (-0.08 [-0.38, 0.20]). Data on this variable is sparse and somewhat unreliable; as it mostly comes from indirect measures and different methods may be used to determine whether an individual is mature (e.g. body size, egg development in females), there is inconsistency in how age of sexual maturity is identified across species.

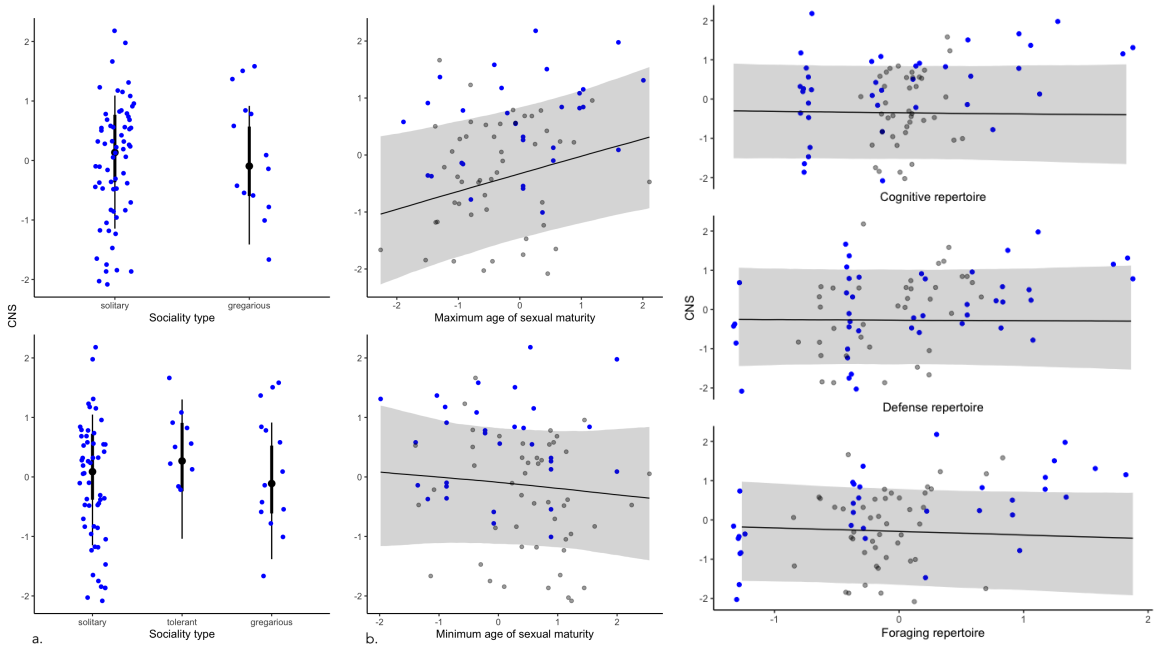


Figure 4. (a) Posterior predicted CNS (medians with highest density continuous interval) for each category of sociality. Top shows results for solitary vs. gregarious categories; bottom is solitary, tolerant/in-between, and gregarious categories. CNS is logged and standardized. (b) Posterior predicted CNS for maximum age of sexual maturity (top) and minimum age (bottom). Black lines indicate posterior medians and gray shaded area highest density continuous intervals. Blue dots are observed data. Grey dots are imputed values (posterior medians) for species missing data. CNS and ages are logged and standardized.

Posterior predicted CNS values for hunting/foraging repertoire. Black lines indicate posterior medians and gray shaded area highest density continuous intervals. Blue dots are observed data. Grey dots are imputed values (posterior medians) for species missing data. CNS and repertoires are logged and standardized.

Behavioral repertoire

The ABH predicts a positive relationship between brain size and behavioral repertoire, as for both social and asocial learners larger brains can store and manage more adaptive information leading to a larger set of flexible behaviors.

Overall, our analyses did not support this prediction, as we did not find evidence for a positive relationship between our measures of behavioral complexity and brain size. The effect of the combined cognition measure (summed from cognitive repertoire from lab studies and social behaviors in the wild) was centered around 0 (-0.02 [-0.19, 0.18]). Defense repertoire was also centered around 0 (-0.01 [-0.24, 0.23]). Conversely, the estimate for foraging repertoire was somewhat negative (-0.10 [-0.32, 0.15]). (Figure 4c).

Therefore, our proxies for behavioral complexity did not show a consistent effect on brain size. This contradicts both our predictions and previous findings of links between behavioral complexity and brain size in other species[8,79]; c.f.[6]. However, as these variables had large amounts of missing data and biases in the distribution of observed behaviors across species, our findings are not conclusive. The need for additional research, in the lab and especially in the wild, is discussed below in the context of overall limitations of the current study.

Summary

	m.meandepth	m.benth	m.dhab	m.phab	m.soc	m.smmean	m.hunt	m.def	m.cog	average
Intercept estimate	-0.335	-0.406	-0.29	-0.218	-0.306	-0.384	-0.316	-0.261	-0.346	-0.318
Intercept 95% CI	-1.449 to 0.806	-1.564 to 0.768	-1.431 to 0.831	-1.345 to 0.933	-1.455 to 0.838	-1.537 to 0.766	-1.653 to 0.789	-1.39 to 1.014	-1.523 to 0.844	
ML estimate	0.658	0.672	0.661	0.667	0.639	0.659	0.682	0.66	0.677	0.664
ML 95% CI	0.499 to 0.812	0.511 to 0.833	0.499 to 0.82	0.51 to 0.819	0.473 to 0.797	0.451 to 0.854	0.514 to 0.838	0.501 to 0.816	0.525 to 0.818	
WoS estimate	0.218	0.134			0.256	0.143				0.188
WoS 95% CI	0.045 to 0.396	-0.031 to 0.304			0.081 to 0.44	-0.082 to 0.351				
Articles read estimate			0.216	0.128			0.239	0.217	0.183	0.197
Articles read 95% CI			0.003 to 0.417	-0.071 to 0.338			0.063 to 0.436	0.035 to 0.404	0.015 to 0.361	
Benthic estimate	0.481	0.577	0.407	0.39	0.48	0.513	0.398	0.382	0.441	0.452
Benthic 95% CI	0.002 to 0.964	0.075 to 1.065	-0.126 to 0.919	-0.102 to 0.896	-0.004 to 0.962	-0.016 to 1.044	-0.091 to 0.889	-0.124 to 0.889	-0.054 to 0.942	
Mean depth estimate	-0.221		-0.266	-0.311	-0.227	-0.282	-0.245	-0.25	-0.233	-0.254
Mean depth 95% CI	-0.382 to -0.062		-0.448 to -0.086	-0.491 to -0.128	-0.39 to -0.067	-0.466 to -0.097	-0.417 to -0.071	-0.42 to -0.083	-0.393 to -0.075	
Combined cognition estimate									-0.02	-0.020
Combined cognition estimate 95% CI									-0.194 to 0.174	
Defense repertoire estimate								-0.009		-0.009
Defense repertoire 95% CI								-0.244 to 0.23		
Diet breadth estimate			-0.093							-0.093
Diet breadth 95% CI			-0.463 to 0.314							
Diet breadth:benthic estimate			0.132							0.132
Diet breadth:benthic 95% CI			-0.273 to 0.516							
Foraging repertoire estimate							-0.096			-0.096
Foraging repertoire 95% CI							-0.323 to 0.146			
Mean lifespan estimate						-0.032				-0.032
Mean lifespan 95% CI						-0.277 to 0.221				
Mean age at maturity estimate						0.183				0.183
Mean age at maturity 95% CI						-0.073 to 0.392				
Predator breadth estimate				0.036						0.036
Predator breadth 95% CI				-0.183 to 0.246						
Predator breadth:benthic estimate				0.241						0.241
Predator breadth:benthic 95% CI				-0.102 to 0.537						
Mean latitude estimate			0.076	0.086		0.046	0.075	0.066	0.039	0.065
Mean latitude 95% CI			-0.081 to 0.23	-0.058 to 0.227		-0.102 to 0.192	-0.064 to 0.213	-0.075 to 0.206	-0.101 to 0.172	
Sociality estimate					-0.215					-0.215
Sociality 95% CI					-0.578 to 0.168					

(a)

Predictor	Estimate	95% CI
Maximum age maturity	0.27	-0.26 – 0.83
Sociality	-0.29	-0.74 – 0.19
Benthic habitat	0.24	-0.21 – 0.68
Predator breadth*benthic habitat	-0.26	-0.79 – 0.27
Maximum depth	-0.21	-0.43 – 0.02

(b)

Table 2. (a) Coefficient table of mean estimates and 95% CIs for variables (rows) and corresponding models (columns). It should be noted that the 'average' column is mean of posterior means of all models and coefficients should not be interpreted equivalently across models and the meaning will differ depending on included covariates (see code for DAG in Supplementary Information). Remaining coefficients and models are in Supplementary Table 1. (b) Mean estimates and 95% CIs of brain size for main predictors using species with multiple brain/body measurements.

In summary, our findings are inconsistent with social theories of brain evolution[13,18], 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 with what has been theorized for and received some support among the aforementioned social vertebrates[1,5], age at sexual maturity did not show a consistent positive effect. This suggests that the length of the juvenile period is not a factor in the evolution of cephalopod brains.

Our findings are consistent with 'ecological' theories of brain size evolution (e.g.[7,8]), including formal models, such as the models from which the ABH was derived, which incorporate ecology. In particular, depth and habitat appeared to be reliable predictors of brain size, with shallower-living and benthic species tending to have larger brains. If we consider shallower and benthic habitats to be relatively more complex than deep sea and pelagic habitats, this is in line with the idea that environmental variability selects for greater cognitive capacities and larger brains[80]. This is indicated to some extent by studies of benthic and pelagic biodiversity; for instance, pelagic food webs tend to have lower species diversity than do benthic ones, possibly leading to greater specialization among benthic foragers[59,81]. We also found some support for levels of predation, measured through the breadth of predator taxa, as predicting larger brains, consistent with some previous evidence with fish[82], as well as overall theorizing on selection for behavioral flexibility and intelligence in cephalopods concurrent with their evolutionary loss of defensive hard shells[53,83]. 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[56,80].

However, our measure of predator breadth suffers from missing data, overgeneralization of taxonomic categories, and difficulty with accurate measurements for many species. 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[7,84]. While our results similarly support some aspects of the cognitive buffer hypothesis[85], i.e. selective pressures for cognitive ability from a variable environment, this predicts that large brains will preferentially be selected in longer-lived species[34], 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.

Limitations and future directions

One limitation of this analysis is the sparsity of cephalopod data overall and 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 should be interpreted with this in mind.

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[66] and Maddock and Young[52,65,66] (updated by Nixon & Young[52,65,66]), with the inclusion of a few more recent brain analyses (Chung et al.[86,87], Montague et al.[88]), 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. Still, research effort did weakly predict larger brains in our statistical models (Table 2a).

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 analyses on the 36 species in our dataset with additional (one or two) brain and mantle length measures, also using the consensus phylogeny. For these species, the two alternate CNS and ML measures were averaged, or if only one alternate measure was available that was used. The results of these analyses are summarized in the table above. The results are largely consistent with the estimates from our main analyses, with overall positive effects for maximum age at sexual maturity and benthic habitats and overall negative effects for sociality and maximum depth, although the 95% CI include 0 in all cases and the estimates are closer to 0 (around +/-0.25 for all predictors) (Table 2b). The only effect in an opposite direction from our main analyses is the model interacting predator breadth and benthic habitats, which has a primarily negative instead of a positive estimate. Future research using additional reliable and comparable brain data, both for the species in the current dataset and other species without current brain measurement data, should provide additional insight into processes of brain evolution across the cephalopod family tree.

Additionally, although there is extensive behavioral data on a few species, especially the common octopus (*Octopus vulgaris)* and common cuttlefish (*Sepia officinalis*), similar data are lacking for the majority of species. Our measures of ecological and behavioral complexity based on field observations may also not have accurately represented the actual distribution of such behaviors across different species. For instance, among species with available data, our measure of diet breadth (count of taxonomic categories found to be eaten by a particular species) did not correlate strongly with our measure of hunting/foraging behaviors (0.15, $p = 0.41$). Similarly, defense repertoire was not significantly correlated with breadth of predator taxa (-0.38, $p = 0.15$). Although we controlled for research effort, this might not have been sufficient to account for the

extent to which variables like diet breadth, number and variety of predators, foraging strategies, and other behaviors were simply not described in the literature for a large proportion of species in our dataset. There are also biases in the types of observations; as noted above, there are numerous lab studies explicitly on learning capacities and other behaviors in certain species while others had a large amount of literature primarily on fisheries or other topics not related to cognition or behavior. However, this is an issue with any large database project using secondary data not originally collected on topics related to the focus of the database. Collecting all the relevant data needed here would be impossible for any research group.

Our findings contrast with the link shown by previous research between sociality and brain size among primates and other vertebrate species such as birds. That said, there is much we have to learn about the dynamics of social interactions in extant cephalopod species, such as the communication systems of various squid species[89] and social tolerance towards conspecifics at clustered den sites among some octopus species[90]. Our results also did not indicate that a longer juvenile period, which in other species is associated with a period of social learning from parents and conspecifics, predicted a larger brain among cephalopods, which usually die after mating, usually between one and three years of age, and do not engage in parental care. The life history of most cephalopod species is distinct from that of mammals, with a generally greater proportion of their (much shorter) lives spent in a pre- or non-reproductive adulthood stage[91] and reproduction coinciding with the start of senescence. Rather than interacting with or learning from conspecifics, cephalopods spend this period primarily avoiding their numerous predators. Therefore, the theoretical framing of the links between the juvenile period, sociality, and brain size in other taxa is not easily transferable to cephalopods.

While our analyses did not support a clear association between larger brains and behavioral complexity, as captured through cognitive measures, conspecific interactions requiring various forms of social cognition, and hunting and defense behaviors, the data for these variables are sparse and require further research in the lab and field. As our analyses used whole brain size as the focal outcome, they also 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[92,93]. Among cephalopods, this includes research on relative lobe size and how these link with ecological factors[52,65,66]. We did find support for effects of ecological variables, particularly habitat and depth, and this likewise should be an avenue for further research that could produce more precise results.

Cephalopods, then, provide a unique comparison to the taxa that have most often been the subject of comparative brain evolution studies[54,70]. In addition to focusing on a previously neglected group in this literature, our study evaluates – and finds broad support for – predictions explicitly derived from the ABH model - a general theory for the evolution of expanded brains and intelligence[38]. Modeling is essential to theory development for the study of complex systems[94], and should accompany data collection and collation as we continue to research the evolution of diverse intelligences across the animal kingdom. Although the ABH is a general theory not designed specifically for cephalopods, it offered reasonable testable hypotheses for the present study, but because the underlying mathematical model was never designed with non-vertebrate, let alone cephalopod, life history in mind, further models are needed to move us toward a general theory of brain evolution. The next step toward a fully general theory and

theoretical framework of brain evolution[95] would also need to model and test the evolution of brains in insects, which represent approximately half of animal biomass[96].

Methods

Data collection

Brain and body size data were taken mainly from Wirz[66] and Maddock and Young[65], updated by Nixon & Young[52], combined with a few newer species-specific brain data estimates[86–88,97,98]. 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[50,52,99–102];[52].

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 on 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), gregarious (usual or obligate schooling), or tolerant/aggregative (an in-between category with individuals sometimes observed as congregating outside of reproductive contexts and appearing tolerant of closeby individuals). 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* [103], an interface to the probabilistic programming language *Stan* [104]. They generally follow the operationalization of Bayesian multilevel regression models from McElreath[105] as implemented in brms by Kurz[106]. 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[107]. 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

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[108] using sequence data from GenBank[109]. 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[110,111], 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*[112] is shown on the consensus phylogeny in Figure 5. Relative brain size is somewhat phylogenetically conserved, with larger measures appearing among the incirrate octopuses and cuttlefish.

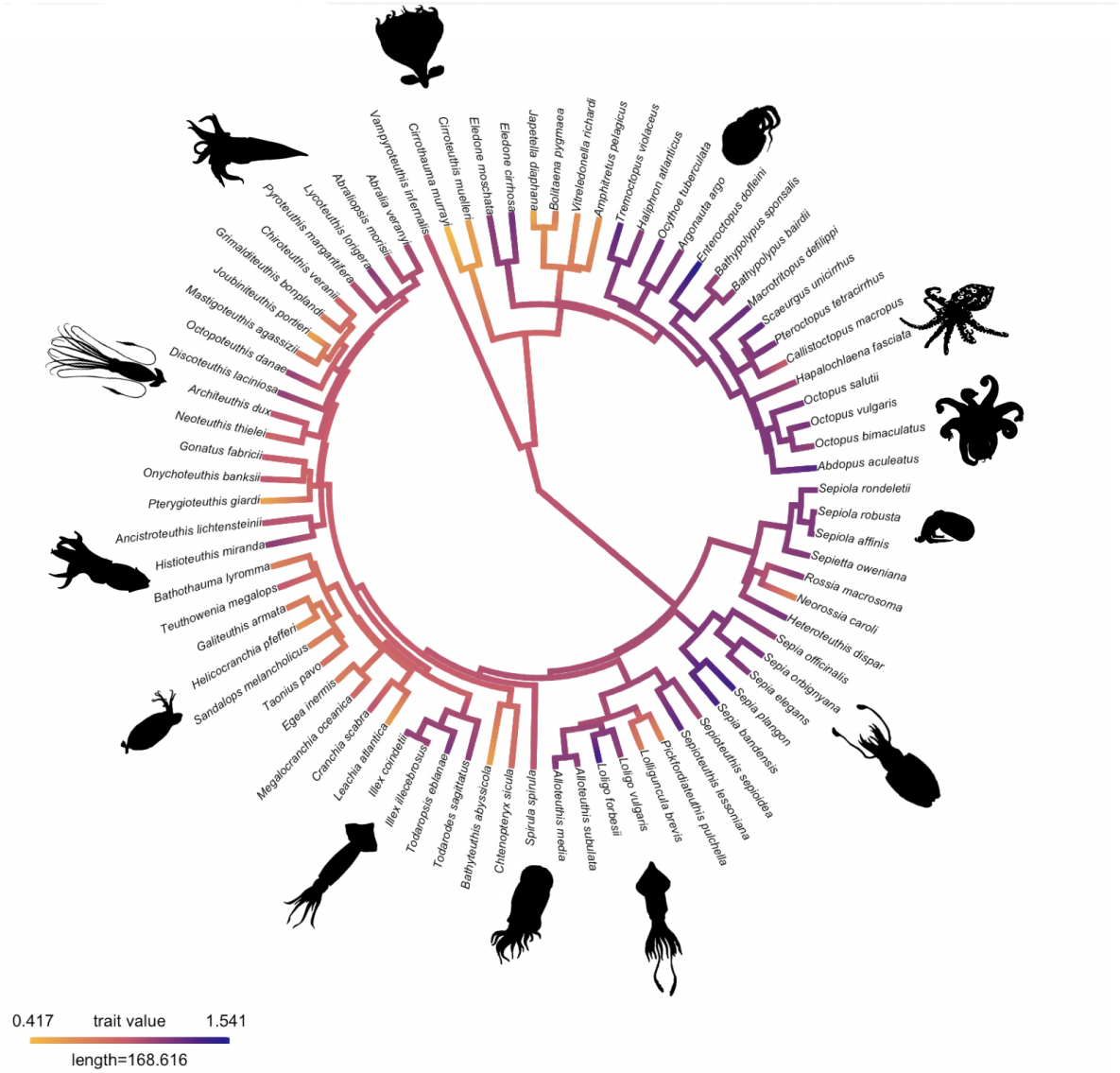


Figure 5. Ancestral state reconstruction of relative brain size (CNS/ML) on a log scale. Images from phylopic.org (Keesey 2024).

Author contributions

KB: Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration
TB: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration
AL: Conceptualization, Methodology, Validation, Investigation, Data curation, Writing – review & editing, Visualization, Project administration
NG: Investigation, Data curation
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JO: Investigation, Data curation
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MM: Conceptualization, Methodology, Validation, Software, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition

Data Availability
Analysis code and data are openly available at www.github.com/kcbasava/ceph-brain-evolution. The pre-registration document can be found at www.osf.io/5dyfz.

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