

The social and cultural roots of whale and dolphin brains

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Encephalization, or brain expansion, underpins humans' sophisticated social cognition, including language, joint attention, shared goals, teaching, consensus decision-making and empathy. These abilities promote and stabilize cooperative social interactions, and have allowed us to create a 'cognitive' or 'cultural' niche and colonize almost every terrestrial ecosystem. Cetaceans (whales and dolphins) also have exceptionally large and anatomically sophisticated brains. Here, by evaluating a comprehensive database of brain size, social structures and cultural behaviours across cetacean species, we ask whether cetacean brains are similarly associated with a marine cultural niche. We show that cetacean encephalization is predicted by both social structure and by a quadratic relationship with group size. Moreover, brain size predicts the breadth of social and cultural behaviours, as well as ecological factors (diversity of prey types and to a lesser extent latitudinal range). The apparent coevolution of brains, social structure and behavioural richness of marine mammals provides a unique and striking parallel to the large brains and hyper-sociality of humans and other primates. Our results suggest that cetacean social cognition might similarly have arisen to provide the capacity to learn and use a diverse set of behavioural strategies in response to the challenges of social living.

Many apparently intelligent and encephalized animals are social¹. The social brain hypothesis (SBH)², originally developed to explain large brains in primates, argues that large brains are an evolutionary response to complex and information-rich social environments. The 'cognitive'³ or 'cultural' niche⁴ has allowed humans to colonize almost every terrestrial ecosystem. Whales and dolphins (cetaceans) have the largest nervous systems of any taxonomic group, and rank highly on every putative measure of neuroanatomical complexity⁵. Many cetaceans are also organized in hierarchical social structures and display an astonishing breadth of cultural and prosocial behaviours, providing a rare parallel to humans and other primates in terms of social, behavioural and neuroanatomical complexity⁵. However, as yet, there is little evidence for associations between large brains, social structures, and social and cultural behaviours in cetaceans.

Large-brained cetaceans may both be adapted to the challenges of living in and maintaining sophisticated social structures and benefit from the advantages of access to other members of their group. Cetaceans show overwhelming evidence for sophisticated social and prosocial behaviour⁶ (including complex alliance relationships⁷; social transfer of hunting techniques⁸; cooperative hunting⁹; complex vocalizations including regional group dialects¹⁰, vocal mimicry¹¹, and 'signature whistles' unique to individuals¹²; interspecific cooperation with humans¹³ and other species¹⁴; alloparenting¹⁵; and social play¹⁶), but the many scattered reports of these behaviours have never been collated across species. Collating information from the literature across species to develop an index for behaviours such as innovation, new behaviours and socially complex behaviours has been used to relate behavioural differences to brain size in both birds^{17–21} and primates^{22–25}, but such an exploration has not yet been attempted for the cetaceans.

Results and discussion

To evaluate the extent to which cetacean brains are social, we compiled a comprehensive dataset for body mass, brain mass

(Fig. 1a), group size and social organization characteristics (see Supplementary Table 1 and Supplementary Fig. 1). First, we tested for the most straightforward evidence for the SBH by examining both a linear and a quadratic relationship between log group size and brain size controlling for body size (we also present the results for log brain size, residual brain size and encephalization quotient (EQ) in the Supplementary Information) using phylogenetic generalized least-squares analysis, by implementing the 'gls' function in the R package 'nlme'²⁶, with a Pagel correlation structure. To evaluate the impact of phylogenetic uncertainty, we estimated model parameters using model averaging (AICcmodavg²⁷) over 1,000 candidate trees²⁷; we also present model summary statistics using the consensus tree. We evaluated the relationships between the independent variables of body size and indices of sociality (linear, nonlinear and categorical) and brain size as the dependent variable. Brain size was not predicted by a linear relationship with group size but was predicted by a quadratic relationship (Table 1 and Supplementary Table 5). Because these results suggested that mid-sized groups have larger brain size, we then used a kmeans cluster analysis (Supplementary Fig. 2) to assign species into social categories based on mean reported group size. These classifications may be informally characterized as (1) ephemeral aggregations (individuals are usually observed alone, but can aggregate at food sources or during migration), (2) mid-sized associations, and (3) large groups (or 'mega-pods') of dozens to hundreds of individuals (see Methods). We found that these social categories were also strongly associated with log brain size (as well as other brain measures, except EQ; Table 1, Fig. 2a and Supplementary Fig. 6). Cetaceans found in mid-sized social groups had the largest brains (in both absolute and relative terms), followed by those that form large communities (mega-pods); those predominantly found alone or in small groups had the smallest brains. We also evaluated EQ because it is often used in investigations of cetacean brain evolution^{28,29}, but our analyses contribute to a growing body of research

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suggesting that EQ does not provide results congruent with other brain size measures³⁰.

The relationship that we observed between social structure and brain size suggests that social cognition may play a key role in cetacean encephalization. To this end, we systematically and exhaustively searched the literature for examples of sophisticated social behaviour in cetaceans, creating a ‘social repertoire’ score by cataloguing the presence of within-group alliances, caregiving or alloparenting, interspecific cooperation, group hunting, social defence, social play, social learning and complex vocalizations for each species. Because these data are based on observations made in the field and in captivity, there is inevitably variation in the reliability and reproducibility of the reports. Although we ultimately made all data binary (a species either had been observed to exhibit a given behaviour [1] or had not [0]), in Supplementary Table 2 we have linked each behaviour to all independent empirical reports (if more than a single report exists). In this way, a sense of the replicability of each behaviour can be obtained by examining the number of accompanying references. Whereas certain behaviours have been reported only once to date and remain controversial, others (such as humpback whale song transmission) have been confirmed many times and can be considered established facts. Although it is crucial to keep in mind the variable reliability of each behaviour, we reasoned that trying to quantify this variability and incorporate it into our models would only have exacerbated the problem by introducing subjective assessments or other sources of bias (see Methods and specifically Supplementary Table 2 for further details of our search strategy and criteria).

We next used a principal components analysis to reduce the social repertoire scores to a single axis that explained 70% of the total variance (Supplementary Fig. 3). Of course, absence of evidence for social behaviours in a given species may reflect a lack of research effort rather than a true absence of such behaviours. We therefore controlled for research effort in two ways: first, by assessing the number of papers in the *Zoological Record* for each species and incorporating the \log_{10} publication number as a factor in our analyses; and second, by correcting the social repertoire score by taking the residuals from a phylogenetic regression of social repertoire and research effort (termed ‘corrected social repertoire’ visualized for all species in Fig. 1b). This corrected social repertoire score was highly correlated with the raw social repertoire score ($r=0.82$, 95% CI 0.70–0.90, $t=9.60$, $P<0.001$). We then examined (i) whether the corrected social repertoire score differed between species, and (ii) the relationships between social structure, corrected social repertoire score and brain size.

Corrected social repertoire score was significantly associated with brain size controlling for body size, with absolute brain mass and with residual brain size (Fig. 1c, Table 2 and Supplementary Table 6). These findings suggest that the relationship between social structure and brain size is partly driven by increasing social-behavioural flexibility: a diverse repertoire of social behaviours pays the greatest dividends when all individuals are recognizable to one another and interact regularly. These conditions are met when groups are cohesive and predictable. It is therefore reasonable that our results show that large relative brain size, cohesive social bonds, and broad social repertoires tend to co-occur in the same species.

In primates, non-social ‘ecological’ factors, such as home range size, high-energy diets^{31,32}, or the diversity of food sources and foraging skills, are also associated with brain size^{31,33}, most plausibly because of the strong energetic requirements involved with metabolically supporting a large brain³². Encephalization in cetaceans appears to have begun millions of years after the transition and adaptation to an aquatic environment^{34,35}, suggesting that secondary changes in ecological flexibility within cetaceans could be associated with large brain size. We collated reported diet items (see Supplementary Table 1; details in Methods) as a measure of

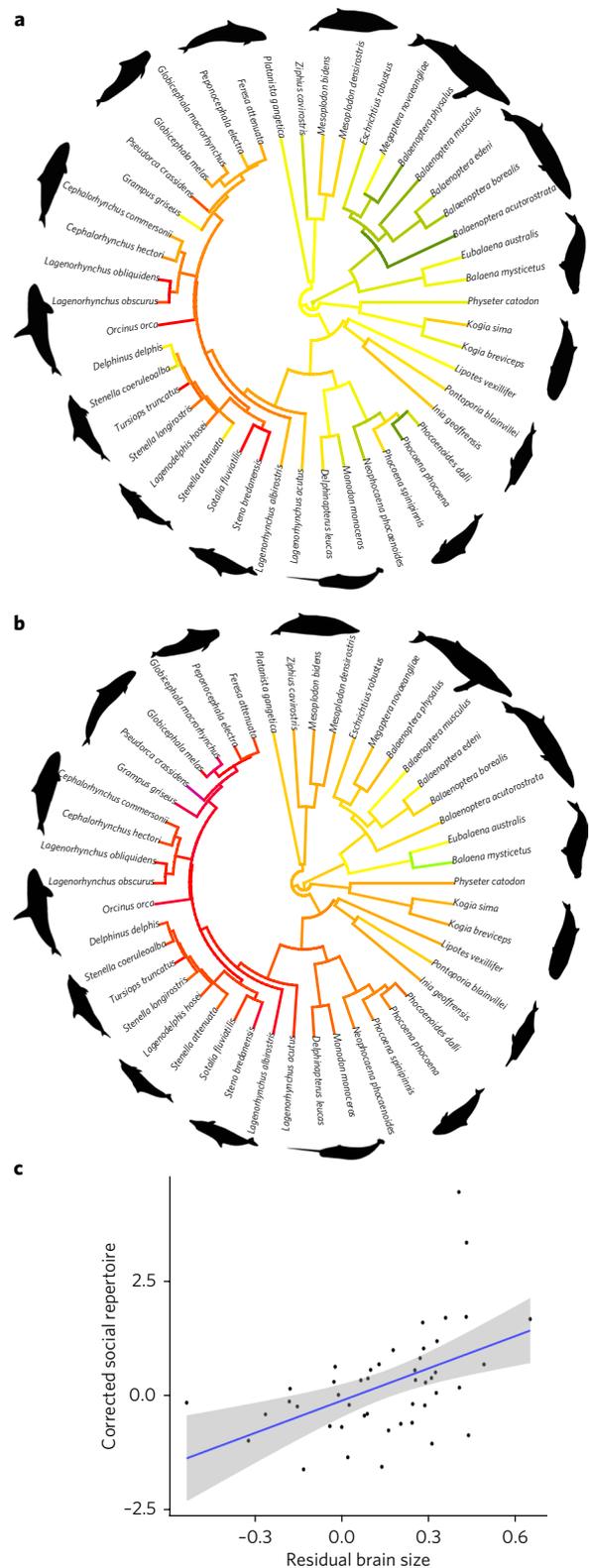


Fig. 1 | Distribution of residual brain size and social repertoire scores.

a, Residual brain size; **b**, corrected social repertoire scores across cetaceans. Red corresponds to large brain size or high social repertoire score, and green to low values. **c**, Scatterplot of the relationship between corrected social repertoire size and residual brain size ($n = 46$). The estimated value of λ (0.18) for the corrected social repertoire score was significantly different from both a Brownian motion model ($\chi^2 = 36.91$, $P < 0.001$) and a non-phylogenetic model ($\chi^2 = 3.69$, $P = 0.03$). Credit: silhouette images, Chris Huh.

Table 1 | The relationship between measures of sociality and absolute cetacean brain size, controlling for body size in 46 species of cetaceans. Body size, brain size and group size are all \log_{10} -transformed. Pagel's lambda refers to the estimated degree of phylogenetic autocorrelation derived using maximum likelihood

Variable	Factor		λ^a	Estimate ^a	CI ^a	F ^b	P ^b
Brain size	log group		0.88	-0.006 ± 0.02	$-0.04, 0.03$	0.18	0.67
	Body size			0.46 ± 0.04	0.39, 0.53		
Brain size	Quadratic log (group size)	log group size	0.70	0.42 ± 0.06	0.15, 0.40	9.86	<0.001
		$(\log \text{ group size})^2$		-0.04 ± 0.01	-0.06, -0.02		
Brain size	Social structure category	Mid-sized groups	0.86	0.42 ± 0.03	0.36, 0.48	204.07	<0.001
		Mega-pods		0.13 ± 0.08	-0.02, 0.28		
		Body size		0.05 ± 0.08	-0.11, 0.21		
				0.46 ± 0.04	0.38, 0.54	149.40	<0.001

Pairwise comparisons between a baseline category of ephemeral aggregations with mid-sized groups and mega-pods are reported. F-values are reported for the global term for social structure.

^aEstimates and confidence intervals (CIs) were estimated using model averaging over 1,000 phylogenetic trees; bold CIs indicate where the range does not extend past zero. ^bParametric analysis of variance (ANOVA) statistics are derived from a gls model using the consensus tree.

dietary richness. This measure was significantly associated with brain size controlling for body size, such that species with larger relative brain size had richer diets (Table 2 and Supplementary Table 6); absolute brain size alone did not predict dietary richness (Supplementary Table 6). Geographic (latitude) range also was marginally associated with relative brain size and strongly associated with absolute brain size (Table 2 and Supplementary Table 6), such that larger-brained species occur across a wider latitudinal range. That both dietary richness and latitude range are associated (albeit to a lesser degree) with brain size provides tentative evidence that large-brained cetaceans are more ecologically flexible.

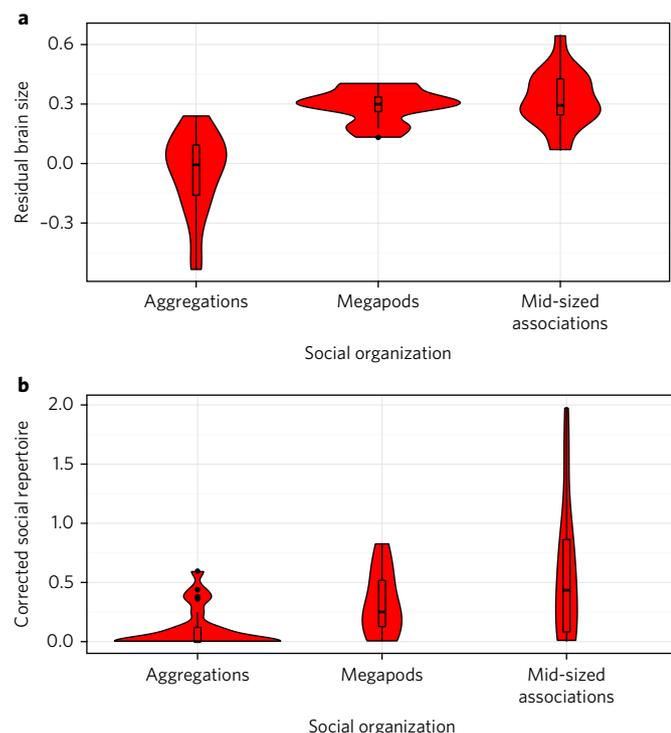


Fig. 2 | Mid-sized social groups are associated with larger brain size and higher social repertoire scores. a, Relationship between social structure and larger brain size (both absolute and residual); **b**, relationship between social structure and higher social repertoire scores ($n = 46$). Violin plot outlines represent relative density of points, internal boxplots show first and third quartiles, and the whiskers show the largest and smallest values within $1.5 \times$ of the 25th and 75th quartiles.

Thus, as is the case in primates³⁶, multiple traits are associated with cetacean brain size. Whereas univariate analyses are unable to disentangle relationships, multiple regression contains the ability to evaluate probable causality and indirect relationships. To disentangle the relationships between brain size, body size, social behaviour and ecology, we used a modified phylogenetic path analysis, whereby for each variable we evaluated all possible candidate models incorporating permutations of other variables apart from the variable of interest. The best-fit model for each variable was the one with the lowest Akaike information criterion (AIC) and fewest parameters (see Methods); all variables included in the 'best model' for each variable are connected by arrows in Fig. 3. Parameter weights were calculated by summing model weights over all models incorporating each parameter. The direction of causality was inferred by comparing model weights between each pair. Brain and body size predicted dietary richness and social repertoire score; brain size alone predicts latitude range, and brain size is best predicted by a quadratic relationship with group size (Fig. 3).

Our analyses demonstrate that cetacean brain evolution is best explained by the demands associated with maintaining and coordinating cohesive social groups and the advantages of living in such groups; social repertoire is broadest in species found in mid-sized groups with typically strong social bonds, and in those species with the largest brains. Although previous studies have identified links between brain size and sociality^{37,38} or social group size^{39,40}, few studies have evaluated the behaviours and cognition underpinning social living. Apart from anthropoid primates, a simple linear relationship between group size and relative brain size has not been found in most mammalian taxa³⁸. This suggests that the factors driving brain evolution in cetaceans are more complex than the mere number of individuals in the group. Our social repertoire score provides a window into the behaviours that are enabled by investment in cognitive architecture. Our investigation is similar to studies in birds^{17,18} and primates^{22–24} that also evaluate how behavioural repertoires are associated with encephalization. Although these studies have been criticized for providing correlative evidence for adaptive explanations of encephalization⁴¹, our study provides yet more evidence across taxa that brain, behavioural and social evolution are inextricably linked. Moreover, our results are consistent with theoretical models that predict how culture, behavioural richness and cognition are intertwined and can create a positive feedback loop or ratchet⁴²: larger brains can support a larger social repertoire and a larger repertoire can support a greater carrying capacity, potentially offering learners greater opportunity and variety for learning. A large social repertoire combined with sufficiently high-fidelity transmission between conspecifics could have triggered the emergence of the cumulative

Table 2 | Phylogenetic least squares regression for the relationship between absolute brain size, body size, corrected social repertoire, dietary richness and latitude range across 46 species. Body size and brain size are log₁₀-transformed

Variable		λ^a	Estimate ^a	CI ^a	F ^b	P ^b
Corrected social repertoire	Brain size	0.00	2.41 ± 0.78	0.88, 3.93	9.52	0.004
	Body size		-1.02 ± 0.28	-1.56, -0.469	-13.26	<0.001
Dietary richness	Brain size	0.00	1.36 ± 0.53	0.31, 2.41	6.49	0.01
	Body size		-0.49 ± 0.19	-0.87, -0.12	6.70	0.01
Latitude range	Brain size	0.95	71.76 ± 36.28	0.67, 142.86	9.19	0.04
	Body size		3.036 ± 19.44	-35.07, 41.15	0.02	0.88

^aEstimates and confidence intervals (CIs) were estimated using model averaging over 1,000 phylogenetic trees; bold CIs indicate where the range does not extend past zero. However, where the maximum likelihood lambda estimate was zero, all models are identical so the consensus estimates are given. ^bParametric ANOVA statistics are derived from a gls model using the consensus tree.

culture characteristic of the past few million years of human evolution. Our results corroborate previous work in cetaceans^{1,43} and other mammals^{37,44}, and demonstrate that the richness of cooperative social behaviours increases with brain size and group stability in whales and dolphins.

Our results are also consistent with behavioural richness emerging as an outcome of social learning (for example through social observation) and support the idea that the availability of socially acquired information in cohesive social structures is a component of social intelligence and general cognitive abilities in cetaceans, as in primates²³. Additional support for the notion that sharing of information may be an important component of cetacean social cognition comes from a recent study linking the complexity of cetacean social vocalizations (non-echolocative ‘whistles’) to sociality and mean group size⁴⁵. Moreover, the large proportion of auditory cortex in the cetacean brain⁴⁶ suggests that sociality, communication/vocalization ability and brain size may have all coevolved in the order Cetacea. This is consistent with information-based explanations for social cognition and complexity^{42,47}.

Various aspects of cetacean neuroanatomy corroborate our findings for the coevolution of brain size, social structure and social repertoire. An enormous proportion of neocortex is dedicated to audition and probably vocalization in cetaceans, especially in the highly social odontocetes⁴⁶, which possess more sonically complex social vocalizations than the less-social mysticetes⁴⁵. Cetaceans also show enlargement of the anterior insula and anterior cingulate cortex⁴⁸; social cognitive skills such as ‘mentalizing’—the ability

to imagine, predict and empathize with the mental states of others—have been hypothesized to rely critically on these regions⁴⁹. Taken together, these findings support the notion that cetacean neuroanatomy is geared toward, and has coevolved alongside, sophisticated social cooperation and coordination. The unique cytoarchitectural organization of cetaceans—especially the apparent absence of layer IV and less easily differentiable cortical lamination than in primates—has been used to argue against the possibility of sophisticated cognition in this order⁵⁰, as has evidence that adult neurogenesis is absent in cetacean brains⁵¹. Recent work, however, suggests that cetacean cytoarchitecture is more complex than initially thought⁴⁸ and may be characterized by unique neuronal morphological types⁵². Our results provide additional evidence that cetacean nervous systems—irrespective of any cytoarchitectural or neurophysiological idiosyncrasies that they may exhibit—are capable of supporting, and indeed are integral to, sophisticated social behaviour. The notions that adult neurogenesis or a typical six-layered cortical organization are prerequisites for complex social and cognitive behaviour^{50,51} may therefore need to be reconsidered. Another more recent critical view argues that large cetacean nervous systems serve a heat-production function, as an adaptation to life in a relatively cold aquatic environment⁵³. This ‘thermogenesis’ hypothesis has been compellingly refuted on both theoretical and empirical grounds^{54,55}, however, and our results provide further evidence against it.

In summary, cetacean social and brain evolution represent a rare parallel to those in humans and other primates⁴³. We suggest that brain evolution in these orders has been driven largely by the challenges of managing and coordinating an information-rich social world. Although these challenges may increase with group size, it is not group size itself that imposes the challenges. In both primates and marine mammals, structured social organization is associated with higher levels of cooperation and a greater breadth of social behaviours. Thus, we propose reframing the evolutionary pressures that have led to encephalization and behavioural sophistication to focus on the challenges of coordination, cooperation, and ‘cultural’ or behavioural richness.

Methods

Data acquisition. Data were collated from online databases (especially ref. ³⁶), three major marine mammal encyclopaedias^{57–59} and an extensive body of published primary research (see specific references in Supplementary Tables). All references are grouped by species in Supplementary Table 1 (brain mass, body mass, social organization and other basic variables) and Supplementary Table 2 (all examples of social and prosocial behaviours collated to create our ‘social repertoire’ score). Where multiple values were available for any given measure, the weighted mean was used.

Putative measures of sociality. We explored three putative measures of sociality: mean group size; ‘social structure’ (derived from observed group size; see below); and documented social and prosocial behaviours (‘social repertoire’). We aimed to go beyond simply using mean group size as a proxy for social complexity because of an expanding body of evidence that the reality of this relationship is far more

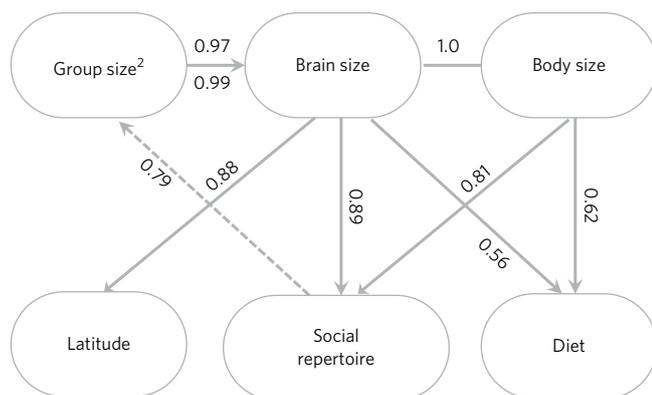


Fig. 3 | Model of likely relationships between brain size, behaviour and ecology in cetaceans. Paths were determined via a model selection approach using AIC. Parameter weights are on each of the arrows (the sum of weights for all models including each pair of variables; see Supplementary Information). Weights are reported for both linear (top) and quadratic (bottom) terms for group size and brain size, whereas the model between social repertoire and group size is linear. The dotted arrow from repertoire to group size suggests a feedback loop ($n = 46$).

complex than a simple linear relationship. For instance, the stability of social bonds has been shown to be more predictive of relative brain size than simple group size alone³⁸.

Mean group-size values were gathered from as many sources and independent sightings as possible, and were weighted by the number of observations or field sightings on which they were based (for example, if a given study reported a mean observed group size of 10 for a particular species, and this mean was based on dozens of field sightings, the mean was weighted proportionately to reflect the large number of sightings on which the values were based). Specific references for each species are provided in the main database (Supplementary Table 1). Mean group size was \log_{10} -transformed for all analyses.

All species ($N=90$) were classified into social structure categories using kmeans clustering of group size. To determine the optimal number of categories of social groups, we used an AIC scree plot (Supplementary Table 2) and 6 indices ('KL', 'CH', 'Hartigan', 'CCC', 'Scott' and 'Marriot'; see package for details) using the NbClust package in R (ref. ⁶⁹). The scree plot and four out of six indices all supported three as the optimal number of clusters. Although the terms that we might use to label these clusters are subjective, we believe that a reasonable nomenclature for the three clusters could be described as follows: 1 = solitary/small/ephemeral aggregations (that is, individuals are often spotted alone, or in frequently changing associations or temporary aggregations during migrations or at food sources); 2 = mid-sized associations (often described as regular associations between dyads or small groups that extend beyond simple and usually temporary mother-offspring pairs; and 3 = large groups or 'mega-pods' (large groups of animals (>50) regularly observed together at the same time in field observations).

In order to collate data not just on social structure per se (that is, whether a species tends to be solitary or to coalesce in socially cohesive groups), but also on prosocial behaviour of various kinds (such as cooperative group hunting or social transfer of knowledge), we exhaustively searched the literature for examples of such behaviours in every species, using review papers on cetacean culture and sociality^{61,62}, three major marine mammal encyclopaedias^{57–59} and the citations lists of the *Zoological Record* online archive. After consulting all of these sources, additional searches were conducted using Google Scholar (<http://scholar.google.com>), examining titles and abstracts of the first 200 results that appeared using a search string specifically focused on social and prosocial behaviours, specific to each species (for example, for *Sousa teuszii*, the search query would be alliances OR caregiving OR alloparenting OR cooperative OR cooperation OR play OR social OR language OR teaching OR vocalizations OR whistle OR hunting "*Sousa teuszii*"). When the title or abstract suggested that the report was of relevance to our study, the text was consulted in detail.

We included not only 'prosocial' behaviours in the narrow sense of behaviours that benefit others at a cost to the individual, but rather all behaviours that might assist in forming alliance relationships or indicate cooperation for mutual benefit, or potentially even for altruistic purposes. We classified all relevant published findings into one of eight categories: (i) alliance formation (for example, males cooperating to take turns in positioning a female for copulation); (ii) caregiving behaviour (for example, pushing an injured conspecific to the surface to breathe) and/or alloparenting (for example, allomaternal babysitting or nursing of calves); (iii) interspecific cooperation (for example, cetacean species cooperating with human fishermen in a mutually beneficial fashion); (iv) cooperative group hunting (for example, coordinated 'bubble-net' fishing by humpback whales (*Megaptera novaeangliae*)); (v) social defence from predators (for example, coordinated 'rosette' patterns adopted by sperm whales (*Physeter macrocephalus*) to protect calves against predation from orcas); as 'clumping' or grouping may be an incidental (non-prosocial) response to predation, only cases in which species adopted clear-cut coordinated patterns of social defence were included; (vi) social play behaviour (for example, social play among conspecifics); (vii) social transfer of behaviour or information (for example, horizontal transfer of 'songs' among humpbacks (*Megaptera novaeangliae*), or vertical transmission of migration routes among belugas (*Delphinapterus leucas*)); and (viii) complex vocalizations (for example, vocal imitation of humans, conspecifics or other species; evidence for individual-specific 'signature' whistles; evidence for group-specific vocal 'dialects').

All data were entered in a database (Supplementary Table 2). To quantify results for statistical analyses, we tallied one point for each distinctive behaviour falling into any of these eight categories, based on published, peer-reviewed research. Each behaviour (for example, a particular form of cooperative hunting) could only be awarded a single point within a category; multiple published observations of the same behaviour were included in the database for reference purposes, but did not increase the total score for that behaviour. Similarly, each category was limited to a total score of three (3) points, so that if a species had a high facility within a certain range of social or prosocial behaviour (or, relatedly, if such a form of behaviour had been intensively researched and therefore many varying examples had been reported in the literature), this could not unduly affect the overall social repertoire score for a given species. With eight categories, this resulted in a maximum social repertoire score of 24, although no species approached this maximum. In all analyses of social repertoire, 'research effort' (number of published reports per species) was controlled for, to mitigate the attention given to certain species over others (further details below).

'Ecological' theories of intelligence and brain evolution posit that environmental factors may be a major driver of brain size. Two of the most

prominent examples from primate research are dietary richness and geographical range^{44,63}: species inhabiting a wide range of environments imply the need to map larger spatial ranges and also a greater diversity of environments to which the species must be able to adapt. Dietary richness refers to the number of different prey types or foodstuffs that a species consumes, and therefore the number of potentially differing predation or foraging strategies (respectively) that the species must be able to execute. To test the hypothesis that these factors may be predictive of large brains in cetaceans, we sought to test variables analogous to the 'behavioural ecology' variables used in studies of encephalization in primates and other mammals^{44,63,64}. We therefore compiled data on geographical range (indexed by observed latitude range in degrees) and dietary richness for all cetacean species. Latitude range was used as a measure of geographical range and environmental/habitat complexity in the absence of more detailed measures: although a given group or member from a species is unlikely to inhabit the entire range, ecological hypotheses would predict that the species' brain must be adaptable and complex enough to inhabit environments as varied as tropical and arctic waters (in the case, for instance, of the most wide-ranging species, such as blue whales (*Balaenoptera musculus*) or orcas (*Orcinus orca*)).

For dietary richness, we followed numerous marine mammal researchers and encyclopaedias in dividing prey species into four basic types: invertebrates, cephalopods, fishes and 'other' (including marine mammals). Each cetacean species was assigned a dietary richness score of 1–4 based on how many of these categories constitute its known prey. We relied on many published sources for this data, but in particular refs ^{56,59}. In primates, the difficulty in locating ephemeral food sources or in extracting the edible portions has been proposed as a driver of encephalization^{32,65}. We followed similar logic here: the hunting of diverse classes of prey (for example, surface feeding on swarms of zooplankton versus hunting other highly intelligent marine mammals, including other cetaceans in some cases) evidently requires knowledge, and sometimes learning, of disparate and occasionally complex foraging and predation strategies. The benefits of a diverse array of feeding strategies and prey types may therefore have influenced encephalization: small (relative) brain size may have constrained the number and/or novelty of foraging or predation strategies, favouring enlarged brains as a means of increasing access to diverse food resources requiring correspondingly diverse cognitive-behavioural strategies for their procurement. All data on these two variables are summarized in Supplementary Table 1.

Statistics. One approach to evaluate the richness of the social repertoire of different species would be to sum all occurrences of behaviours of interest. However, there is no a priori reason that all behaviours co-evolve across the phylogeny. Therefore, to determine whether the behaviours could be reduced to fewer explanatory variables, we used a polychoric principal components analysis (PCA), which infers a latent Pearson correlation and thus allows for dichotomous variables⁶⁶. This was executed in the R 'psych' package⁶⁷, using the 'polychoric' function to find the correlation matrix, then extracting principal components analyses using the 'principal' function and finally using the 'factor.scores' function to extract species-specific social repertoire scores. All categories besides 'social defence' loaded onto the first factor and were retained in the analyses. This first factor explained 70% of the variance in the data (Supplementary Table 3).

Research effort (the amount of time and resources dedicated to study of a given species) is a potential confound. To control for research effort, we tabulated the number of studies reporting on a given species, as indexed in the online archive of the *Zoological Record* (1864 to present; see Supplementary Fig. 4 for histogram). We included all publications that included the species, rather than a subset (such as publications on behaviour or biology). Our goal was to avoid any bias on our part in the subset search terms we chose. Thus, our measure captured research effort of any kind and not just how interesting a given species is to behavioural researchers. The correlation between our final social repertoire score and research effort was weak ($r=0.25$, $P=0.07$). Species with no known examples of social or prosocial behaviour, but also <50 publications in the *Zoological Record*, were not included in the social repertoire analysis (with relatively little research conducted, it seemed imprudent to conclude that a species engages in no social/prosocial behaviours; these excluded species are indicated by grey shading in Supplementary Table 2). Conversely, if a species showed no examples of social/prosocial behaviour, but did have ≥ 50 publications in the *Zoological Record* archive, we included it in our analysis, with an overall social repertoire score of 0. Here, we assumed that if a reasonable amount of research (50 or more studies) has yielded no reports whatsoever of social/prosocial behaviours, the species is indeed likely to engage in little such behaviour. Resulting scores were standardized so that the minimum was zero and then adjusted for research effort by dividing by the \log_{10} of number of research papers identified. We also incorporated research effort as a covariate in analyses to avoid potential statistical issues with ratios. We chose this approach rather than taking residuals from a regression of social repertoire against research effort as residuals are problematic for ecological data: using residuals results in biased parameter estimates⁶⁸.

Controlling for brain–body allometry. Brain size scales with body size in a predictable allometric relationship⁶⁹, which suggests that a scalable component of brain size represents increasing demands on the control of metabolism and coordination as body size increases. To control for these non-higher cognitive aspects of brain size, an EQ (ref. ⁶⁹) is commonly used for understanding variation in cetacean brains⁶⁹. An alternative approach to partial out the effects of allometry, whereby brains necessarily increase with body size, is to take residuals from a linear regression between brain and body size. These residuals identify where brains are larger than expected for a given body size (positive residual) and where they are smaller than expected (negative residual). However, the relationship between brain size and body size in cetaceans is strongly nonlinear even after log-transforming each variable (see Supplementary Fig. 5). Brain size residuals taken from an ordinary least squares (OLS) regression can penalize small-brained species as OLS can underestimate the slope (and overestimate the intercept) where both x and y have measurement error (in this case, error is expected to occur in measures of both brain and body size). Moreover, because species are not independent, it is questionable whether a phylogenetic regression should be used, but these are also conservative. Because EQ is a ratio, it can often have a right-skewed distribution. A preferable option is to incorporate body size as a covariate in the analyses, which avoids the issues mentioned above. That said, empirical data from primates suggest that absolute brain size, rather than any relative measure, is a better predictor of cognitive performance^{1,30,64}. To demonstrate the impact of brain measures on the results, we present the results for brain size + body size, absolute brain size, EQ and residual brain size.

Disentangling multiple relationships. Incorporating multiple variables creates issues with whether there are direct or indirect relationships between variables of interest. For non-phylogenetic data, it is possible to use confirmatory path analysis⁷⁰. However, incorporating this approach with comparative data requires a new framework. One approach has been suggested⁷¹ in which one tests for conditional independencies between pairs of data. This approach has two shortcomings for complex datasets. First, it requires a clear decision about causality relationships between variables. Second, as the number of variables increases, so does the number of candidate models in a factorial way. Thus, either a subset of candidate models need to be identified a priori or the number of variables needs to be constrained in small datasets. As we have a relatively large number of variables, we opted to use an alternative, but related, approach to identify conditional independencies. For each variable, we used an information criterion approach and selected the model with the lowest AIC. Where model fit was indistinguishable (that is, the difference in AIC between best-fit models was <2 ; see ref. ⁷²), we selected the model with the fewest parameters. We then calculated model weight in order to estimate the relative importance of each variable based on AIC differences⁷². The relative weight of evidence for each candidate model was calculated by:

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\text{AIC}\right)}{\sum \exp\left(-\frac{1}{2}\Delta_i\text{AIC}\right)}$$

where w_i is the weight for each model, and $\Delta_i\text{AIC}$ for each model is the difference between each model and the best-fit model identified. For variable weights, we summed weights over all models including each variable in turn. This approach is similar to the comparison of AIC in conditional independence path models, except that here we have not constrained the candidate models, as we had neither good a priori reasons to choose a subset nor a clear hypothesis for directionality—both of which are critical for the conditional independence approach.

Cetacean phylogenetic tree reconstruction. We downloaded both the cetacean consensus tree and a 1k tree block from the 10kTrees website (www.10kTrees.harvard.edu). To quantify phylogenetic signal in our ‘social repertoire’ score, we used the ‘fitContinuous’ function in the ‘geiger’ package⁷³ in R to calculate the maximum likelihood value of Pagel’s lambda (λ)^{74,75}. A value of λ approaching 1 is consistent with a Brownian motion model of evolution, whereas a value of 0 suggests independent trait evolution⁶⁸. We used a likelihood ratio test to compare the maximum likelihood lambda model inferring no phylogenetic signal ($\lambda = 0$) and Brownian motion ($\lambda = 1$). The LR test follows a chi-squared distribution, with one degree of freedom.

Phylogenetic regression. To evaluate the level of phylogenetic signal in the data, we used the fitContinuous function in the geiger package⁷³, together with a consensus phylogenetic tree downloaded from 10kTrees⁷⁶. Brain size, body size and group size were \log_{10} -transformed for all analyses. All phylogenetic regressions were performed using the gls function in the nlme package⁷⁶ in R, with a Pagel correlation structure and an maximum-likelihood-optimized λ value⁷⁴. To explore the impact of phylogenetic uncertainty, we also ran models over a 1k tree block and used model averaging to estimate coefficients⁶⁹. To determine whether species’ social repertoires can be reduced to fewer explanatory factors, we applied a polychoric PCA in the ‘psych’ package in R, which is appropriate for binary or ordinal data.

Ancestral state reconstruction. To visualize likely transitions across the tree, we evaluated likely social transitions using the ‘ace’ function in R package ‘APE’⁷⁷. The probability of different states is plotted as a pie chart at each node (Supplementary Fig. 7).

Data availability. Data are available in Supplementary Tables 1 and 2.

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Author contributions

K.C.R.F., M.M. and S.S. conceived the project and wrote the manuscript. K.C.R.F. and M.M. collated the data, with some assistance from S.S. S.S. primarily conducted statistical analyses, with some assistance from M.M. and K.C.R.F.

Competing interests

The authors declare no competing financial interests.

Additional information

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