

# Phylogenetically controlled life history trait meta-analysis in cetaceans reveals unexpected negative brain size and longevity correlation

Nikita E. Groot<sup>1</sup>, Rochelle Constantine<sup>1</sup>, Ellen C. Garland<sup>2</sup>, Emma L. Carroll<sup>1</sup> 

<sup>1</sup>School of Biological Sciences, The University of Auckland—Waipapa Taumata Rau, Auckland, New Zealand

<sup>2</sup>School of Biological Sciences, University of St. Andrews, Fife, Scotland

Corresponding author: School of Biological Sciences, The University of Auckland—Waipapa Taumata Rau, New Zealand. Email: [e.carroll@auckland.ac.nz](mailto:e.carroll@auckland.ac.nz)

## Abstract

The identification of patterns in trait evolution is essential to understand the interaction of evolutionary forces, and provides useful information for species management. Cetaceans are a phylogenetically well-resolved infraorder that exhibit distinct trait variation across behavioral, molecular, and life history dimensions, yet few researchers have applied a meta-analytic or comparative approach to these traits. To understand cetacean trait evolution, we used a phylogenetic generalized least squares approach to examine the cognitive buffer hypothesis (CBH). A large brain should buffer individuals against environmental challenges through increasing survival rates, and a longer lifespan should buffer individuals against the cost of extended development for larger brains according to the CBH, leading to an expected positive correlation between brain size and lifespan. In contrast to this expectation, previously observed in taxa including primates, we found a negative correlation between brain size and lifespan in cetaceans. This suggests cetaceans experience selective pressures different from most other mammals in these traits but may be more similar to some social mammalian carnivores that display alloparenting. We also provide a comprehensive dataset to explore additional aspects of trait evolution but which would greatly benefit from studies on behavioral ecology across cetaceans and increased focus on data deficient species.

**Keywords:** review, phylogenetic analysis, cognitive buffer hypothesis, behavioral evolution

Investigating the evolution of behavioral adaptations or traits requires an extensive understanding of species history, unless a comparative approach is taken. By extracting the findings of behavioral and trait research across many species and controlling for phylogeny, the underlying patterns of trait evolution may be revealed (Harvey & Pagel, 1991). Behavioral traits are being recognized as increasingly important in an evolutionary and conservation context. For example, culture—the sharing of information and behaviors by members of a group through social learning (Allen, 2019; Frigaszy & Perry, 2003; Heyes, 1994; Hoppitt & Laland, 2013; Whitehead & Rendell, 2004)—has been described in a variety of animals such as birds, primates, cetaceans, and insects, and has been described as a secondary system of inheritance alongside genetic inheritance (Whiten, 2019). Non-human culture is interesting from a comparative standpoint in helping us to understand human evolution, and has more recently drawn attention through its conservation implications (Brakes et al., 2021). The social learning mechanisms inherent in culture have important implications for population viability and species responses to change (e.g., Brakes et al., 2019).

However, research examining the evolution of culture and its associated traits such as social learning often neglect cetaceans due to perceived inscrutability of their traits and behaviors (e.g., Heldstab, 2017; Isler & van Schaik, 2009). Cetacea is a phylogenetically well-resolved infraorder nested

within Artiodactyla, composed of whales, dolphins, and porpoises. Despite displaying wide variation in behavioral and life history traits (e.g., Bouveroux et al., 2019; Hunt et al., 2019; Sargeant et al., 2005), this infraorder lacks in-depth trait research. This partly results from research constraints, as many fare poorly in captivity (Lott & Williamson, 2017), and many species are inaccessible for field observations (e.g., Hooker et al., 2019). However, some species have been studied in-depth (e.g., Mann & Karniski, 2017), although this is typically limited to a few populations. Despite these challenges, cetaceans are an ideal group for conducting trait meta-analyses because of their well-defined phylogeny and widely acknowledged diversity. In particular, cetacean trait diversity presents an underutilized opportunity to use a comparative approach in understanding the evolution of social learning and culture, and how these correlate with other traits such as lifespan, mortality, and communication behaviors (Whiten, 2021).

The cognitive buffer hypothesis (CBH) offers one potential explanation for the evolutionary relationship between complex behavior (particularly culture and social learning), physiology and life history. It attempts to summarize the benefits, and the energetic and developmental costs of brain size and behavioral complexity, across taxa (Sol, 2009). The CBH suggests that greater behavioral plasticity and cognitive abilities, which are generally expected to

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occur alongside larger brains relative to body size, provide fitness benefits through higher survival and better adaptation to environments (Figure 1). The CBH also suggests that because larger brains (in general, but especially relative to body mass) and greater behavioral complexity take more time to develop and thus delay reproduction, natural selection should drive a buffer-like, concurrent extension of the lifespan that would otherwise be negatively impacted (Sol, 2009). Therefore, under the CBH, species with larger brains and greater behavioral complexity are expected to live longer. The CBH commonly assumes that high encephalization is both driven by, and enabling of, a greater degree of social learning and behavioral flexibility (Jiménez-Ortega et al., 2020; Sol, 2009; Street et al., 2017).

Street et al. (2017) identified a significant relationship between social learning, encephalization, and longevity in primates, suggesting this was strong evidence in support of the CBH. Further work seems to agree that a positive correlation between lifespan and brain size exists in primates, and additionally rodents, but not other clades including cetaceans (DeCasien et al., 2018). Similar support for the CBH has been discovered for birds, though the direction of causality and the mechanism for the relationship is still debated (Jiménez-Ortega et al., 2020; Minias & Podlaszczuk, 2017; Vágási et al., 2016). Cetaceans, however, have been purposefully excluded from some analyses of the CBH (e.g., Heldstab, 2017), and only examined to a limited extent by others (DeCasien et al., 2018).

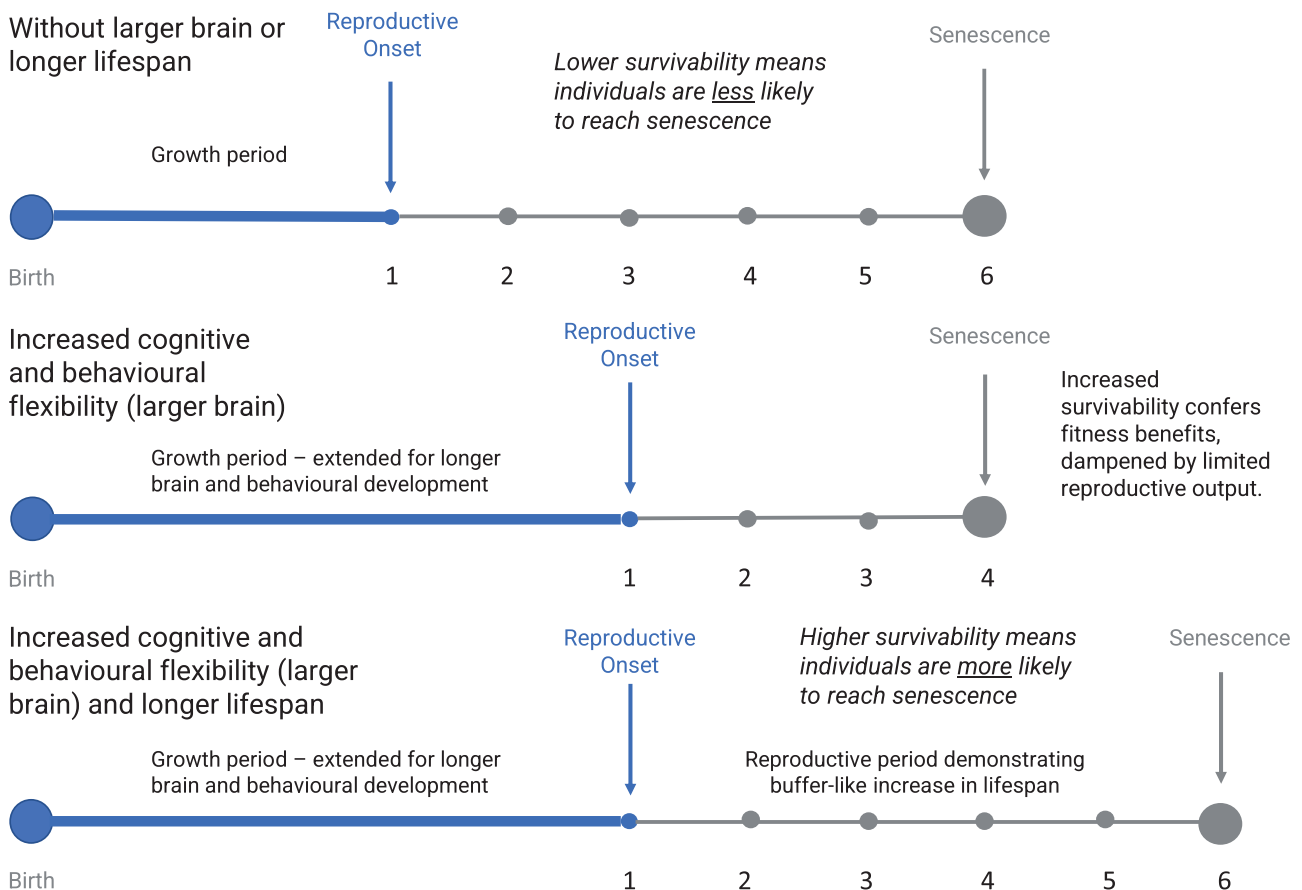
Here, we compiled a database of cetacean behavioral, morphological, and life history traits to explore the CBH, which has proven relevant to other cultural species (e.g., primates), though not yet explored in-depth in cetaceans. We expected to observe a positive relationship between brain size, longevity, and behavioral complexity (e.g., a more complex learned component of foraging behavior) as previously observed in other species such as primates (Street et al., 2017) and to some extent, birds (Jiménez-Ortega et al., 2020). If lifespan tends to increase with brain size and behavioral complexity, this could indicate support for the CBH.

## Methods

### Phylogenetic data compilation

We used the “Cetacean Tree of Life” (McGowen et al., 2020); a phylogenetic tree based on maximum likelihood (ML) (confirmed by Bayesian inference) of concatenated loci and coalescence analyses of gene trees, to inform phylogenetic relationships. Of the 92 cetacean species identified by the Society for Marine Mammalogy (Committee on Taxonomy, 2021), those which were not phylogenetically well-resolved and which were severely data-deficient were excluded. This left 77 species, 73 of which were already represented in McGowen’s “Cetacean Tree of Life.”

We modified the phylogenetic tree by removing non-cetacean outgroups and adding four species (*Platanista gangetica*,



**Figure 1.** A depiction of the cognitive buffer hypothesis (CBH), showing the hypothetical evolutionary trajectory of a larger brain and longer lifespan. Numbers represent reproductive opportunities, ending at reproductive senescence.

*Cephalorhynchus hectori*, *Sotalia guianensis*, and *Sousa sahulensis*; Supplementary Figure S1) using R (version 3.6.3; R Core Team, 2021) and the packages “ape” (version 5.6-2; Paradis et al., 2019) and “phytools” (version 1.0-3; Revell, 2021). The phylogenetic relationships of these species were known, either from previous phylogenetic analyses (McGowen et al., 2009), or from further research not yet represented in the original tree (M. McGowen, personal communication, July 12, 2021). Of these 77 species, 13 were mysticetes (baleen whales) and 64 were odontocetes (toothed whales, dolphins, and porpoises).

### Trait data compilation

Trait data (defined in Tables 1 and 2; detailed information can be found in Supplementary Tables S1 and S2) were collated from published articles, reports, open-access data collections, supplemented by books and encyclopedias (Supplementary Table S3). Where no other sources were available, data were also gathered from reports to the Scientific Committee of the International Whaling Commission and theses (Supplementary Table S3). For morphological and life history trait (i.e., length, mass, brain mass, lifespan, male, and female age at first reproduction, gestation, weaning, calving interval; Table 1) data and group size estimates, we used the search terms “cetacea,” “mysticete,” “odontocete” and the trait name in Google Scholar and Scopus. We drew upon large databases including AnAge (De Magalhaes & Costa, 2009), PanTHERIA (Jones et al., 2009), and PHYLACINE (Faurby et al., 2018). Original sources were identified where possible. Where these databases did not have the trait values of interest for a species, we then used its scientific name as a search term in place of Cetacea, mysticete, or odontocete in Google Scholar and Scopus. Where different sources provided different values for the same species or a single source gave multiple individual values, we used the mean. Where a source provided a range, we used the midpoint (following Gonzalez-Lagos et al., 2010; Fox et al., 2017).

We obtained behavioral trait (i.e., sociality, group foraging behavior, learned component of foraging, acoustic communication; Table 2) values by a similar process. We again used the terms “cetacea,” “mysticete,” and “odontocete” plus trait-specific terms, and species names where gaps in the data appeared. For sociality “group” or “social” was used as the trait-specific terms. For group and learned foraging behaviors, we used “foraging” or “hunting.” For acoustic communication, we used “sound” or “vocalization” or “communication.” Non-continuous trait values (A1–D7 subcategories, Supplementary Tables S1 and S2) were stored in binary (e.g., cyclical social stability, 1 = yes, 0 = no, NA = unknown). This is because phylogenetic generalized least squares (PGLS) frameworks can manage non ordinal discrete variables with multiple states if these are recoded as separate binary characters (Garamszegi, 2014).

To examine the state of the literature, we summarized the available data by the number of values available across species per trait, and additionally by contributions of individual cetacean families to the total data available on each trait (Figure 2). From this summary, we determined that behavioral complexity could not be examined here as part of testing the CBH, as behavioral traits (A1–D7) were too data-deficient (less than 15 species with known trait states) for analyses.

For those traits with sufficient coverage across taxa, we checked for normality in R (version 3.6.3; R Core Team, 2021) using the Shapiro-Wilk test (Shapiro & Wilk, 1965),

and for homogeneity of variance using Levene (Schultz, 1985) and Bartlett (Tobias & Carlson, 1969) tests. Trait collinearity was assessed using variance inflation factors (Mansfield & Helms, 1982). When deciding which traits to include in models, we selected traits which displayed a more normal distribution and equal variance. Traits showing large variation (e.g., Mass, Lifespan, Female first Reproduction, Group Size) were log-transformed; however, for the Odontocete-only analysis (see below), Female first Reproduction deviated more from the normal distribution when log-transformed so unlogged data was used in this instance. For traits that were highly correlated, such as the age at first reproduction for males and females, we chose the trait for which we had a larger sample size.

### Examining the CBH

We examined the CBH using PGLS analyses from the “nlme” package (version 3.1-153; Pinheiro & Bates, 2000; Pinheiro et al., 2021). The PGLS approach examines trait relationships after correcting for phylogenetic signal, using a matrix of expected variance and covariation given a phylogenetic tree and model of trait evolution (e.g., Brownian motion or Pagel’s  $\lambda$ ; Blomberg et al., 2012). The log of lifespan was used as the response variable in all models. Response predictors were either EQ, or EQ and female age at first reproduction. While it is inappropriate to include predictors with strong collinearity in PGLS models (Mundry, 2014), we also ran additional models to confirm our results using brain mass and body mass as predictors, similar to Overington et al. (2009), therefore accounting for potentially inflated type II error caused by residual analyses. We ran each model (where possible, given sample size and computational restrictions) for each of three datasets containing (a) all species, (b) mysticete species only, or (c) odontocete species only.

PGLS models employed ML so that model fits could be compared even when fixed effects were not identical (McNeish, 2017), and were fitted using different statistical distributions for the response variable (reflecting different models of trait evolution: Brownian motion or Pagel’s  $\lambda$ ). Estimates of Pagel’s  $\lambda$  can inform whether a model of Brownian motion which assumes phylogenetic nonindependence is appropriate (Freckleton et al., 2002). Pagel’s  $\lambda$  typically ranges from 0 to 1, respectively indicating total phylogenetic independence of a trait (0), to trait variation being proportional to phylogeny (1). Furthermore, Pagel’s  $\lambda$  relaxes assumptions of Brownian motion, therefore is better equipped to fit models of trait evolution based on the data and tree provided (Freckleton et al., 2002). Estimates of Pagel’s  $\lambda$  can also inform our understanding of trait evolution itself; values above one, in the context of trait evolution, suggest its rate of evolution is higher at the phylogeny’s roots than at the tips, and have also been interpreted as showing that traits are more similar than would be expected under a Brownian model of evolution (Freckleton et al., 2002; Münkemüller et al., 2012; Pagel, 1999).

The majority of the data across traits were naturally right skewed and slightly bimodal prior to log transformation, as expected given the significant differences in various character traits of the two cetacean infraorders. Although running phylogenetic analyses means these differences should be accounted for, we also separately examined each infraorder. This served to check for skewed data for one or both infraorders, and to examine whether different evolutionary processes operate in the infraorders. Odontocete data tended to be more normally distributed, while mysticete data was largely right skewed. The

**Table 1.** The name and description of traits included in analyses. Non-bolded trait names indicate values which were directly taken, without alteration or processing (e.g., mean, median or binary coding), from existing literature.

Trait name	Trait description	Variable type
<i>Morphological &amp; Physiological</i>		
Length (m)	Average length of mature specimen (meters)	Continuous
Mass (kg)	Average mass of mature specimen (kilograms)	Continuous
Brain Mass (g)	Average brain mass (grams)	Continuous
<b>Encephalization Quotient (EQ)<sup>1</sup></b>	$\frac{\text{Absolute brain mass}}{0.12(\text{body mass})^{67}}$	Continuous
<i>Life History</i>		
Lifespan (y)	Species' maximum lifespan calculated by molecular methods where available, else by observation (years).	Continuous
Age at First Reproduction (Male and Female) (y)	Age at which a male or female of the species typically produces their first offspring (years).	Continuous
<b>Proportion of Life as Juvenile (Male and Female)</b>	Proportion of maximum lifespan spent immature (pre-reproductive).	Continuous
Gestation (mon)	Average gestation time in months.	Continuous
Weaning (mon)	Average time between gestation and weaning (end of lactation) in months.	Continuous
<b>Years Dedicated to Single Offspring (y)</b>	Average number of years taken to raise one offspring indicated by combined time of gestation and lactation/time until weaning.	Continuous
<b>Proportion of Life Dedicated to Single Offspring</b>	Proportion of maximum lifespan on average dedicated to raise one offspring.	Continuous
Calving Interval (y)	Average number of years between calves.	Continuous
<b>Proportion of Life Between Calves</b>	Average calving interval as a proportion of maximum lifespan.	Continuous
<i>Behavioural</i>		
Group Size	Average group size from observations.	Continuous
<b>Sociality</b>	Aspects of the social structure or social interactions which influence con-specific relationships, group organization and group composition. Subcategories include Primary Unit, Stability, Tolerance, Offspring Membership, Alloparenting, Maternal Grouping, Male Alliance, and Post-reproductive lifespan.	Binary
<b>Group Foraging Behaviours</b>	The interactive behaviour between individuals foraging in proximity. Subcategories include Competitive, Non-Competitive, Information Share/Foraging Communication, and Co-operative Foraging.	Binary
<b>Learned Foraging Behaviours</b>	The apparent presence or absence of learned patterns of foraging site fidelity (with or without contextual dependencies) and/or specific foraging techniques. Subcategories include Site Fidelity, Contextually Relevant Fidelity, and Learned Foraging Behaviors.	Binary
<b>Acoustic Communication</b>	The presence or absence of various sound-making traits ranging from song to signature vocalizations. Subcategories include Song, Cultural evolution of vocalizations, Social Sounds, Social Sound Variety, Vocal Imitation, Membership Vocalizations, and Signature Vocalizations.	Binary

bowhead whales' (*Balaena mysticetus*) relatively long lifespan may have contributed to this skew across life history traits; we therefore also examined the mysticete dataset with the bowhead whale removed (Table 3, dataset "Cognitive Buffer 4").

The analysis was structured to explore the traits with the largest sample size. As models require complete data to be fitted, increasingly complex models had decreasing sample sizes. We examined model fits through diagnostic plots (e.g., residual analyses and quantile–quantile plots). Models of the same sample size (e.g., 2a–f, 3a–c, Table 3) were compared using delta AICc ( $\Delta\text{AICc}$ ) and AICc weights, which are well-suited to examining smaller sample sizes and models of phylogenetically controlled trait relationships (Johnson & Omland, 2004).

## Results

### Distribution of trait data across Cetacea

At least one trait for each of 73 cetaceans included in analyses was found in the literature, with average mass recorded for

all but two species. The quantity of data available for brain mass and encephalization quotients results from an extensive review by Ridgway et al. (2016). Data were available for less than 60% of species for most traits, and less than 25% of species for behavioral traits (Figure 2; Table 2). As such, we determined that all of Group Foraging Behaviors (B), Learned Foraging Behaviors (C), and Acoustic Communication (D), and additionally the Tolerance (A3), Offspring Membership (A4), Alloparenting (A5), Maternal Grouping (A6), Male Alliance (A7), and Post-reproductive Lifespan (A8) were too data deficient to be included in further analyses. This reflects both a skew in the literature and the difficulty in finding and defining conclusive evidence of trait presence or absence. These data limitations prevented us from assessing how EQ, as a biological proxy for cognitive capacity and behavior, compared to direct behavioral observations. It was also not possible to consider whether social learning or behavioral repertoire factored into the mechanisms or benefits hypothesized to explain the CBH (Sol, 2009).



**Table 2.** Behavioural trait subcategory definitions and examples. For sociality dimensions defined by Prox and Farine (2020), some examples listed in the example column are explicitly drawn from the discussion and supplementary materials of that paper.

Trait Code	Trait	Definition	Example
A.	Sociality	Aspects of the social structure or social interactions which influence conspecific relationships, group organization and group composition. The first three subcategories below were identified using statistical analyses by Prox & Farine (2020) as best able to capture patterns of mammalian social organization. Prox and Farine (2020) build upon Kappeler (2019), who also published a sociality framework based on qualitative literature review with largely overlapping dimensions of organization, structure, mating, and care systems.	
A1.	Primary Unit	<p>“the largest stable unit that has a temporally consistent membership”</p> <p>(A1.1) Individual: “Individuals change their social environment frequently.”</p> <p>(A1.2) Pair/Family: “Pairs of individuals persist over time and do not separate without forming new pairs. Families [...] are small groups [...] composed of mostly related individuals”</p> <p>(A1.3) Group: Similar to a family, only larger and without necessarily being related, potentially fissions into subunits or fuses with other groups. (Prox &amp; Farine, 2020)</p>	Resident killer whales live in “clans” or “pods” which under this framework are designated as having a primary unit of “group.” Short-finned pilot whales ( <i>Globicephala macro-rhynchus</i> ) are considered “pair/family” and both gray whales ( <i>Eschrichtius robustus</i> ) and bottlenose dolphins are considered “individual” (Prox & Farine, 2020).
A2.	Stability	<p>“the general stability of group membership,” likelihood of repeat observations of the same group member composition.</p> <p>(A2.1) Fluid: “Individuals are likely to be observed with different associates over the course of short time periods and groups change membership constantly over time”</p> <p>(A2.2) Cyclical: “Group memberships change with regular periodicity”</p> <p>(A2.3) Long-lasting: “A social constellation is maintained over longer time periods. Individuals may have changed groups only a few times in their lifetime”</p> <p>(A2.4) Permanent: “Individuals are not known to change groups during adulthood” (Prox &amp; Farine, 2020)</p>	Resident killer whale populations are considered “permanent,” sperm whales ( <i>Physeter macrocephalus</i> ) are considered “long lasting,” gray whales are considered “fluid” (Prox & Farine, 2020), while Commerson’s dolphins ( <i>Cephalorhynchus commersonii</i> ) are considered “cyclical.”
A3.	Tolerance	<p>“how primary units interact with other primary units”</p> <p>(A3.1) Open: “Primary units can freely join other primary units.”</p> <p>(A3.2) Tolerant: “Primary units can mix, but some low level of agonism or local avoidance can be observed” (Prox &amp; Farine, 2020)</p>	Short-finned pilot whales are considered “tolerant” while Hector’s whales and long-beaked common dolphins ( <i>Delphinus capensis</i> ) are “open” (Prox & Farine, 2020).
A4.	Offspring Membership	<p>“The time offspring spend with their natal primary unit”</p> <p>(A4.1) None: “No parental care is given during the time the society component is monitored”</p> <p>(A4.2) Short/limited: “The members of one generation of offspring disperse before or when a new generation of offspring is born.”</p> <p>(A4.3) Extended: “Generations of offspring overlap, or the next reproductive event is delayed until parental care for current offspring is completed”</p> <p>(A4.4) Philopatric: “The majority of offspring of the society component stays in the group after reaching maturity” (Prox &amp; Farine, 2020)</p>	Gray whales are classed as “short/limited” while Hector’s dolphins ( <i>Cephalorhynchus hectori</i> ) are “extended” and beluga ( <i>Delphinapterus leucas</i> ) are “philopatric,” though due to having both male alliances and loosely matrilineal groups, bottlenose dolphins would class as both “none” and “extended” (Prox & Farine, 2020).
A5.	Alloparenting	The presence or absence of alloparenting (care for another’s offspring).	Sperm whales are known to ‘babysit’ offspring other than their own while foraging (Whitehead, 1996).
A6.	Maternal Grouping	The presence or absence of social groupings mainly comprised of maternal females.	Sperm whales tend to form distinct maternal groups of females and immature individuals (Gero et al., 2008).

Table 2. Continued

Trait Code	Trait	Definition	Example
A7.	Male Alliance	The presence or absence of social groupings mainly comprised of males “allied” for access to females.	Blainville’s beaked whales form groups consisting of only males, apparently for reproductive gain (Baird, 2019).
A8.	Post-reproductive lifespan	Average number of years and proportion of lifespan females of a species spend in a post-reproductive state.	27% of adult female years in beluga populations are lived by post-reproductive females (Ellis et al., 2018) while killer whales live up to 15.78 years beyond reproductive senescence (Aimé et al., 2017). “Grandmothering,” where maternal females living beyond reproductive senescence with direct benefits to the survival of offspring and grand offspring, occurs often in socially learning species with matrilineal structures (Aimé et al., 2017)
<b>B.</b>	<b>Group Foraging Behaviours</b>	The interactive behavior between individuals foraging in proximity.	
B1.	Mutually Beneficial Foraging/Independent Foraging	Individuals foraging in a group appear to unintentionally increase, or have no effect upon, the foraging success of another individual in that group (not including those in a mother-calf dyad). This trait excludes apparent intentional co-operation, but captures a distinct lack of competition.	In some populations, male killer whales forage individually and in deeper waters than those used by their matriline (Beerman et al., 2016), while Blainville’s beaked whales forage in groups but catch fish independently (Arranz et al., 2011; Madsen et al., 2013).
B2.	Information Share/Foraging Communication	Individuals positively influence conspecific foraging success by communicating about food.	Humpback whales appear to produce vocalizations which coordinate or communicate feeding behaviour (Cerchio & Dahlheim, 2001; Parks et al., 2014).
B3.	Co-operative Foraging	Individuals positively influence conspecific foraging success through co-operative behaviours beyond communication.	Humpback bubble-net feeding requires a degree of co-operation and perhaps even role differentiation, though as with all marine mammals the latter theory is difficult to prove (Sharpe, 2001).
<b>C.</b>	<b>Learned Foraging Behaviors</b>	The apparent presence or absence of learned patterns of foraging site fidelity (with or without contextual dependencies) and/or specific foraging techniques.	
C1.	Site fidelity	Apparent vertical or horizontal transfer of migratory routes to feeding grounds (with no apparent temporal preference beyond proximity during annual migration).	Gray whales exhibit feeding ground fidelity, with 72% of calves born in a 12 year period returned annually to the feeding ground of their mother (Bröker et al., 2020).
C2.	Contextually relevant fidelity	Learned preferences and/or routes to feeding groups influenced by temporal context.	Mammal hunting killer whales flexibly choose foraging sites specifically when that site is most productive (many prey), as well as choosing the prey type which their primary hunter is most often successful in catching (Hoelzel, 1991).
C3.	Foraging Behaviors	Population-specific foraging behaviors exist in a species, indicating foraging traditions, high innovation and/or high behavioural plasticity.	Bottlenose dolphin populations possess unique foraging innovations and even exhibit cultural homophily, meaning that their social organization is influenced by their foraging behaviour (Methion & Diaz López, 2020), while humpback whales display cultural transmission of feeding behaviors (Allen et al., 2013).
<b>D.</b>	<b>Acoustic Communication</b>	The presence or absence of various sound-making traits ranging from song to signature vocalizations.	
D1.	Song	Structured, stereotyped repetition of sounds grouped into units and vocal phrases	Pygmy blue whales ( <i>Balaenoptera musculus brevicauda</i> ) express sound series (“themes”) repeated in generally regular intervals, which might be comprised of (for example) “three quasi-tonal multi-harmonic sounds” also called “song” (Gavrilov et al., 2011).

Table 2. Continued

Trait Code	Trait	Definition	Example
D2.	Cultural evolution of vocalizations	Song and non-song repertoires. The order of vocal phrases and units in a song varies (between singers/locations) and changes temporally including learned imitation of new songs. Changes in call types are transmitted among groups.	Humpback whale song patterns correlate with their migration patterns, indicating cultural transmission of song (Owen et al., 2019).
D3.	Social Sounds	All non-song vocalizations and percussive sounds used in social settings.	Blue whales ( <i>Balaenoptera musculus musculus</i> ) use type-D calls and singular song phrases in social settings (Lewis et al., 2018).
D4.	Social Sound Variety	More than five distinct social communications, composed of varying sounds and call types	Humpback whales have a large repertoire of vocalizations and produce percussive sounds (such as pectoral fin slaps) which they use specifically and primarily in social settings (Dunlop et al., 2007).
D5.	Vocal imitation	Heterospecific vocalizations imitated	Killer whales engaged in a “do-as-I-do” paradigm quickly and recognizably imitate familiar and novel human sounds (Abramson et al., 2018).
D6.	Membership vocalizations	Sounds indicating group or population membership	Killer whale groups or ‘acoustic clans’ can be further divided into pods and family groups with greater associative strength based on differences in vocalizations (Ford, 1984). Furthermore, sperm whales are typically grouped into vocal clans (e.g., Rendell & Whitehead, 2003)
D7.	Signature vocalizations	Sounds indicating individual identity	Bottlenose dolphins produce and interpret “signature whistles” unique to a specific individual (Jamik & Sayigh, 2013).

Except for behavioral traits (Table 2), most cetacean families were well represented relative to their size (Figure 2). Two small families each with one species, Neobalaenidae (pygmy right whales *Caperea marginata*) and Iniidae (Amazon river dolphins *Inia geoffrensis*) were poorly represented across traits, while the equally small Eschrichtiidae (gray whales *Eschrichtius robustus*) was well represented across all traits (Figure 2). The relatively large family Ziphiidae ( $n = 23$  species), representing beaked whales, was never overrepresented, and is especially lacking research on reproductive and behavioral traits (Figure 2).

### Examination of the CBH

PGLS models of the log of lifespan by EQ consistently produced a slight, negative, statistically significant ( $p < .05$ ) correlation (Table 3). We also produced models of lifespan by body mass and brain mass to confirm this relationship (Table 3, Figure 3b, Supplementary Figure S2).

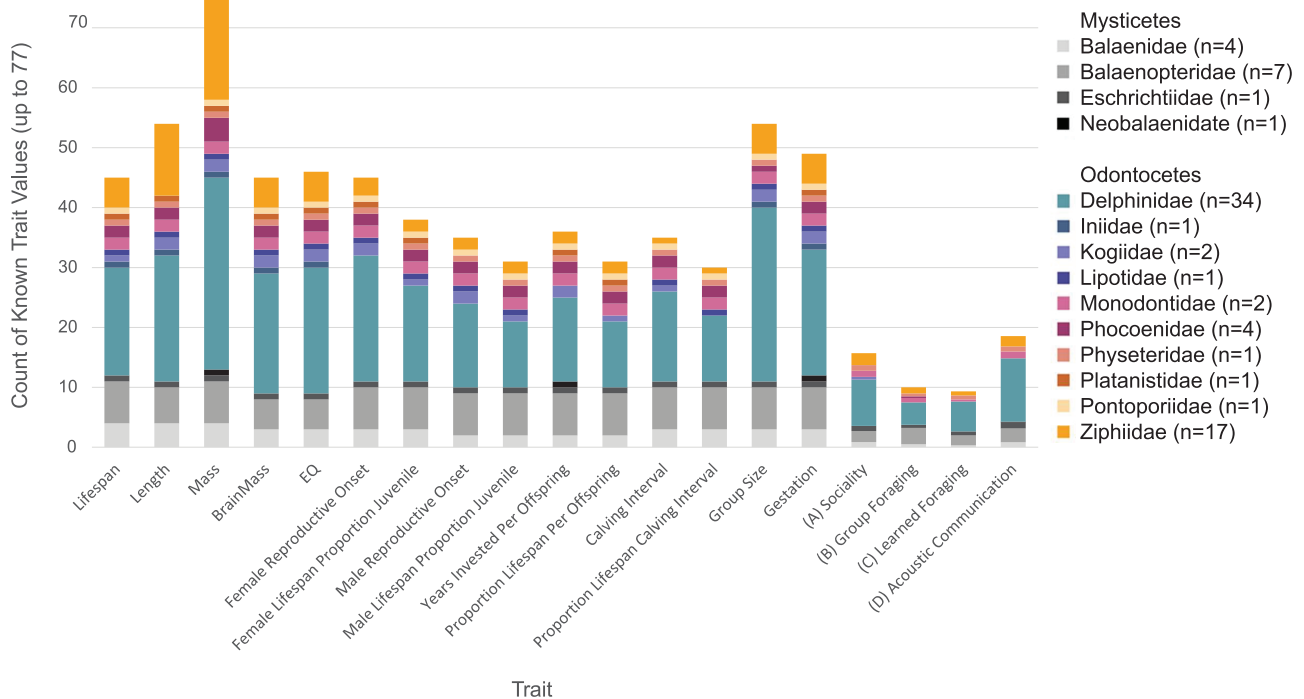
Considering both infraorders (hereafter cetacean dataset), the best fitting model was an additive model where the log of lifespan was predicted from EQ and the log of female first reproduction, using a Brownian motion structure (Table 3, model 2a, Figure 3a). The same model using Pagel’s  $\lambda$  showed the same relationship and a similar fit, followed by the model of the log of lifespan by EQ and the log of female first reproduction with an interactive term (Table 3).

For the mysticetes, we had data for up to nine of 15 extant species (60%; 64% of phylogenetically resolved species in our tree) and three extant families (one family containing one species not included). The model predicting the log of lifespan by EQ using Pagel’s  $\lambda$  ( $\lambda = 1.06$ , Table 3, model 4b, Figure 3c) proved the best fit for the mysticete data, even when the bowhead whale was removed. Removing the bowhead decreased effect size from  $-0.92$  to  $-0.54$  and the statistical significance from  $p = .05$  to  $p = .1$  when considering the simplest model of the log of lifespan by EQ (Table 3).

For the odontocetes, we had data for up to 28 of 77 extant species (36%; 44% of phylogenetically resolved species in our tree), encompassing all 10 extant families. The best fitting model was an additive combination of EQ and female first reproduction predicting the log of lifespan using Pagel’s  $\lambda$  ( $\lambda = 1.04$ , Table 3, model 8a, Figure 3d); both factors had statistically significant effects ( $p < .01$ ).

Where the average age of a species’ female first reproduction was included as a predictor with an interactive term, relationships between predictor and response variables consistently dropped below significance ( $p > .05$ ), and interactions were not significant ( $p > .05$ , Table 3). The significance of an additive female first reproduction term differed by infraorder (never significant for mysticetes) and structure (only significant when Pagel’s  $\lambda$  was used), however, was positively correlated as expected for odontocetes (Table 3). This positive correlation was steeper in the cetacean dataset, which would suggest that the mysticetes are skewing this relationship when included alongside odontocetes (Table 3).

Models of lifespan by brain and body mass also depict a negative relationship between brain mass and lifespan across datasets, though significance decreased, likely because the predictors are highly correlated. The interaction between predictors was significant in odontocetes and for the cetacean dataset, but not for mysticetes. In the cetacean and odontocete



**Figure 2.** Availability of trait data by cetacean families ( $n$  = number of species). For sociality, foraging, and acoustic communication traits, the average number of known trait values across subcategories (rather than the total) was used (see Table 1 and Supplementary Table S1 for trait definitions).

datasets, the relationship between lifespan and body mass was also negative.

Overall, best fitting models consistently depict a significant negative relationship between lifespan and EQ (Table 3). The relaxation of Brownian motion assumptions by use of Pagel’s  $\lambda$  significantly improved model fit when considering each infraorder separately, however, not when considering the overall cetacean dataset.

### Discussion

The evolutionary drivers of social behaviors and culture in non-human animals are an increasingly discussed and researched topic (Whiten, 2021; Whiten et al., 2022). Cetaceans are amongst the few classes of mammals in which cultural evolution (Whitehead, 2017), as well as social structures of varying complexity, have been described, making them a natural choice for comparative meta-analyses. Cetaceans also present an interesting group for comparative phylogenetic analyses of trait correlates due to their vast trait diversity and phylogenetic resolution. To date, there have been limited investigations which include cetaceans into the different hypotheses suggested to underpin social and behavioral traits, such as the CBH, described here, but also others such as the cultural brain hypothesis (Muthukrishna et al., 2018) or social brain hypothesis (Dunbar, 2009). Our review of cetacean trait literature reveals gaping holes in behavioral data and highlights a number of smaller cetacean families which are currently data-deficient. However, we also highlight the importance of considering cetaceans when investigating evolutionary theories of the brain and behavior.

### CBH in cetaceans

Our results show that unlike other mammals, including primates and rodents, cetaceans do not show a positive relationship between brain size and lifespan. The negative correlation

we observed here between lifespan and encephalization, which is more pronounced in mysticetes, is counter to some of the predictions of the CBH. Among mammals a positive relationship between encephalization and lifespan has been observed (Gonzalez-Lagos et al., 2010), but an exception has been the negative relationship described in Carnivoran families with allomaternal care (Isler & van Schaik, 2009). Theoretically, the presence of helpers reduces the costs of reproduction and increases reproductive success also alleviating the pressure for an extended lifespan buffer (DeCasien et al., 2018; Isler & van Schaik, 2009). DeCasien et al. (2018) additionally observed that though encephalization predicts problem-solving ability, the same carnivores with allomaternal care performed worse on problem-solving tasks than those without allomaternal care. It is theorized that the cognitive benefits of increased encephalization could be directed into improving reproductive success, rather than into decreasing extrinsic mortality. This could also be applicable to some or all cetaceans, but particularly odontocetes, as many species demonstrate alloparental care (e.g., Augusto et al., 2017; Gero et al., 2009). The presence of alloparents may decouple the coevolution of a higher encephalization and a lengthened lifespan as predicted by the CBH; however, alloparenting is not the only potential confound.

The lifespan and EQ traits relevant to the CBH were better represented across cetacean families than were behavioral traits. Given the size of each infraorder, the datasets analyzed are large enough to be robust (i.e., 13/14 families across the infraorder were represented). However, while unlikely, it cannot be ruled out that the relationship observed here is the result of unidentified confounds or research bias. Methods of estimating age in cetaceans can be imprecise and given longevity is typically from ~25 to 70 years, with some even longer, studies spanning an individual’s life are rare (Luque et al., 2009; Nielsen et al., 2018). Furthermore, the use of EQ as an



**Table 3.** Model comparison for the Cognitive Buffer Hypothesis (CBH). Only species with complete trait data for each variable in a model could be used. Because of data sparsity, this meant that models of increasing complexity had decreasing sample size. Therefore, basic models were additionally run using the datasets with reduced sample size used for more complex models. The log of maximum lifespan was always used as the response variable, with predictor variables including encephalization quotient (EQ) or the logs of body mass and brain mass. The natural data or log of female reproductive onset (Fem1stReprod or Log Fem1stReprod) was considered in some models. Italicized models exhibit poor distribution of residuals or large deviations from normality. Bolded models represent best fit by AICc. AICc only compared models of the same sample size.

Cetacea											
sampling from 77 species											
Model, Response Distribution	N	Intercept ± SE	p	Predictor (Coefficient ± SE)	p	Predictor (Coefficient ± SE)	p	Interaction Coefficient ± SE	p	DF	ΔAICc
1a Brownian	37	1.94 ± 0.47	<.01	EQ (-0.09 ± 0.04)	.02					3	—
<b>2a Additive, Pagel's λ</b>	<b>33</b>	<b>1.51 ± 0.4</b>	<b>&lt;.01</b>	<b>EQ (0.8 ± 0.3)</b>	<b>&lt;.01</b>	<b>Log Fem1stReprod (0.45 ± 0.15)</b>	<b>&lt;.01</b>			<b>4</b>	<b>0</b>
2b Additive, Brownian	33	1.51 ± 0.4	<.01	EQ (-0.8 ± 0.03)	<.01	Log Fem1stReprod (0.45 ± 0.15)	<.01			5	2.34
2c Interaction, Brownian	33	1.52 ± 0.47	<.01	EQ (-0.08 ± 0.1)	.42	Log Fem1stReprod (0.44 ± 0.29)	.14	0.01 ± 0.11	.97	5	2.79
2d Interaction, Pagel's λ	33	1.52 ± 0.49	<.01	EQ (-0.08 ± 0.01)	.39	Log Fem1stReprod (0.44 ± 0.29)	.14	0.01 ± 0.11	.95	6	5.34
2e Brownian	33	1.96 ± 0.41	<.01	EQ (-0.09 ± 0.03)	<.01					3	5.78
2f Pagel's λ	33	1.96 ± 0.43	<.01	EQ (-0.09 ± 0.03)	<.01					4	8.27
<b>3a Interaction, Brownian</b>	<b>36</b>	<b>2.06 ± 0.58</b>	<b>&lt;.01</b>	<b>Brain mass (-0.11 ± 0.07)</b>	<b>.14</b>	<b>Body mass (-0.26 ± 0.24)</b>	<b>.3</b>	<b>0.05 ± 0.03</b>	<b>.05</b>	<b>5</b>	<b>0</b>
3b Interaction then Additive, Brownian	36	2.63 ± 0.66	<.01	Brain mass (-0.18 ± 0.09)	.05	Body mass (-0.62 ± 0.27)	.04	Interaction (brain and body mass) 0.09 ± 0.03	<.01	6	0.43
3c Interaction, Pagel's λ	36	2.31 ± 0.63	<.01	Brain mass (-0.13 ± 0.08)	.12	Log Fem1stReprod (0.21 ± 0.17)	.16	0.07 ± 0.03	.03	4	1.32
<b>Mysticeti</b>											
baleen whales											
Model (Size) Response Distribution		Intercept ± SE	p	Predictor (Coefficient ± SE)	p	Predictor (Coefficient ± SE)	p	Interaction (Coefficient ± SE)	p	DF	ΔAICc
<i>4a. Interaction model of EQ and female reproductive onset: the data could not support computation of necessary eigenvalues to run this model.</i>											
<b>4b Pagel's λ</b>	<b>9</b>	<b>2.26 ± 0.3</b>	<b>&lt;.01</b>	<b>EQ (-0.76 ± &lt;0.01)</b>	<b>&lt;.01</b>					<b>4</b>	<b>0</b>
<i>4c Additive, Pagel's λ</i>	<i>9</i>	<i>2.39 ± 0.33</i>	<i>&lt;.01</i>	<i>EQ (-0.65 ± 0.12)</i>	<i>&lt;.01</i>	<i>Log Fem1stReprod (-0.2 ± 0.22)</i>	<i>.39</i>			<i>5</i>	<i>9.15</i>
4d Brownian	9	2.25 ± 0.55	<.01	EQ (-0.92 ± 0.39)	<.01					3	21.86
4e Additive, Brownian	9	1.72 ± 0.61	.03	EQ (-0.72 ± 0.38)	.1	Log Fem1stReprod (0.49 ± 0.31)	.17			4	26.02
4f Interaction, Brownian	9	1.03 ± 0.69	.2	EQ (2.28 ± 1.91)	.28	Log Fem1stReprod (1.18 ± 0.52)	.07	-3.25 ± 2.03	.17	5	34.3
5a Interaction, Brownian	9	-10.27 ± 10.7		Brain mass (1.22 ± 1.29)	.39	Body mass (2.96 ± 2.33)	.25	-0.3 ± 0.28	.33	5	-
<b>6a (Ex. B. mysticetus)</b>	<b>8</b>	<b>2.05 ± 0.36</b>	<b>&lt;.01</b>	<b>EQ (-0.54 ± 0.27)</b>	<b>.1</b>					<b>3</b>	<b>0</b>
<i>6b (Ex. B. mysticetus)</i>	<i>8</i>	<i>2.4 ± 0.5</i>	<i>&lt;.01</i>	<i>EQ (-0.52 ± 0.27)</i>	<i>.11</i>	<i>Log Fem1stReprod (-0.4 ± 0.4)</i>	<i>.35</i>			<i>4</i>	<i>7.82</i>
<b>Odontoceti</b>											
toothed whales											
Model (Size) Response Distribution		Intercept ± SE	p	Predictor (Coefficient ± SE)	p	Predictor (Coefficient ± SE)	p	Interaction (Coefficient ± SE)	p	DF	ΔAICc
7a Brownian	28	1.8 ± 0.55	<.01	EQ (-0.08 ± 0.04)	.08					3	—
<b>8a Additive, Pagel's λ</b>	<b>24</b>	<b>1.5 ± 0.47</b>	<b>&lt;.01</b>	<b>EQ (-0.07 ± &lt;0.01)</b>	<b>&lt;.01</b>	<b>Fem1stReprod (0.04 ± &lt;0.01)</b>	<b>&lt;.01</b>			<b>5</b>	<b>0</b>

Table 3. Continued

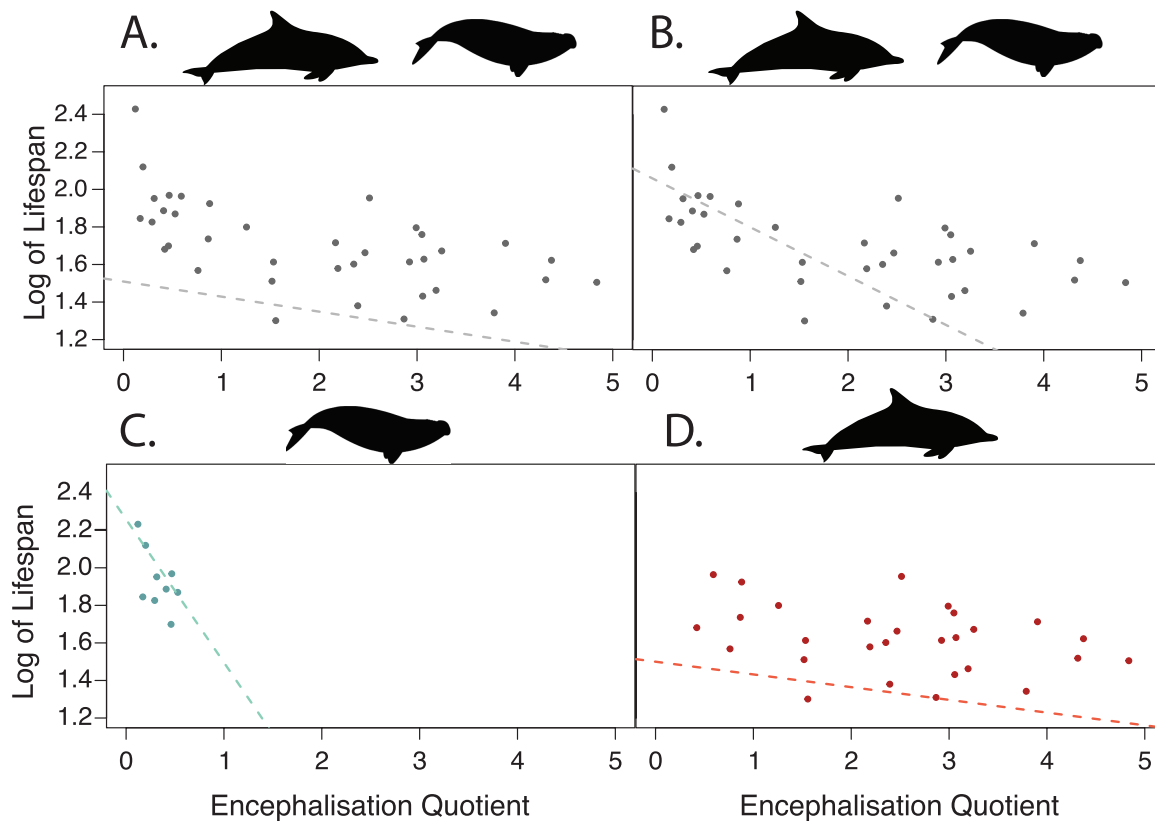
		sampling from 77 species										
Cetacea												
8b	Interaction, Pagel's λ	24	1.57 ± 0.49	<.01	EQ (-0.09 ± 0.03)	.02	Fem1stReprod (0.03 ± 0.02)	.16	0.004 ± 0.01	.57	6	4.28
8c	Additive, Brownian	24	1.52 ± 0.39	<.01	EQ (-0.07 ± 0.02)	.02	Fem1stReprod (0.04 ± 0.01)	.01			4	30.83
8d	Interaction, Brownian	24	1.57 ± 0.44	<.01	EQ (-0.09 ± 0.08)	.29	Fem1stReprod (0.03 ± 0.03)	.31	0.002 ± 0.01	.81	5	33.99
8e	Pagel's λ	24	1.82 ± 0.46	<.01	EQ (-0.07 ± 0.3)	.02					4	35.76
8f	Brownian	24	1.81 ± 0.43	<.01	EQ (-0.07 ± 0.03)	.02					3	38.53
9a	Interaction, Brownian	27	1.94 ± 0.52	<.01	Brain mass (-0.08 ± 0.07)	.24	Body mass (-0.33 ± 0.21)	.13	0.06 ± 0.02	.02	5	—

indirect proxy for intelligence and behavioral flexibility is not ideal; brain mass cannot be proven to directly correlate with behavioral flexibility or cognitive capacity, even controlling for body mass. Though these results appear robust, previous work from an indirect examination of lifespan and encephalization in Cetacea, using an older phylogeny, reported no relationship (DeCasien et al., 2018), therefore our results should be interpreted cautiously.

It is possible that the negative correlation between lifespan and EQ presented here reflects a relationship present in some but not all species, or which is skewed by particular groups. Clearly the relationship between lifespan and encephalization is different in mysticetes compared to odontocetes, based on the observed differences in relationship strength, steepness, and significance. Given the small sample size for many odontocete taxa, there may be further distinctions not yet evident. This distinction, especially given its persistence despite the application of phylogenetic comparative methods, suggests the underlying evolutionary processes acting upon lifespan or encephalization are likely to be different (currently and/or historically). Furthermore, the influence of the bowhead whale on the relationship between encephalization and lifespan should be highlighted. The bowhead whale possesses a uniquely long lifespan (but a relatively small brain) and an impressive host of mechanisms to support its longevity (Keane et al., 2015). Its removal from the mysticete dataset also removes the significance of the relationship between encephalization and lifespan.

The data presented here offer some evidence that other selection pressures are causing some (or all) cetaceans to develop longer lifespans independently of, or more powerfully than, the mechanisms described in the CBH. One distinction between mysticetes and odontocetes is their mechanism of feeding, and their diet. Dietary and ecological explanations for neurobiological and behavioral evolution focus largely on the selection pressures resulting from the energetic demands of the brain, and whether individuals benefit from flexibility in foraging behaviors (Rae, 2018). This would make sense depending on which species were sampled; the blue whale targets small prey and benefits little from techniques beyond its usual lunge-feeding behavior, with foraging efficiency and body size primarily limited by prey availability (Goldbogen et al., 2019). In contrast, the killer whale's rapid adaptive radiation might largely be attributable to its flexibility in adopting new feeding techniques (Foote et al., 2016). However, the humpback whale and Bryde's whale (*Balaenoptera edeni*) have benefitted from foraging flexibility (Allen et al., 2013; Constantine et al., 2018), highlighting this is not restricted to either odontocetes or mysticetes.

The CBH is not necessarily limited to predictions about lifespan; it also suggests that higher encephalization may be selected for in species which would benefit from behavioral flexibility due to food scarcity (Sol, 2009). Luo et al. (2017) examined this prediction in frogs, finding compelling evidence for an alternate hypothesis which described constraints on the mechanisms critical to the CBH. The encephalization of frogs experiencing food scarcity due to seasonal variability were suspected to be limited by the food scarcity itself, due to the energetic demands of developing a larger brain (Luo et al., 2017). This "expensive brain framework" also served to explain observations of reduced encephalization in migrating birds due to the competing energetic demands of migration (Sol et al., 2010). The expensive brain hypothesis described



**Figure 3.** Relationship between log lifespan and encephalization quotient (EQ) for each dataset, with the trendline reflecting the best fitting PGLS models of the cognitive buffer hypothesis (CBH), as indicated by  $\Delta AIC_c$ : Panel A: all cetacean model 2a; Panel B: all cetacean model 3a (using brain and body mass as predictors); Panel C: mysticete model 4b and Panel D: odontocete model 8a. Note that the best fitting all cetacean and odontocete models include female age at first reproduction as an additional predictor not visualized above.

in DeCasien et al. (2018) also expects that lifespan should be longer in species with larger brains to compensate for the costs of prolonged growth phases, akin to one of the CBH trait relationships described in Sol (2009). Research on energetic allocation or resource availability may be relevant to understanding patterns of brain size, behavior, and lifespan in cetaceans, especially for species that undertake long-distance migrations (e.g., mysticetes). To investigate these patterns, it would likely be necessary to separate resident and migratory populations, and populations occupying resource rich or poor environments, to compare encephalization either within or between species.

It is also important for future work to consider the mechanism behind the evolutionary relationship between lifespan and brain size. As well as the CBH, other hypotheses support such a relationship including the expensive brain hypothesis, described above, and the delayed benefits hypothesis. DeCasien et al. (2018) described the latter as where selection pressure comes from the additional benefits long-lived species would receive from a larger brain, compared to a shorter-lived species. By analyzing the likelihood of ancestral trait states in primates and rodents, DeCasien et al. (2018) determined that larger brains likely evolved before longer lifespans in primates, attributing this direction of selection pressure to the expensive brain hypothesis (where it overlaps with the CBH, in that longer lives evolve to offset developmental costs). However, they found that in rodents, longer lifespans likely evolved before larger brains, in line with the “delayed benefits hypothesis” where the longer lifespan instead allows the full benefits of a larger brain to be realized (and therefore

selected for). Similarly, Jiménez-Ortega et al. (2020) posit that an extended lifespan is a necessary pre-adaptation for a larger brain, in order for the benefits of increased cognitive abilities to be strongly selected upon. Analyses of ancestral trait states such as in DeCasien et al. (2018) would be interesting to conduct in Cetacea following our findings, and may help to disentangle the direction of selection pressures. Our work provides a foundation for building datasets that will allow future work to tease apart the different drivers for the observed pattern in lifespan and brain size—and later, behavioral complexity—in cetaceans, and to contrast them with other taxa.

#### Limitations on analyses linked to paucity of behavioral data in many cetacean species

Behavioral data are lacking for almost all species of cetacean. This is attributable to two primary factors; first, that these data are often more time consuming to collect, even with new technology. Especially for long-lived species like cetaceans, it is important to conduct long-term studies which can observe changes in behavior through the different life stages (Mann & Karniski, 2017). Second, unlike mass or gestation time, behavior can be interpreted differently by different observers and using different techniques (e.g., Mann, 1999; Whitehead, 2004). Furthermore, even where behavioral observations are made, researchers may make little attempt to integrate their data with the literature, or to ascribe meaning or intent to their observations, limiting further use. This leads to the exclusion of cetaceans from large-scale trait analyses which draw upon behavior.

Frameworks for cataloguing, defining and describing social and foraging behaviors accessible (but not limited) to cetaceans already exist (Lang & Farine, 2017; Prox & Farine, 2020). A framework for communication data is noticeably absent, though was partially incorporated into Lang and Farine's (2017) work on social predation. The data we present began to build upon a number of acoustic communication traits such as the presence of signature whistles or vocal imitation. Such traits may be consistent with a domain-specific approach to cognition and behavioral correlates (van Horik & Emery, 2011; Shaw & Schmelz, 2017). Mann (1999) provides a review of behavioral sampling methods for cetaceans which remains highly relevant and new tools such as drones are enhancing behavioral studies (e.g., Torres et al., 2018). Brakes et al. (2021) provide direction and a framework for examining culture and social learning across taxa, and integrating behavior into population and conservation research. Researchers have repeatedly highlighted and encouraged the use of comprehensive, integrative, multidimensional, and multidisciplinary approaches in further research (e.g., Cade et al., 2021; Watt et al., 2019; Wiley et al., 2011). Thus, a number of options for addressing gaps in marine mammal knowledge already exist.

Another key problem for behavior research (especially in cetaceans) is trait absence. There remains no ideal approach to determining whether a lack of observations in the literature reflects research skew or trait absence. Weighting of data by research effort might at least account for this problem (as done in Street et al., 2017). Due to the volume and complexity of the data presented here, this was infeasible at the time. However, it is unlikely that accounting for research skew would have influenced our findings; most species trait values were based on a limited number of observations.

Species that were well represented in behavioral traits also showed greater non-overlapping variability; research focusing on different populations described the same species as occupying different trait states. For example, the primary unit ("largest stable unit that has a temporally consistent membership," Prox & Farine, 2020) and group stability of the bottlenose dolphin differs between populations and over time (Bouveroux & Mallefet, 2010; Elliser & Herzog, 2011; Karniski et al., 2018; Mann et al., 2000; Mann & Smuts, 1998; Möller et al., 2001; Prox & Farine, 2020). Such variability has driven some to separate such species into behaviorally distinct ecotypes for behavioral analyses: Lang and Farine (2017) coded the killer whale into "Killer Whale (Type B), Killer Whale (Punta Norte), Killer Whale (Resident) and Killer Whale (Transient)" when developing a framework for describing social predation behavior. It is possible that these differences in behavior result from differences in researcher biases, observation times and methods, or interpretation. Research on these killer whale ecotypes indicate that these differences may be behavior-driven (e.g., Foote et al., 2016). Behavioral flexibility allows a group to occupy a new niche, and then social learning perpetuates the new behaviors within the group. Population expansion following founder effects and reproductive isolation can conserve or accentuate allelic differences in the colonizing group, leading to genetically distinguishable populations, which may later be called "ecotypes." However, some caution that such distinctions should not be made hastily (de Bruyn et al., 2013).

It is recommended that future work take a similar approach to that of Prox and Farine (2020), considering ecotypes within

species separately to reflect their distinct behavioral differences. This would also align with current goals suggested for population management in species capable of social learning (Brakes et al., 2021; Whitehead, 2017), and presents opportunities for deeper insight into the causes of trait variation (Powell et al., 2017). This is especially important given the extensive evidence to suggest that culture has important influences on population genetics, and can separate sympatric populations (Kopps et al., 2014) or alter selection pressures (Foote et al., 2016).

## Conclusions

Our research indicates that the relationship between lifespan and brain size in cetaceans does not follow the predictions of the CBH, despite sharing many similarities with mammals which do demonstrate the expected positive relationship. Disentangling the potential explanations for the relationship between brain size, lifespan (and ideally, behavior) will require further research on cetacean traits, particularly in those families currently underrepresented in the literature. When possible, we recommend that further work account for metabolic rates as well as mass and consider the influence of alloparenting and migration. Furthermore, it would be valuable to examine behavioral complexity and causes of mortality in addition to brain size and lifespan.

## End Note

1 The trait "EQ" was calculated using species averages, however an additional trait designated "IndivEQ" was calculated using the brain and body masses of individual specimens. These traits did not yield significant differences; however, EQ was available for three more species than was IndivEQ.

## Supplementary material

Supplementary material is available online at *Evolution* (<https://academic.oup.com/evolut/article/77/2/534/6887610>)

## Data availability

Life history and trait data underpinning analyses, and R code used in the analysis, can be found on dryad: <https://doi.org/10.5061/dryad.j6q573nj4>.

## Author contributions

All authors designed research, N.E.G. conducted research under supervision of E.L.C., R.C., E.G., all authors contributed to writing and editing.

*Conflict of interest:* The authors have no conflicts of interest to declare.

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