Coevolution of social network structure and life history in toothed whales

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Abstract

Toothed whales offer a 34 million year-long natural experiment for the evolution of complex mammalian societies. However, quantitative comparative analyses of social structure in these species are lacking. Here, we draw on existing social network analyses to compare social structure across toothed whales. We consider published measures of two social network traits across all toothed whales: modularity (Q), which captures divisions or “cliques” in a social community, and social differentiation (S), which estimates how much whales vary in their relationships – whether they associate equally with others or form special bonds with specific individuals. Combining these with a recently published database of life history traits, we applied phylogenetic multilevel models with the objective of exploring the origins of social network structure in toothed whales. We identified 98 measures of modularity and 89 measures of social differentiation from 23 toothed whale species. Social network structure was more similar among closely related species (i.e., showed strong phylogenetic signal), despite substantial intraspecific variability. Toothed whales with longer lifespans and larger bodies tended to form more modular social networks, as did those where males were proportionally larger than females. Similar, but weaker patterns were found between life history traits and social differentiation. Results from causal coevolutionary models provide preliminary evidence that social structure has been both a cause and consequence of changes in life history. Our findings reveal the correlated evolution of social network structure and life history traits in toothed whales, shedding new light on the origins of social relationships.

Significance Statement

Social relationships are key determinants of biological fitness in many species, yet most comparative evolutionary analyses rely on coarse proxies like group size, which may not capture the true complexity and consequences of social behavior. We show that social networks can be a powerful tool for mapping the evolution of social structure across the historical diversification of species. This study paves the way for a new body of research exploring how traits like body size and longevity have shaped, or been shaped by, social relationships. Moreover, as the first implementation of a new type of dynamic coevolutionary model in non-humans, our study recasts social structure as a causal leader in life history evolution across species.

Introduction

Why species vary in their reliance on social relationships is a fundamental question in behavioral ecology. For humans and other animals, social relationships can be an important determinant of health, survival, and reproduction (1, 2). More broadly, when the benefits of social living outweigh its costs, social structure, defined as the characteristics and pattern of social relationships across a community (3, 4), should be subject to selection. However, social structure is unlike traits such as body size or aggression in that it is necessarily an emergent product of multiple, interacting individuals. More specifically, networks form via dynamic feedbacks between individual behavior and network structure itself (5). Evidence from multiple species suggests that social structure can be highly variable within communities. Some of this plasticity is cyclical and predictable, for example, several species show seasonal changes in social structure. But social structure can also shift rapidly in response to a variety of factors such as the loss of community members (6, 7), changes in resource availability (8), and even natural disasters (9, 10). Thus, a key question is whether phylogenetic history predicts variation in social structure, or if plastic responses to local ecological and demographic conditions play a more dominant role.

Numerous theoretical models aim to explain species-level variation in social structure. Socioecological models focus on ecological factors such as resource distributions and have been applied to taxa such as primates and ungulates. There is also growing theoretical work suggesting that social structure should reflect life history traits. For example, Silk et al. propose that differentiated social relationships will be more likely to evolve in species with longer lifespans (11). However, empirical tests of these models have often been unsatisfactory. A major challenge is that it is very difficult to quantify social structure or the quality of social relationships across species. Existing empirical studies of social evolution often rely on general categories of “social organization”, representing the composition of social communities (i.e., whether individuals are group-living or solitary), or group sizes (12). However, these measures do not necessarily provide insight into social structure, i.e., the relationships within those communities. Indeed, many studies have relied on variation in group sizes, though group size may be unrelated to the complexity of relationships experienced by individuals (13). For example, terrestrial ungulates and offshore dolphin species can be found in herds or super-pods of thousands of animals, but this does not imply any sort of maximum in terms of the complexity of pairwise relationships between individuals. In fact, social complexity is argued to involve at least two major axes. “Organizational complexity” refers to the division of relationships and social roles, more common when social partners are related (e.g., many eusocial insects, kin-based packs of wolves, *Canis lupus*; 14), while “relational complexity” refers to the diversity of relationships in a community, e.g., how many types of relationships exist, and how animals interact to form and maintain these relationships (15). In light of the multi-faceted nature of social complexity, quantitative tests of the origins of social structure across animal populations have been largely absent.

Comparing social networks across populations and species is a promising avenue for developing and testing theory on social evolution (16). Social networks are models that represent the pattern of relationships between individuals within a social community. While it is widely recognized that inferred social networks are highly contingent on sampling and analytic decisions, in certain contexts they can be comparable (17). Here we focus on two properties of networks: modularity, which refers to the division of a community into sub-units, and social differentiation, which refers to the variability of dyadic relationships. Crucially, these measures map onto theory of organizational and relational social complexity, respectively, allowing us to expand the scope of comparative social analysis beyond measures like group size or general categories of social behavior.

Toothed whales (Odontocetes) exhibit a wide range of social structure, with some of the clearest evidence of complex social relationships outside of primates. Accounting for the majority of cetacean species (79 of 94; 18), this taxon contains examples of social traits otherwise exclusive to humans such as menopause (5 species; 19), using learned vocalizations as symbolic markers (20), and forming mental concepts for specific social partners (21). Toothed whales vary along a continuum of fission-fusion communities, where individuals associate widely and form ephemeral groups, to more stable social units centered on female kin. There is currently no consensus on what causes this apparent variation in social structure among species. In fact, whether species-specific differences are even supported by quantitative investigation remains to be seen.

Existing theory has identified several factors potentially important to toothed whale social structure. Generally, larger species (e.g., killer whales, sperm whales) appear to form stable kin-based units, likely resulting in more modular social networks (22). Similarly, high maternal investment and the need for allocare have been suggested to underlie cooperation in female-based groups of toothed whales, and sperm whales specifically (23, 24). Sexual size dimorphism may also be important: in some species, females may form stable social units to protect against harassment by proportionally larger males (25). Finally, it is likely that ecological factors also play a role. In particular, the predictability of resources and the risks of predation in open aquatic environments have been identified as possible drivers of both toothed whale social organization and the formation of cooperative bonds (26).

Here, we implement the first (to our knowledge) quantitative phylogenetic study of social network structure in toothed whales. Social network analysis is often applied to photo-identification data in whale and dolphin populations, revealing a diversity of social structures. However, direct comparisons between networks are rare (e.g., 27) and generally qualitative. Ironically, the challenges of studying toothed whales in the wild may make them a good candidate for comparative social network analysis. Unlike more accessible species where researchers have many degrees of freedom in collecting social data (e.g., using biologgers, traps, photographs, etc.), most cetacean researchers rely on *in situ* photographic data from which individual whales are identified and assumed to be associating within groups. Based on existing theory (11, 22), we predict that species with “slower” life histories will be more likely to rely on stable groups (higher modularity) and specific social relationships (higher social differentiation). We also consider whether life history traits impact the plasticity of social structure, i.e., whether intraspecific variability is greater in species with slower or faster life histories.

Results

Published measures of toothed whale social networks

We conducted a systematic literature review to identify measures of two key social network traits across as many toothed whale populations and species as possible. Our review returned 591 articles for initial screening, of which 241 were deemed suitable for a more detailed assessment, and 88 were retained in the final database. With an additional 9 studies identified via secondary searches, our database included 100 studies in total (including 3 studies of sperm whales carried out as part of the present article; See supplementary materials). Studies were globally distributed, though some regions were less represented than others (e.g., Indian Ocean), and most concentrated on populations closer to shore (Figure 1). We identified 98 measures of modularity from 87 articles and 20 species, as well as 89 measures of social differentiation from 71 articles and 21 species. The large majority of these networks were not sex-specific (94%), and most used the half-weight index (HWI) to represent pairwise relationships (77%).

As expected, social network measures were absent for most toothed whale species (55 of 78). In particular, studies on arctic whales, porpoises, and oceanic dolphins in offshore environments were rare or completely absent. Studies were also absent for most beaked whales excepting Bairds' beaked whales (*Berardius bairdii*) and northern bottlenose whales (*Hyperoodon ampullatus*), though this was not surprising given that this taxon has often been challenging to study and some species have never been identified alive (28). Despite these limitations, the resulting database offers relatively broad coverage for comparative network analysis (in a recent review, Albery et al. found that studies used a median of 12 networks across 4 species; 16). Our dataset also included species from the most basal group in the tree (*Physeteroidea*), implying that reconstructed ancestral states will represent the last common ancestor of toothed whales.

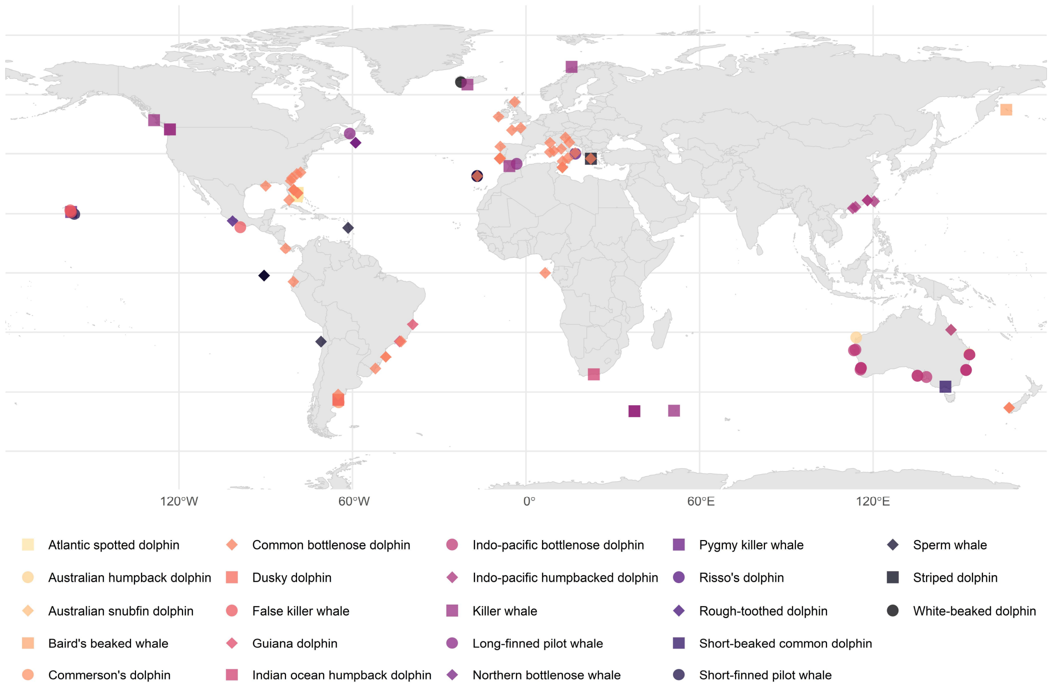

Figure 1 – Global distribution of study sites based on articles providing estimates for population-wide social network modularity and/or social differentiation (N = 100 studies).

Overview of toothed whale social network traits

The resulting comparative database allowed us to compare and visualize the distribution of social network characteristics across species. Mean social differentiation by species was always greater than 0.5, suggesting that well-differentiated relationships are prevalent in toothed whales. Species-level means in modularity included values below 0.3 for 4 species in our sample (*Delphinus delphis*, *Hyperoodon ampullatus*, *Sotalia guianensis*, *Stenella frontalis*), suggesting the absence of important divisions in the community. It is important to note that there was substantial inter-specific variability in these measures, however. For species with estimates of both social differentiation and modularity, we detected a broadly positive relationship between measures (Figure 2). Interestingly, sperm whales (Physeter *macrocephalus*) stood out from the main cluster of values by having exceptionally modular social networks with moderate social differentiation.

Using simple models with no additional predictors, we found that phylogeny explained a great deal of variance in life history traits *and* social networks: modularity (posterior mean $R^2{}_{phylo}$ = 0.76, CI 0.59 – 0.89), social differentiation ($R^2{}_{phylo}$ = 0.62, CI 0.29 – 0.85; Figure S2). In other words, more closely related toothed whales had more similar social networks. When incorporating phylogenetic and additional species-specific varying effects, phylogeny still appeared to explain a greater proportion of variance in both modularity ($R^2{}_{phylo}$ = 0.74, CI 0.52 – 0.89, $R^2{}_{species}$ = 0.04, CI 1.00 × 10^{-4} – 0.19), and social differentiation (R^2_{phylo} = 0.44, CI 0.02 – 0.81, $R^2_{species}$ = 0.19, CI 1.20 × 10^{-3} – 0.53). Phylogeny tended to explain more variation in life history traits than in social measures (female lifespan, R^2_{phylo} = 0.91, CI 0.69 – 0.99; female body length, R^2_{phylo} = 0.98, CI 0.96 – 0.99; female age at sexual maturity R^2_{phylo} = 0.86, CI 0.64 – 0.97). One exception to this was sexual size dimorphism (SSD; R^2_{phylo} = 0.54, CI 0.02 – 0.87), which we calculated as the ratio of female to male body length. These estimates of phylogenetic signal will include additional drivers of covariance between species, both present and historical. In other words, they should not be interpreted as the direct causal legacy of phylogeny. Nevertheless, that phylogeny explained so much variance in Q and S supports the idea that clade-level differences in social network structure can be identified and are not overwhelmed by population-specific plasticity.

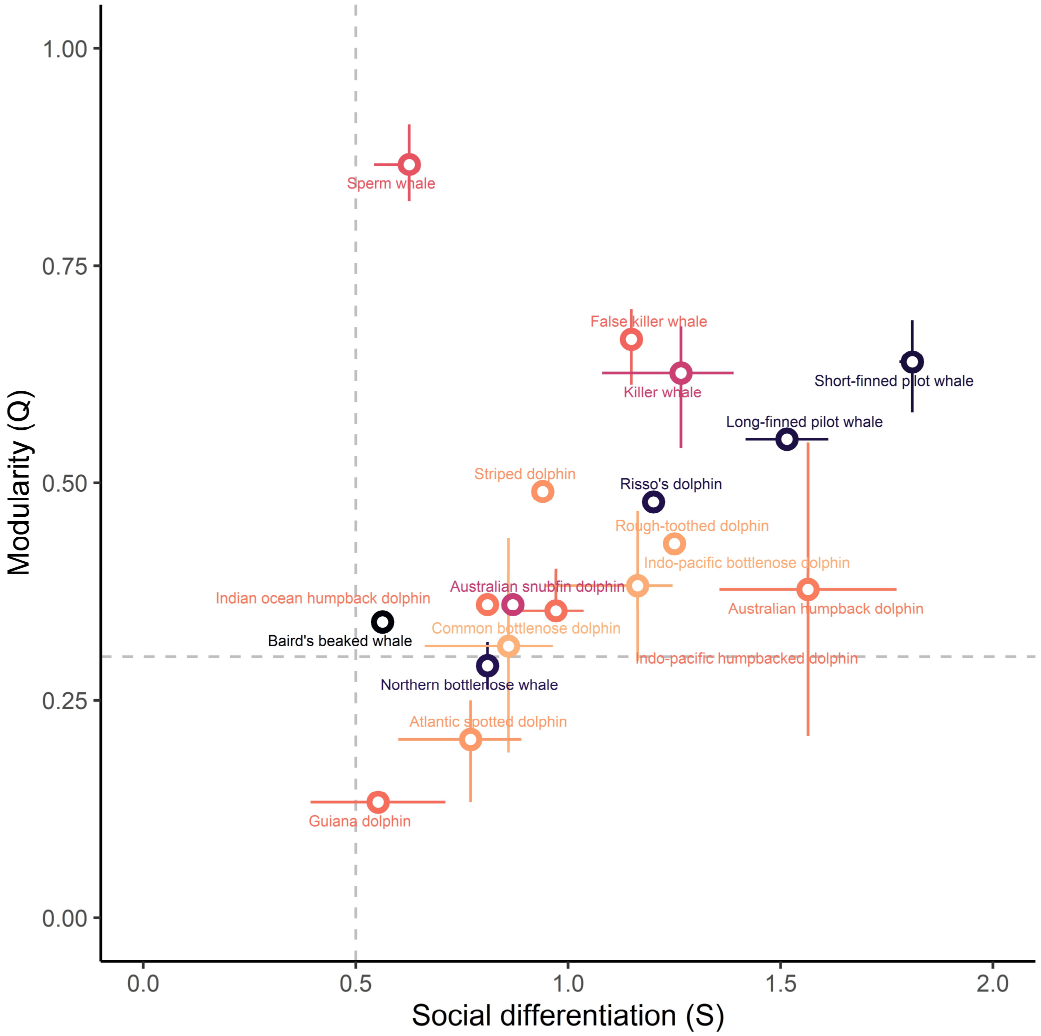

Figure 2 – Empirical relationship between social network modularity and social differentiation across toothed whales. Points represent means, across studies, while lines represent 50% inter-quartile intervals, calculated for species with at least two measures of the given trait. Typically, values of Q above 0.3 (dashed horizontal line) are considered to imply the presence of social divisions within a community, while values of S above 0.5 (dashed vertical line) are considered to imply the presence of well-

differentiated social relationships.

Predictors of social structure in toothed whales

Toothed whales with longer lifespans form more modular social networks (β = 0.4, pd = 98.4%, where β is the effect of of a 1-SD increase in lifespan on modularity on the logit scale; Figure 3A), over and above phylogenetic covariance. Modularity was also greater in larger toothed whale species, regardless of whether body length was log-transformed (β = 0.55, pd = 97.3%; when body length was log-transformed: β = 0.53, pd = 98.2%). A positive but less certain relationship was identified between modularity and age at maturity (β = 0.29, pd = 94%). Species where females were similar in size or (more rarely) larger than males also formed less modular networks, i.e., were less likely to form distinct social units (β = -0.64, pd = 99.8%). Though broadly similar patterns were observed for social differentiation, S, these effects were generally weaker and less certain (Figure 3 G-J). The traits most strongly associated with social differentiation were lifespan (β = 0.1, pd = 89.7%, where β is the effect of a 1-SD increase in lifespan on social differentiation on the log scale), age at maturity (β = 0.09, pd = 89.8%), and sexual size dimorphism (β = -0.12, pd = 88.5%). This can be interpreted as weak evidence that extended juvenile periods and lifespans are linked to the formation of specific social bonds. Broadly, we find stronger evidence that organizational social complexity (more specifically, social network modularity) is related to life history traits, when compared to relational social complexity. This may be related, in part, to the smaller sample sizes available for social differentiation given the exclusion of studies that did not report using the likelihood method for estimation. Sample sizes varied across these models due to the availability of measures of each trait (See Table S6 for the number of observations and number of groups for each varying effect).

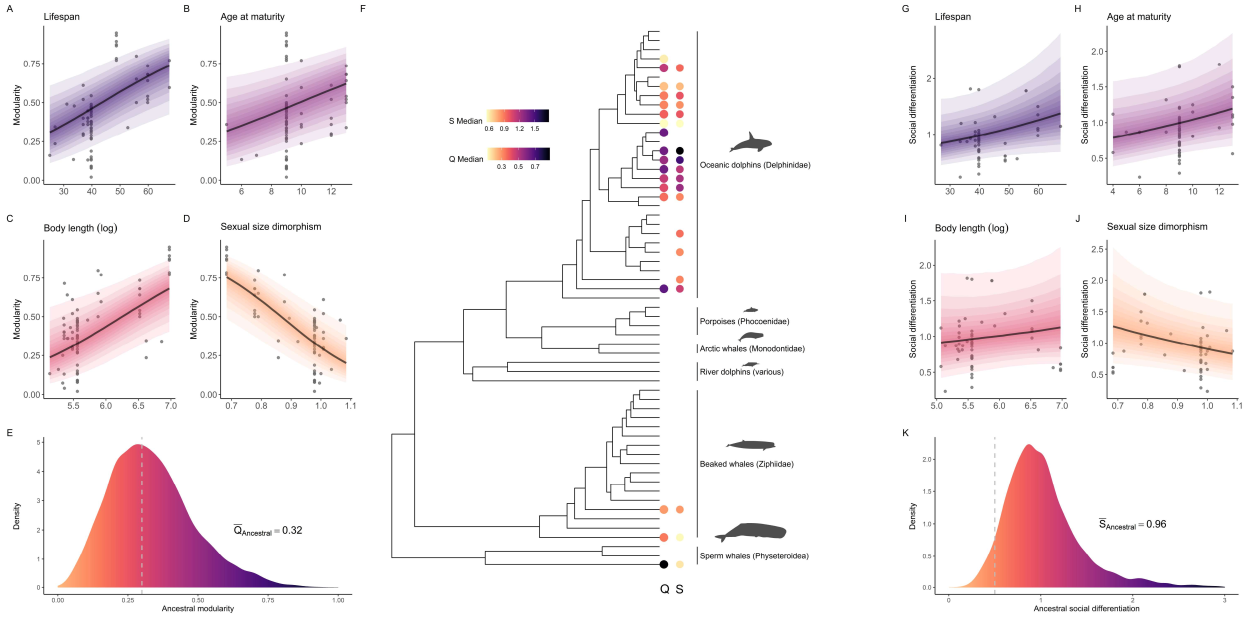

Figure 3 – (A-D) Predicted probabilities of modularity as a function of toothed whale life history traits. (E) Posterior of the estimated modularity of the common ancestor to all toothed whales included in our sample, with $\bar{Q}$ showing the median of the posterior and the dashed line showing a typical threshold for non-trivial divisions in a community. (F) Phylogenetic tree of toothed whales showing median observed modularity and social differentiation. (G-J) Predicted probabilities of social differentiation as a function of toothed whale life history traits. (K) Posterior of the estimated social differentiation of the common ancestor to all toothed whales included in our sample, with $\bar{S}$ showing the median of the posterior and the dashed line showing a typical threshold for differentiated social relationships.

We used these models to infer the social structure of the last common ancestor to all toothed whales. Predictions for these ancestral states were uncertain, with a range of social network structures being possible (Figure 3E,K). However, based on fossil evidence that early odontocetes were approximately 2.5 m in length (29), our model predicts that ancestral toothed whales were most likely to form social networks with some clustering, given a median predicted modularity of 0.32, just above the typical threshold for divisions within a community (30). However, the posterior probability of ancestral modularity being greater than 0.3 was just 55%, meaning that non-modular networks were almost equally likely. Based on the same assumed ancestral body size, there was a somewhat clearer picture for ancestral social differentiation, with a 99% posterior probability of ancestral toothed whales having non-homogenous relationships ($S > 0.3$) and a 95% probability of ancestral toothed whales having well differentiated relationships ($S > 0.5$). In other words, a reliance on specific social relationships (rather than homogenous patterns of social association) has likely been a component of whale behavior for at least 34 million years.

Intraspecific variation in social structure

Several studies in our literature search highlighted variation in social structure within the same population. For example, strong seasonal differences in social differentiation were observed in bottlenose dolphins (change in S from 0.72 to 0.20; 31) and dusky dolphins (*Lagenorhynchus obscurus*, change in S from 0.58 to 1.12; 32). Across populations, substantial intraspecific differences in social network measures were evident. For example, we found descriptions of Australian humpback dolphin (*Sousa sahulensis*) populations that were entirely fluid (Q = 0.04; 33) and that formed distinct social units (Q = 0.715; 34). Intraspecific variation in social network structure was most obvious for bottlenose dolphins, which are perhaps the best-studied species of cetaceans in many respects. Though findings were generally consistent with the expectation that bottlenose dolphins form fairly fluid social networks with well-differentiated relationships, there was substantial variation in both S and Q across populations (Figure 2).

Generally, we caution that variability in observed social network traits will include genuine biological plasticity as well as measurement error, differences in analytic methods, etc. Though we were only able to quantify intraspecific variation in social network structure for 12 species, a clear pattern emerged where dolphins generally displayed the greatest variability, while larger species such as sperm whales and killer whales showed more limited variability. This was supported by phylogenetic models, with smaller toothed whales showing a wider range of modularity (effect of body length on variability: β = -

0.69, pd = 99.3%), as well as species where females were similar in size or larger than males (effect of sexual size dimorphism on variability: β = 0.55, pd = 98%).

Evidence for coevolutionary patterns

While the previous analyses reveal patterns of trait association among extant species, a more satisfying approach is to test how these traits co-evolved over time (35). The results of the coevolutionary models were mostly uncertain, with wide posteriors straddling zero for cross-selection (i.e., bidirectional) effects between social structure and life history (Figure S2). However, we found strong evidence that social modularity influenced subsequent extensions in body length (Figure 4A). More specifically, toothed whales with more divided social networks tended to become larger over evolutionary history, while whales with more fluid or cohesive networks tended to become smaller (Figure 4B). This effect was clear when considering un-transformed body lengths (99.8%), but less certain when considering log-transformed length (87.3%). Otherwise, we found weak evidence that changes in both lifespan and sexual size dimorphism (SSD) may have influenced subsequent changes in modularity (lifespan promoting increases in modularity: 87.4%, females being similar or larger in size to males promoting decreases in modularity: 92.6%). While these findings do not provide exclusive support for a specific evolutionary pathway (e.g., social structure to life history, vice versa, or reciprocal causation), they show that the formation of stable social groups may likely promoted subsequent changes in life history. There was little evidence of temporal precedence between social differentiation and life history traits (Figure S2), perhaps relating to its somewhat lower phylogenetic signal.

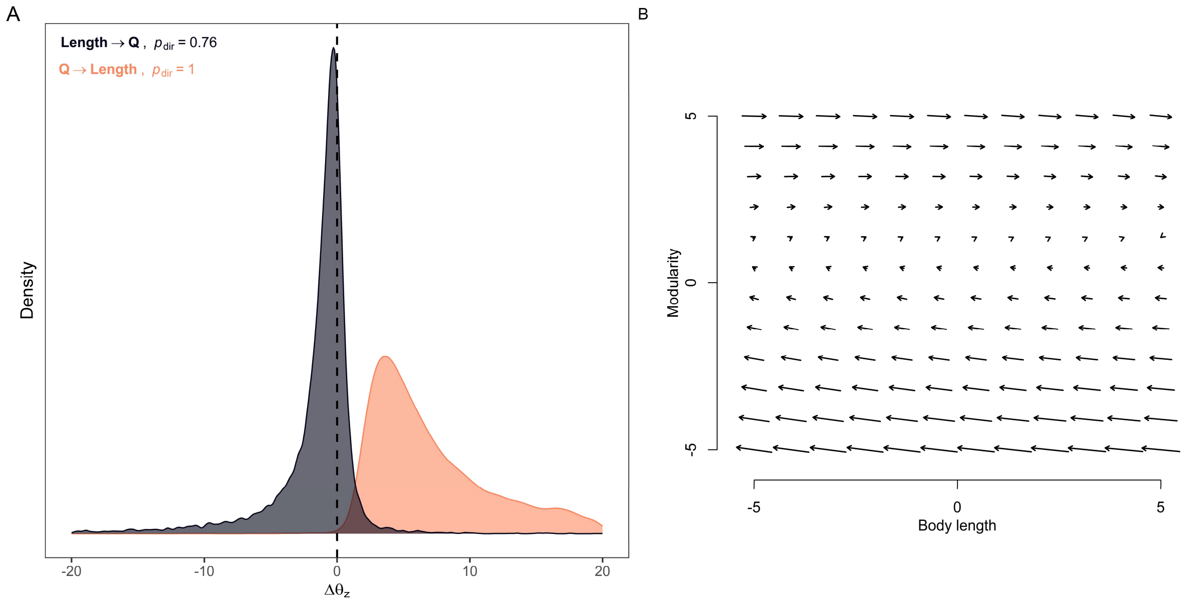

Figure 4 – Changes in social network modularity promote changes in body length in the evolution of toothed whales, but not vice versa (i.e., a unidirectional effect). (A) Posteriors of estimated change in body length and social network modularity resulting from a median absolute deviation increase in the opposite trait. (B) Flowfield diagram showing expected evolutionary changes from a given position in trait

space: whales with lower modularity will evolve to be smaller while whales with higher modularity will evolve to be larger. Variables are shown on the latent scale, with the length of arrows indicating the strength of change. Effects for both panels were estimated using a generalized dynamic phylogenetic models (GDPMs).

Discussion

Social evolution has been a focus of even the earliest comparative phylogenetic research (36). However, progress has been limited by a reliance on coarse proxies of social behavior such as categories of social organization, or group size. Our study leverages existing social network analyses to investigate the phylogenetic roots of social relationships in toothed whales. While social network measures are strongly influenced by sampling and analytic decisions, these findings suggest that they can capture broad patterns and offer insights into the factors underlying social evolution. Quantitative comparisons of social networks across populations or species remain relatively rare, often include just a few species or populations, and are often targeted at primates (16). Here we apply this approach to toothed whales, providing the first evidence, in any taxon, that social network structure and life history traits evolve in a correlated manner.

Across toothed whales, species with longer lifespans, larger bodies, and (perhaps) delayed sexual maturity formed more modular social networks (Figure 3). In other words, they were more likely to rely on stable social units or groups (e.g., as in killer whales, sperm whales), often based on female kinship (37). The same was true of species with sexual size dimorphism, specifically where males tended to be larger than females. Weiss et al. highlight three potential drivers of social network structure in toothed whales: maternal investment, sexual dimorphism, and ecology (22). Adjudicating between these factors is expected to be difficult however, due to the covariance between them – in fact, all three are expected to be closely associated with body size. In any case, our analysis provides empirical evidence that this constellation of life history traits evolves in tandem with social structure. Moreover, our analysis shows that lifespan may also be important. Stable social groups, and relationships within them, may be associated with lifespan via several mechanisms. First, stable social relationships may reduce the risk of extrinsic mortality, supporting extended lifespans (2), but see (38). Reciprocally, longer lifespans should allow individuals to invest in specific relationships where benefits might be delayed (11). This would also predict a strong link between social differentiation and lifespan, i.e., that longer-lived species would have a greater diversity of relationship types, including cooperative social bonds. However, we only found weak evidence for this in our analyses (Figure 3). This weaker effect, compared to modularity, may indicate that “relational” social complexity is less tied to life history in toothed whales, and/or may reflect the smaller sample size available for measures of social differentiation.

This study complements research on evolutionary links between life history (and lifespan specifically) and other measures of social behavior. For example, Kamilar et al. found no effect of group size on longevity in a phylogenetic analysis of 253 mammals, with a potentially negative relationship in artiodactyls (39). A comparative analysis of 39 bird species found that cooperative breeding strategies were more likely to evolve in species with longer lifespans (40). More recently, a study of 152 species from various taxa found that species classified as more social (using a hierarchy of 5 categories) were more likely to live longer, aligning with our findings (41). However, this study relied on a continuum of social complexity where “social” was defined by the presence of stable groups, implying a precedence of organizational over relational complexity (15), and highlighting the definitional challenges that comparative social network approaches may help to overcome.

While phylogenetic signal was slightly lower for social differentiation when compared to modularity (Figure S1), both were more similar among more closely related species. Previous attempts to quantify the phylogenetic signal of social behavior have provided mixed results. For example, though studies on primates have indicated that social organization is fairly conserved (42, 43), a meta-analysis suggested that measures like group size or time spent socializing appear largely independent of phylogeny (44). Generally, behavioral traits are expected to be more flexible and thus show reduced phylogenetic signal than physical traits like body size (45). This was supported by our analysis, with all life history traits except sexual size dimorphism showing greater phylogenetic signal than social traits. As expected, we detected high instraspecific variability in social network structure, with smaller species showing greater plasticity than larger species.

There appeared to be a generally positive relationship between modularity and social differentiation across species (Figure 2). This was not unexpected, as social divisions necessitate some degree of differentiation in relationships, but allows us to consider deviations from the general trend. For example, sperm whales stand out as forming the most modular networks (reflecting kin-based social units) but only moderate social differentiation compared to other species. One possibility is that the prevalence of alloparental care results in more similar relationships within sperm whale units, as a greater reliance on a single mother-offspring bond (in other species) could contribute to the overall diversity of social relationships. Indeed, sperm whale calves are often the most central individuals of their social community (46). More broadly, this social strategy may differ from other species such as pilot whales, which appear to be investing in differentiated relationships while relying on the organizational stability provided by more modular networks (Figure 2).

There has been a great deal of caution around comparing social networks given that their topology can be influenced by both sampling and analytic decisions. For example, chacma baboon (*Papio ursinus*) networks constructed using interaction vs. proximity data differed, though some broad characteristics such as the differentiation of social relationships were consistent (47). Amidst these challenges, social networks offer a major advantage over the potentially subjective classifications that are often relied on (e.g., “group-living”, “solitary”), by quantifying patterns of social relationships. In addition to the fact that field methods for studying social behavior in cetaceans are more constrained than in some other taxa (i.e., relying almost exclusively on photo-identification), the vast majority of studies in our database used the same software, SOCPROG (30), to quantify network structure, likely resulting in greater overlap in analytic methods.

Scale can also be a challenge for comparative analysis of social networks (17). For example, our analysis required making decisions about what constitutes a “population”, particularly for smaller, coastal species (e.g., dolphins). For example, several studies of bottlenose dolphins included spatially and socially distinct (though not isolated) communities (48–51), likely resulting in more divided and differentiated social networks. Thus, part of the variability in social network structure may result from differences in the scale at which animals are studied. However, it is not biologically trivial that dolphin populations can form adjacent but socially divided communities. The capacity to maintain separate communities with some social-spatial overlap may imply that dolphins exhibit aspects of social psychology and cognitive capacities that underlie modularity in other species (e.g., strong concepts of group membership, long-term memory for specific individuals; 52). Indeed, most dolphin populations in our study are considered to exhibit meaningful social divisions (modularity >0.3), though they are generally considered to have fluid social networks.

Dynamic coevolutionary analyses showed that the formation of more modular networks (i.e., stable groups) promoted subsequent evolutionary changes in body size (Figure 4). That a weaker, but still positive, effect was found when using log-transformed body lengths (Figure S2) suggests that the intense modularity of the largest toothed whales is driving some, but not all of this historical pattern. This finding highlights that social structure can be a leader, rather than follower, of life history evolution. That the strongest evidence of a specific causal history involved body length may also simply reflect the fact that of the (highly correlated) life history variables, it had the greatest coverage, and most consistent measurement, across species. The specific mechanisms of this causal precedence are unclear, and may involve mediating pathways. For example, modularity might influence foraging success, which in turn could influence life history variables.

We also found preliminary evidence that life history has shaped social structure: there was a 93% posterior probability that sexual size dimorphism triggered the formation of stable social units (i.e., modularity; Figure 4). This adds a causal dimension to the finding that sexual size dimorphism and modularity exhibit correlated evolution (Figure 3). This would appear to align with the hypothesis that protection from sexual harassment has been a factor in the evolution of stable groups among toothed whale species (25). More specifically, it suggests that stable groups may have, in part, been a response to buffer against changing sex-specific body sizes. We also found weak evidence that lifespan may influence subsequent changes in modularity (*pd* = 87%). While no GDPM identified evidence of bidirectional causation between specific pairs of traits, taken together these findings suggest that social network structure and life history have been intertwined in the evolution of toothed whales.

Together, these findings provide new evidence for the joint origins of life history and social network structure. Evidence that social networks covary with lifespan and age at sexual maturity also support theory that social relationships will be strongly shaped by demography, and vice-versa . Our results suggest that how toothed whales form social relationships varies both between and within species in predictable ways. Moreover, our coevolutionary approach demonstrates that stable social groups can play a leading role in the evolution of other traits, even those as fundamental as body size. These results reify that social relationships are not simply an emergent property of local ecological contexts, but an evolving trait with the capacity to shape other fundamental aspects of species biology.

Materials and Methods

Building a database of social network traits

Species list

We used a recent list of toothed whale species compiled by the Society of Marine Mammalogy for our study (Table S4; 18). We included two *Tursiops* species: *T. truncatus* and *T. aduncus*. Dolphins identified as *T. australis* (a disputed subspecies) were treated as *T. aduncus* in our analysis (See 53). We also did not distinguish between *T. truncatus* and the newly distinguished *T. erebennus* which is found in coastal areas of Eastern United States.

Key social network traits

We consider two measures of social networks, modularity (Q) and social differentiation (S), each of which are based on the pattern of social relationships among members of a population. Modularity represents the degree to which a social network can be divided into distinct sub-units, and ranges from zero to one, with values greater than 0.3 often assumed to imply important divisions (3). Social differentiation is the estimated coefficient of variation of pairwise relationships within a social network. Here we focused on measures of social differentiation calculated using the maximum likelihood method, excluding less accurate techniques such as Poisson approximation. Communities with homogenous relationships, i.e., individuals associate similarly with any other individual, will have lower values of S (e.g., < 0.5), while values greater 2.0 are indicative of highly variable relationships (i.e., preferred and non-preferred social partners). Note that social differentiation is distinct from the Shannon entropy of social associations, which is also sometimes represented as "S" (54). While we expect some imprecision in estimates of Q and S for particular studies and populations, they provide a useful lens into broad patterns of social structure across the toothed whales. Though the empirical relationship between Q and S has rarely been quantified, modularity implies some level of social differentiation (as within- vs. between-group relationships should differ). The opposite is not necessarily true, as it is possible to have highly differentiated social relationships without any overarching group structure of division into social units.

Literature search

We systematically searched the literature for estimates of modularity and social differentiation in toothed whale populations (See Figure S3 for PRISMA diagram). First, we used Web of Science to conduct a systematic search of available literature. This was done by searching for the scientific name of each species with "(social network OR social structure)". The resulting 591 unique articles were screened to identify those in which social structure or social organization was among the primary topics of the article. Here we also excluded review articles, meta-analyses, and studies on captive animals. We also limited our analysis to findings published in English.

Whenever a value of social differentiation or social network modularity was reported, we recorded the following details: the value of the measure, the standard error of the measure (if reported), the method used to calculate associations (e.g., half-weight index, simple ratio index, etc.), and whether the network was restricted to either sex. We also took note of any special circumstances surrounding the measurement that might impact the comparability of the social network to those from other studies. This search was done on August 17, 2024. We supplemented these findings with a secondary search using Google Scholar, which allowed full text searches for each scientific species name with "modularity" or "social differentiation". We also examined the works cited sections of found articles as well as a recent review of toothed whale social networks (22), to identify any studies that we had missed. Any potentially useful articles were then assessed manually and any reporting empirical measures of Q or S were included in the comparative database.

Extracting independent measures of social network structure

Comparing social networks is challenging as both sampling and analytic decisions can impact network structure and associated metrics (17). Our protocol for extracting social network measures from the toothed whale literature was guided by the joint aims of 1) identifying broadly comparable measures, and 2) avoiding pseudo-replication when multiple studies were conducted on the same populations. While cetacean social networks are generally estimated using similar techniques (pairwise or group-based associations from photo-identification data), the scale of sampling can vary substantially across studies, and is likely to impact both modularity and social differentiation. To address this potential bias, we focused our analysis on social networks calculated at the population scale. This meant excluding analyses where Q or S was calculated within populations (e.g., based on associations within pre-defined clusters or social units), and instances where networks may include multiple, non-interacting populations (e.g., separate populations of dolphins along a large coastline). Our sample included regions with partially distinct communities, so long as some interaction between communities had been observed (e.g., 51).

We assessed all studies for geographic and temporal overlap to ensure that our analysis did not include analyses of the same underlying data, or of the same population at a given point in time. When multiple studies reported values of Q or S from the same site and time, we prioritized studies with 1) both males and females analyzed in the same network, 2) that contained the most data (i.e., from the greatest time period), and 3) that reported both Q and S. If overlapping studies each reported one of the two social metrics (Q or S), both could be included in subsequent analyses. Overall, few exclusions were deemed necessary: of 99 studies with useful measures Q and/or S, 14 had measures that were excluded from subsequent analyses. Note that when measures of Q or S were calculated for non-overlapping time periods (e.g., different years), we included the estimated measures for each time period in our analysis. When measures were calculated for multiple sampling periods or definitions of associations (e.g., 55), we selected the version that most closely approximated associations with a sampling period of days, which is typical in analyses of toothed whale social structure. Otherwise, we used the mean of measures calculated using different methods, unless a particular method was demonstrated to be most accurate (e.g., 56). See Table S7 for additional detail on criteria for extracting social network measures. Most studies in our database used SOCPROG (30), an open-source software, to run these analyses.

New analyses of sperm whale social networks

Social network traits are rarely measured at the level of populations for sperm whales, with most studies focusing exclusively on associations within or between stable social units (also noted by 22). To include sperm whales in the present analysis, we conducted our own analyses of social differentiation and modularity of sperm whale populations using three long-term photo-identification studies led by, or associated with, the Whitehead Lab or The Dominica Sperm Whale Project. These studies took place in the waters off the Galápagos Islands, Chile, and Dominica. To enhance comparability with other studies, we used half-weight indices applied to associations defined as photo-identifications within 10 minutes with days as sampling periods (typical decisions for analyzing toothed whale networks). Full detail on these analyses, including fieldwork, data processing, and the resulting values of S and Q are provided in the Supplementary Materials accompanying this article.

Toothed whale life history traits

Though we initially considered several potential sources of life history data (e.g., 57, 58), a new database of toothed whale life history traits available in the *marinelifehistdata* package in R (59), was found to be most comprehensive. In addition to superior species coverage, this database provided sex-specific measures for several key traits including body length and age at maturity. Life history measures of toothed whales are almost always drawn from non-captive populations, avoiding some of the potential biases stemming from life history databases of primates, for example (60). However, heterogeneity in the probability of individuals being included in a sample likely induces some bias in measures of cetacean life history. Historical whaling data is a valuable source of key measures for whales (e.g., body length, age and sex structure), but may involve the selective harvest of older individuals, for example. However, the database we used try to address such biases, e.g., including a parameter to account for age-based differences in sampling rates (See Supplementary information of 19). With the obvious exception of sexual size dimorphism, we focused on female-specific measures of lifespan, age at sexual maturity, and body length for our analyses. This decision was based on the fact that female relationships are ubiquitous and fundamental in toothed whale networks, whereas adult males in some species (e.g., sperm whales), may exhibit distinct social-spatial behavior.

Species-specific measures of *lifespan* were drawn from a database that employs age-specific mortality models to estimate the age by which 90% of adulthood is complete (19, 61). Though both male- and female-specific estimates of lifespan were estimated, we used female lifespan alone as a predictor of network structure in our analyses.

We chose to use *body length* as a measure of size, as it is highly correlated with body mass, but is generally easier to measure in toothed whales thus is available for a larger proportion of species (19, 57). The *marinelifehist* database includes estimates of body length for males and females, though in some instances, due to missing data, sex-specific values were estimated based on mixed-sex measurements or measurements from the opposite sex (See Supplementary Materials of (19) for details). We used the log-transformation of mean female length for our main analyses. However, to ensure the robustness of our results to this transformation, we also re-ran key analyses using un-transformed female body length.

For species where data for both male and female body length were available, we quantified sexual size dimorphism (*SSD*) as the ratio of female:male length. This meant excluding measures where data were only available for mixed-sex groups. There were six species with sex-specific data *and* identical mean lengths reported for each sex. While some of these were expected given identical or very similar size ranges reported in sex-specific data (e.g., for Cuvier's or Goose-beaked whales; *Ziphius cavirostris*), there was at least some evidence of non-trivial sex-specific size differences for three of these species (*Pontoporia blainvillei*, *Lagenorhynchus obliquidens*, *Feresa attenuata*). Accordingly, we were less confident in the assumption that males and females of these species were of similar body length, and excluded them from analyses involving SSD. While males are larger than females in most toothed whale species (SSD < 1), there are several species where females are slightly larger (SSD > 1). This variation, together with an assumption that relatively larger males pose a greater threat, allowed us to assess evidence for the hypothesis that social structure among female whales is influenced by the risk of harassment by male conspecifics (25).

Measures of *age at maturity* (species- and sex-specific means) were drawn from the same database available in the *marinelifehistory* package (61). Additional details on the calculation of age at maturity and body length can be found in the Supplementary Materials of (19).

Phylogenetic relationships

We linked species for which we had social network data to the most recent and comprehensive time-calibrated phylogenetic tree of toothed whales (62). There were two species (the Indian Ocean and

Australian humpback dolphins; *Sousa plumbea* and *Sousa sahulensis*) for which we had social network measures but were absent from the tree. For both we used the inferred phylogenetic position of a close sister taxon (See Table S5).

Modelling relationships between social structure and life history

Next, we fit phylogenetic multilevel models to test whether social network measures S and Q are related to key life history traits. The phylogenetic tree was converted into a covariance matrix that specifies the evolutionary distance between each pair of species. This allowed us to model species-specific varying effects (i.e., random intercepts) that could be correlated with one another based on shared evolutionary history. Here we used a simple Brownian motion model of evolution, whereby traits diverge linearly as a function of evolutionary distance. Given that we had repeated measures of S and Q for several species, we incorporated an additional varying effect to account for species-level differences that were not explained by the pattern of phylogenetic history itself. This additional species-specific effect may may absorb related sources of variation such as species-specific habitat preferences or foraging behavior. We also included a varying effect for populations. Finally, to account for the possibility that measures of Q and S calculated vary depending on the association index used, we also included a random effect for association index. While most of our measures were based on HWIs, we included 15 measures based on the simple ratio index (SRI), 5 measures based on the half-weight index conditional on additional predictors (i.e., generalized affiliation indices or GAIs; 63), and 1 measure based on the social affinity index, SAI (3). Three additional measures from studies that did not report an association index were excluded. Models with modularity and social differentiation as response variables were fit using beta and gamma families, respectively, and were fit using weakly informative priors in the *brms* package in R (64). Specifically, we used normal(0,1) or normal(0,2) priors for model intercepts, and normal(0,1) priors for effects of life history traits on Q or S, and default priors from *brms* for all other parameters (student(3, 0, 2.5) for sd terms, and gamma(0.01, 0.01) for shape parameters).

These models were also used to estimate the social structure of ancient toothed whales (65). One approach for inferring ancestral states is to fit a phylogenetic model with only species and phylogenetic effects, interpreting the intercept as the expected state prior to any subsequent changes. However, when key traits of ancestral species are known, incorporating additional traits to make specific predictions can improve accuracy (see 43). Following their divergence 34 million years ago, ancestral toothed and baleen whales tended to be small, with a body length of approximately 2.5 m (29). Thus, we fit an additional multilevel phylogenetic model with body size in addition to species and phylogenetic effects. We then used this model to predict the social structure for an ancestral toothed whale with no varying effects relating to species or subsequent phylogenetic change, and a body size of 2.5 m.

A series of additional multilevel phylogenetic models were fit with only phylogenetic covariance as a predictor. These allowed us to estimate the total variance explained by phylogeny for each social network and life history trait. For these models, we used weakly informative priors: normal(0,1) for the intercept, and exponential(1) for the variance terms.

Quantifying intraspecific variation in social structure

Recent studies have begun to quantify *variability* in social behavior as an important target for comparative research. For example, intraspecific variation in social organization (IVSO) appears to have been ubiquitous in the evolution of artiodactyls (66), and was present in ancestral primates (43). Here we quantify within-species variability in social network structure as the coefficient of variation (standard deviation divided by the mean) of either modularity (Q) or social differentiation (S), for any species with at least two measures. We then related this intraspecific variability in network structure to the same life history traits as above: body length, age at female maturity, lifespan, and sexual size dimorphism in multilevel phylogenetic models. While this variability will be influenced by several factors such as the non-random sampling of global populations and differences in the scale at which species are sampled, it serves as a coarse measure for population-level plasticity in social structure.

Testing for causal coevolution

Evolutionary correlations between life history traits and social structure could result from several causal histories. Extensions in life history (e.g., increasing body size, delayed maturation, etc.) could facilitate changes in social structure. Oppositely, changes in social structure could drive subsequent changes in life history traits. Alternatively, both life history and social structure could influence each other via bidirectional effects (i.e., coevolution). We used generalized dynamic phylogenetic models (GDPMs), a new type of model for phylogenetic coevolutionary analyses (67), to test which of these explanations was most consistent with toothed whale data. First applied to human behavior and cultural phylogenies (35, 68), these models go beyond "static" estimates of evolutionary correlations to explore the specific temporal sequences of evolutionary change. This allows researchers to estimate bidirectional effects, testing for evidence of directed coevolution, i.e., reciprocal causation.

We fit a series of models exploring the (co)-evolution of each social network trait (Q, S) with each life history trait in our analysis (female body length, log-transformed female body length, female lifespan, female age at maturity, and sexual dimorphism). All measures were scaled prior to model fitting, and we used default priors provided by the *Coevolve* package (67), with Gaussian priors for social network and life history traits. Additional parameters capturing species-level variation were included to account for the inclusion of repeated measures of social network traits. Bayesian imputation was used to accommodate missing observations of either social network or life history traits, allowing us to make the best possible use of the data.

All analyses were organized using the *targets* package and run using R version 4.3.2 (69). Models were assessed diagnostically based on $\hat{r}$, effective sample sizes, and posterior predictive checks. As the GDPMs were computationally intensive, they were fit using the *Beluga* computing cluster of the

Digital Research Alliance of Canada. Unless otherwise stated, effects are reported as posterior means alongside the probability of a directional effect (*pd*). Silhouettes of example species shown in Figure 3 were sourced using the *Rphylopic* package (70), including works by Chris Huh (Licence https://creativecommons.org/licenses/by-sa/3.0/). Data and analysis scripts are available upon request.

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