Quantifying Social Complexity in Cetaceans

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If there’s one fact that scientists who study cetacean sociality can agree on, it might be this: Cetacean societies are complex. Cetaceans live in social worlds that are both dynamic and highly individualised. Most populations exhibit “open” social networks, with every individual in the population interacting (or at least associating) with many partners. These interactions are dynamic: partners change over days, weeks, months and years. Individuals must track and manage their relationships with cooperative partners, potential mates, and competitors across various contexts, with fission-fusion dynamics ensuring that the set individuals in the social environment regularly changes. Some populations show remarkably complex social structure, with multi-level cooperative alliances, culturally defined vocal clans, and large-scale social transmission of novel behaviour (Bigg et al., 1990; Cantor et al., 2015; Connor and Krützen, 2015; Garland et al., 2011). Thus, there is much interest in understanding, quantifying, and comparing social structure and complexity across cetaceans. However, given the difficulties inherent in studying the societies of marine animals, the relevant behavioural measures needed to conduct such analyses are often sorely lacking (Groot et al., 2023).

Why study the diversity of social complexity in cetaceans (or any taxa)? Comparative studies of social complexity are often motivated by the “social brain hypothesis” (Dunbar, 1998). Stated briefly, this hypothesis suggests that the cognitive challenges associated with mapping and managing complex social environments has driven cognitive evolution, leading to enlarged brains. Originally developed as an explanation for the extreme brain sizes and cognitive abilities of humans and other primates, this hypothesis has also been invoked to explain the evolution of the cetacean brain size, particularly the extremely large brains of dolphins and sperm whales (Connor, 2007; Fox et al., 2017; Marino et al., 2007). Further interest in social complexity is driven by hypotheses linking the social environment to the evolution of intricate communication systems (Freeberg et al., 2012; Sewall, 2015), a hypothesis also highly relevant to whales and dolphins which often exhibit complex vocal behavior. Furthermore, understanding which evolutionary pressures lead to social complexity is fundamentally interesting in and of itself. Theoretical and empirical work has investigated how longevity (Lucas and Keller, 2020; Silk and Hodgson, 2021), ecology (He et al., 2019), and kinship (Lukas and Clutton-Brock, 2018) drive social complexity. As a taxa with immense variation in ecology, life history, and social organization, cetaceans represent a unique opportunity to examine and test these hypotheses.

To answer questions relating to drivers and consequences of cetacean social complexity, we need to develop well-motivated, quantitative methods for quantifying social complexity, and then apply these methods to numerous species of cetaceans. In this chapter, we present a new approach to describe and understand the diversity of social relationship complexity in cetaceans. In particular, our method and definition focus on understanding the uncertainty, or unpredictability, of individuals' social environments. First we discuss what social complexity is and we provide our definition of a particular kind of social complexity (relational complexity - *uncertainty* or *unpredictability* that individuals face in their social environment), and a method to measure it. Finally, we summarize this measure of social complexity across multiple species of cetaceans and, building on these initial results, suggest priority areas for future research.

*What do we mean when we say “social complexity”?*

Let’s take a step back, and start with a simple question: what do we, as biologists, mean when we say a society is “complex”? How can we classify or quantify the degree of complexity in a particular animal group or population?

We’ll start with a brief consideration of the term “complexity.” There is a large body of literature on the philosophical and mathematical nature of complexity, much of it beyond the scope of what we can cover here. Some authors have simply argued that “complexity” is the opposite of “simplicity,” but we find this definition somewhat unhelpful in this context as it does not get us any closer to something that can be measured. One widespread concept is that complexity lies somewhere between complete order and complete randomness; there must be structure in complex systems, but not so much structure that the behaviour of the system is entirely predictable (Page, 2010). Slightly more concretely, complex systems have been described as those that have many elements of many different types, which interact in diverse ways (McShea and Brandon, 2010). For a more in-depth discussion and review, see Freeberg et al. (2012).

How can we apply these concepts to societies? Working off the framework introduced by Hinde (1976), we can consider individuals in a society to represent the “elements” of the system which interact socially. Individuals of different types (age, sex etc.), from the perspective of sociality, may occupy different “social roles” (such as helpers and breeders). Moreover, interactions between individuals (elements) scale up to various forms of social relationships (Hinde, 1976) (e.g. cooperative, aggressive, competitive etc.). So, using this framework, we can define a complex society as one in which individuals have many different social roles and/or diverse social relationships. These two features of complex societies were formalized by Lukas and Clutton-Brock (2018) into the concepts of “organizational” and “relational” complexity. Societies with high “organizational” complexity exhibit a wide array of well-defined social roles, often with strong division of labour and cooperative breeding with defined breeders and helpers. In contrast, “relational” complexity is found in societies with diverse social interactions, such as coalition formation, dominance hierarchies, and aggression. These two types of complexity do not, it seems, go hand in hand in animal societies. Indeed, they seem to emerge from different evolutionary pressures, particularly kinship structure (Lukas and Clutton-Brock, 2018).

Here, we will focus on “relational” complexity. Our reasons are two-fold, both motivated more by practicality than scientific interest. First, methods for measuring relational complexity are arguably more developed than methods for measuring organisational complexity, as measuring the latter largely relies on reports of the presence or absence of particular features of social organisation (e.g. cooperative breeding, caste systems). Second, we generally have more information about the structure of social relationships in cetacean societies (Möller, 2012; Rendell et al., 2019; Weiss et al., 2021) than we do about social roles. The literature on social roles in cetacean has revealed some interesting patterns in well-studied species. In killer whales, there appear to be age-sex based roles in social units, with older females being more likely to lead group movement (Brent et al., 2015) and different age-sex classes potentially performing different behaviors during group foraging (Baird and Dill, 1995). Similarly, in bottlenose dolphins, there is consistent differentiation between leaders and followers in group movement (Lewis et al., 2011; Lusseau, 2007) and individuals may specialize in particular roles during group foraging (Gazda et al., 2005), although the underlying factors determining social role are less clear in this species. The presence of alloparental care in several cetacean species is also indicative of organizational complexity within social groups (Augusto et al., 2017; Gero et al., 2009). These findings, however, are typically limited to well-studied species and often describe social roles within specific contexts, making it difficult to conduct broad comparative studies of organizational complexity in cetaceans. Studies aimed at better understanding of social roles within cetacean societies may be a fruitful area for future research.

In addition to the concept of diverse interactions between parts, we would like to add one more key feature of social complexity, motivated by evolutionary hypotheses of social complexity as a driver of cognition and communication: complex societies should pose a challengeto the individuals within them. We do not go as far as Bergman and Beehner (2015) to suggest that measures of social complexity must reflect a *cognitive* challenge, as we wish to avoid circular reasoning in potential tests of the social intelligence hypothesis; there may be many ways for animals to deal with the challenges of complex societies, but we propose that the challenge must be present.

Combining the concept of diversity in interactions and relationships with the idea of social challenge, we propose a broad working definition of relational social complexity: We suggest relational complexity can be operationalized as the *uncertainty* or *unpredictability* that individuals face in their social environment (Figure 1). To illustrate this idea, let’s consider three extreme hypothetical cases. First, think of an animal population where every individual has exactly one social partner, and categorically does not interact or associate with any other individuals. This individual would have an extremely predictable social environment, even if there were cognitively complex factors at play (such as the recognition of their social partner). Second, consider a population where individuals associate with others at random, but all individuals are functionally identical in terms of their social interactions. While each animal may have a wide array of social associates, their social environment is functionally constant; they are best served by behaving consistently in all their social interactions, just like the first animal with a single constant associate. Finally, consider a population with a large, open social network, but where every single relationship is unique and therefore consists of different types of social interactions. Animals in such a population would have very little baseline certainty in the types of interactions they were going to have in any given social group. Under our definition, the first two societies would both have very low social complexity, despite being completely divergent social systems, while the third example would be an extremely complex society.

This definition captures the idea that the highest complexity lies between a completely ordered (i.e. the first example with single, exclusive social relationships) and random (i.e. the second example with random undifferentiated relationships) systems. It also has similarities to Bergman and Beehner's (2015) idea of complexity being “the number of differentiated relationships individuals have” and Fischer et al.'s (2017) quantitative measure of individuals’ diversity in relationship types. The key addition is the conceptual underpinning of social challenge, as represented by the uncertainty in an individual’s social environment.

A picture containing text

Description automatically generated**Figure 1.** Social uncertainty for two hypothetical social structures. In the top row, the focal individual (white) maintains two types of social relationship in their social network, indicated by colour. These relationship types are distinguishable by the association rate (indicated by edge thickness), with one class being very strong relationships and the other being weak. This social network results in a social environment where the focal individual’s associates are almost always of one relationship type, resulting in low social uncertainty. In contrast, in the second row, the focal individual maintains three types of relationship that are less divergent in their rate of association. This results in a much more varied social environment, leading to higher social uncertainty.

*Other concepts of social complexity in cetaceans*

Having established what we consider to be a useful definition of “social complexity” for comparative studies, we now turn to a brief review of how previous work, particularly in cetaceans, has operationalized the concept of social complexity, with an eye towards how these measures relate to social uncertainty.

Perhaps the most well-known method for quantifying social complexity is to measure group size (e.g. Dunbar, 1992; Dunbar and Bever, 1998; Pérez-Barbería et al., 2007). This measure has most prominently been used in studies of primates (Dunbar, 1992; Dunbar and Bever, 1998; Dunbar and Shultz, 2021). In primate species, group size is perhaps a reasonable measure of social complexity. Primate groups are typically sets of bonded individuals, and relationships are highly individualized. It makes sense, then, to assume that each individual in the group represents a distinct relationship that a focal individual would need to manage. Group size has, however, also been used as a measure of social complexity in other mammalian taxa, where the link between group size and variety of social relationships becomes less clear (Dunbar and Bever, 1998; Pérez-Barbería and Gordon, 2005). This is a particular problem in studies of cetaceans. Many cetacean species form extremely large aggregations, and it is unlikely that an individual in these groups maintains individualized relationships of any kind with all the others. When group size has been used in comparative studies of cetacean sociality, it has often been suggested that “mid-sized” groups are perhaps the most complex social system, in contrast to solitary species or huge “mega-pods” (e.g. Fox et al. 2017). Thus, studies of cetacean sociality should not, and typically do not, assume that animals found in larger aggregations inherently have more complex social lives.

A related measure of social complexity, which attempts to capture a more relevant measure of the size of individuals social environment, is social network size (e.g. Dunbar, 1992; Kudo and Dunbar, 2001; Lehmann and Dunbar, 2009). By focusing on the number of *social relationships* individuals maintain, this measure can provide a better indication of the size of individuals’ relevant social environment. As most gregarious primate species form well-defined social units at some level, this measure can be approximated in this taxa by the size of bonded social units (Dunbar, 1992). Such measures are more difficult to acquire in cetaceans as most species do not form social units. We do not know of any comparative study using social network size as a proxy for social complexity in cetaceans, however this concept is often invoked to emphasize the challenges inherent to navigating the open societies maintained by some populations of bottlenose dolphin (*Tursiops aduncus* e.g. Connor, 2007). One thing that’s currently unclear is whether having many social relationships is universally challenging. As with group size, if all partners that individuals maintain relationships with are functionally the same in terms of social interactions, it would perhaps not be particularly challenging to navigate a large social network.

Another way to conceive of social complexity is to use more general descriptions of social systems. Such frameworks may involve describing the strength or stability of social associations, establishing the presence of stable social units, summarizing the size and composition of social units, and determining whether units are situated within a multilevel society (e.g. Prox and Farine, 2020; Shultz and Dunbar, 2007). This general method of classifying species by their social organization requires relatively little quantitative data compared to the other methods, and has therefore been extensively used in studies of terrestrial mammals (Pérez-Barbería et al., 2007; Pérez-Barbería and Gordon, 2005; Shultz and Dunbar, 2007) and birds (Hardie and Cooney, 2023; Shultz and Dunbar, 2010). A similar categorical framework was employed by May-Collado et al. (2007) to examine the co-evolution of tonal sounds and social complexity in cetaceans, where species were classified as solitary, group-living with weak associations, group-living with some long-lasting associations, or group living with stable social units. One potential pitfall here is that it’s not clear what social systems are the most “complex.” It’s often been suggested that multilevel societies, where social units are nested within larger social entities, are particularly complex and potentially cognitively challenging, however this claim has not been carefully examined (Grueter et al., 2020). Indeed, as Rendell et al. (2019) point out, cetacean multilevel societies are typically composed of maternal kin and thus exhibit high within-group relatedness (see Gerber et al., this volume), which is predicted to reduce relational social complexity (Lukas and Clutton-Brock, 2018). Indeed, there is some evidence that individuals in multilevel societies may not always cognitively attend to the different levels of social structure they participate in (Maciej et al., 2013; see King et al. this volume for discussion of social cognition in cetaceans), further highlighting a lack of clear hierarchy of complexity between different social systems.

Another method which has been applied to cetaceans is to use the presence of particular social behaviours, such as group hunting and alloparental care, as indicators of social complexity. This method was utilized by Fox et al. (2017) in their analysis of the relationship between sociality and brain size in Cetacea. Importantly, as the authors point out, this is not a measure of the complexity of social structure, but rather measures the related idea of complexity in social behaviour. This has some similarities with our concept of social uncertainty as a measure of social complexity, as a wider repertoire of behaviours may indicate less predictable social interactions. While Fox et al. (2017) did find a correlation between social group size and their “social repertoire score”, it is not clear whether more complex social structures necessarily correspond to societies that exhibit a wide array of social behaviours. It’s also important to note that some of the features often included in these assessments, such as alloparental care, are more representative of “structural,” rather than “relational”, social complexity (Lukas and Clutton-Brock, 2018).

*Measuring relational social complexity*

As none of the measures previously used in comparative studies adequately capture our concept of “social uncertainty”, we propose that we need to develop and apply other methods for quantifying social complexity in cetaceans. A few years ago, some of the authors of this chapter published a paper (Weiss et al., 2019) presenting a method for estimating social complexity. This method uses data on “association indices” between identified individuals. These take the form of a ratio between the number of occasions each pair was observed together and the number of occasions on which either individual in the pair was observed (together or apart). We won’t go into the technical details of our proposed method here, but the basic idea is that we use a statistical algorithm, called a “binomial mixture model,” to estimate the number of relationship types present in a population, with the types being defined by their average association rate. We then estimate two parameters for each type of relationship: the average association rate, which we’ll call *µ*, and the portion of dyads that belong to that type, which we’ll call *α*. We can then estimate the probability that any given pair of associated animals have a relationship of type *k*:

P(associates have relationship *k*) = *qk* =

How does this get us to a measure of social complexity? We can borrow a measure from information theory, entropy, to quantify the uncertainty in the relationship that any two associated animals have. We’ll call this measure “*S*”, and it can be calculated as:

This is our working measure of relational social complexity. In our original paper, we showed the characteristics of this measure on simulated data, and then estimated the complexity of sperm whale (*Physeter macrocephalus*) and northern bottlenose whale (*Hyperoodon ampullatus*) social networks, finding that sperm whales seemed to have greater social complexity than bottlenose whales. When discussing this measure in the remainder of this chapter, we’ll call it “relational social complexity,” but we emphasize that this is just one measure of social complexity.

In the following sections, we’ll fit this model to datasets from numerous other cetacean species. Our goal here is twofold. First, we hope to provide a general taxonomic overview of relational social complexity in cetaceans to promote further thinking about the causes and consequences of social complexity in this taxa. Second, we provide a comparison of our measure of complexity to some of the measures that have previously been utilized as proxies of social complexity in cetaceans.

*Dataset*

The bulk of our datasets were found during a systematic review carried out in 2021 (Weiss et al., 2021). Of the 181 papers included in that review, 15 included the data necessary to calculate our measure of social complexity (a full list of references can be found in Table 1). In order to expand our overview to baleen whales, we have included data on humpback whale (*Megaptera novaeangliae*) associations published by Wray et al. (2021) and data on fin whale (*Balaenoptera physalus*) associations published by Keen et al. (2021). We have also included data from our own field studies on associations between southern resident killer whales (*Orcinus orcas*). Finally, we include the social complexity estimates for bottlenose whales and sperm whales originally published in Weiss et al. (2019). All told, we obtained relational social complexity estimates from 22 datasets across 11 species. Our sample is strongly taxonomically biased towards the delphinids, and particularly common bottlenose dolphins (*Tursiops truncatus*), which is represented in 9 different datasets. The only other species for which we found multiple datasets was killer whales, with 4 datasets including the southern resident killer whale data.

**Table 1.** Summary of our comparative dataset and data sources

|  |  |  |  |
| --- | --- | --- | --- |
| Species | Common name | Location | References |
| *Balaenoptera physalus* | Fin whale | Kitimat Fjord System, British Columbia CA | Keen et al., 2021 |
| *Berardius bairdii* | Baird’s beaked whale | Commander Islands, Russia | Fedutin et al., 2015 |
| *Cephalorhynchus hectori* | Hector’s dolphin | Porpoise Bay, New Zealand | Bejder et al., 1998 |
| *Globicephala macrorhynchus* | Short-finned pilot whale | Madeira, Portugal | Alves et al., 2013 |
| *Hyperoodon ampullatus* | Northern bottlenose whale | The Gully, Nova Scotia CA | Gowans et al., 2001\* |
| *Megaptera novaeangliae* | Humpback whale | Kitimat Fjord System, British Columbia CA | Wray et al., 2021 |
| *Orcinus orca* | Killer whale | Marion Island, South Africa | Reisinger et al., 2017 |
| Crozet Islands, Indian Ocean | Busson et al., 2019 |
| Salish Sea, Washington USA | Center for Whale Research, 2023 |
| *Physeter macrocephalus* | Sperm whale | Dominica, Caribbean Sea | Gero et al., 2014\* |
| *Sousa sahulensis* | Australian humpback dolphin | Northwest Cape, Western Australia | Hunt et al., 2019 |
| *Tursiops aduncus* | Indo-Pacific bottlenose dolphin | Shark Bay, Western Australia | Foroughirad et al., 2019 |
| *Tursiops truncatus* | Common bottlenose dolphin | Sado Estuary, Portugal | Augusto et al., 2012 |
| Sardina, Italy | Díaz López, 2019 |
| Patos Lagoon, Brazil | Genoves et al., 2018 |
| Savannah, Georgia USA | Kovacs et al., 2017 |
| Laguna, Brazil | Machado et al., 2019 |
| Ria de Arousa, Spain | Methion & Díaz López, 2019 |
| Golfo Dulce, Costa Rica | Moreno & Acevedo-Gutiérrez, 2016 |
| Western Ireland | Nykänen et al., 2018 |

\* Estimates from these datasets were first presented in Weiss et al. (2019)

*Analysis*

For all datasets included, we extracted the numerator and denominator of the simple ratio indices of association between all identified individuals. We then used the flexmix R package (Leisch, 2004) to run a binomial mixture model with a maximum of 5 components on all datasets. We allowed the model to drop empty components during the model fitting process to arrive at a final number of components (relationship classes), along with parameter estimates for the association probability and frequency of occurrence for each class. From these estimates, we then calculated our estimate of relational social complexity as described above.

To examine correlations between our measure of social complexity and possible covariates, we used models with the form:

Where *A* is the phylogenetic correlation matrix, derived from the phylogeny presented in McGowen et al. (2020), *D* is the average denominator of the association index, indicating sampling intensity, and the *σ* are estimated standard deviations, and the *β* are estimated fixed effects. The “…” indicates additional, analysis-specific terms. We set *N*(0,1) priors for fixed effects, and broad half-*t* priors for estimated standard deviations. We added only a single predictor variable at a time to the above model for any given analysis, given the small size of our dataset. We fit these models using the brms R package (Bürkner, 2017).

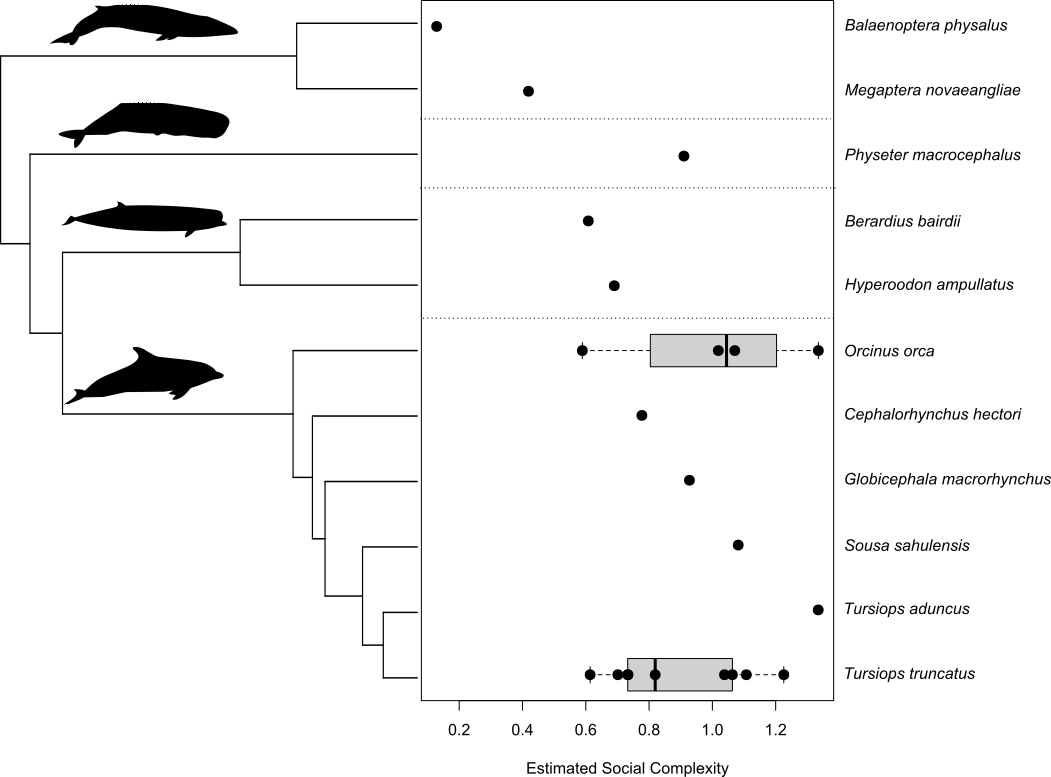
*Social uncertainty across cetacean species*

Across our datasets, the number of identified social relationship types ranged from 2 to 4, with resulting estimates of relational social complexity ranging from 0.12 to 1.33 (Figure 2). The lowest estimated values of relational social complexity were from the two baleen whale datasets, with *S* = 0.12 for fin whales and *S* = 0.42 for humpback whales. Relational complexity was slightly higher in the beaked whale species where we estimated *S* = 0.61 and *S* = 0.69 for Baird’s beaked whales and northern bottlenose whales, respectively.

Among the delphinids, relational social complexity was lowest in Hector’s dolphin (*Cephalorhynchus hectori, S* = 0.77), and peaked in Indo-Pacific bottlenose dolphins and southern resident killer whales (*S* = 1.33). Relational social complexity in sperm whales fits well within the range of complexity estimates for delphinids, most closely resembling that of short-finned pilot whales (sperm whales = 0.91, pilot whales = 0.92). A particularly interesting estimate comes from Australian humpback dolphins (*Sousa sahulensis*), with relational social complexity similar to sperm whales, pilot whales, and killer whales. Importantly, in the two species where we had multiple datasets to analyse, we found a significant degree of variability between datasets. In bottlenose dolphins, estimates of *S* ranged from 0.61 to 1.23, while in killer whales estimates ranged from 0.59 to 1.33.

Examining our estimates of social complexity (and the estimated number of “relationship types”) across species, our statistical model clearly underestimates social complexity. This is particularly obvious in populations that have been studied in detail for many years. For example, in the Shark Bay bottlenose dolphins, our model estimates 4 types of relationships, and a resulting social complexity of 1.33. However, from long-term study, it is known that among males in this population, there are first, second, and third order alliances, and relationships between unallied individuals. Additionally, there are weak and strong female-female relationships. Finally, there are the relationships between males and females, which clearly consist of very different social interactions than intrasexual relationships (see Connor and Krützen (2015) for a detailed overview of this society). Thus, we know there are (at least) 6 different types of social relationship in this population. This discrepancy highlights the degree to which measures of social structure from association, while instructive, inherently underestimate social complexity. There are also clear signs that sampling effort influences our measures, with a strong positive correlation between estimated complexity and average association index denominator (*rs* = 0.66).

By fitting our model described above, we can investigate whether there is evidence for phylogenetic signal in our dataset by quantifying the portion of between-species variance (after accounting for sampling intensity) accounted for by the phylogeny as opposed to uncorrelated species-level differences, which we’ll refer to as *λ*. There is evidence of phylogenetic signal in this dataset, although with such a small dataset there is a good deal of uncertainty (*λ* = 0.86, 95% CI = [0.1, 1]). More broadly, it seems that the main divergence in social complexity occurred between the toothed and baleen whales (although we have few baleen whale data in this analysis). This makes intuitive sense, as large baleen whales are thought to be primarily solitary or live in highly fluid societies (but see Dunlop & Parks in this volume), while toothed whales are generally group-living to some extent. Greater attention to and study of the social relationships of baleens whales will help us expand and refine this picture.



**Figure 2.** Estimated social complexity in cetaceans. Each point represents an estimate from a single dataset. Where multiple estimates were made for a species, boxplots are also drawn. The phylogeny on the left is redrawn from McGowen et al. (2020). Sillouhettes and dotted lines demarcate families (from top to bottom: Balaenopteridae, Physeteridae, Ziphiidae, and Delphinidae).

*How does social uncertainty in cetaceans relate to other concepts of social complexity?*

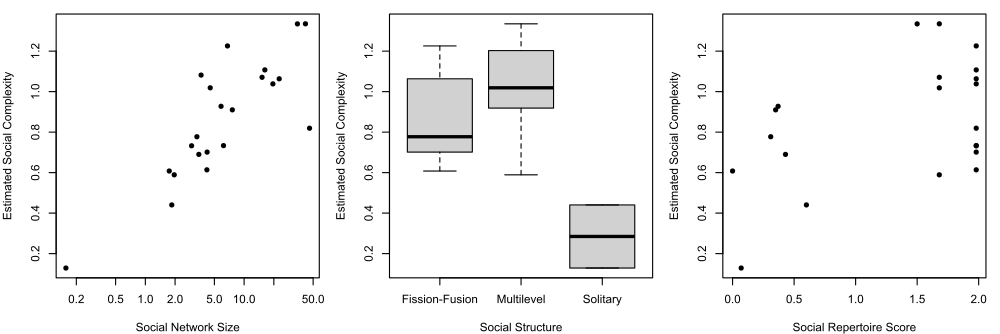
Above, we described three general measures that have been used as proxies of social complexity in previous studies: network size, social structure classification, and social repertoire. While none of these directly measure (or indeed attempt to directly measure) social uncertainty, it may be instructive to determine whether these features correlate with our estimates of social complexity across cetaceans (Figure 3).

First, we can examine how social network size correlates with social relationship complexity. There are two ways to go about estimating social network size in our cetacean association networks. We could count all non-zero association indices as social connections and use the number of social connections per individual as a measure of network size. However, there may be many individuals who associate in aggregations but don’t maintain a social relationship. An alternative way to approach this question is to use the output of our mixture models to estimate the size of the social network that individuals experience. In our analysis, we naturally segment dyads into those with “no relationship” (i.e. the relationship class with the lowest association rate, typically very close to zero) and those with some stronger relationship (all other classes). Therefore, we can measure social network size as the average number of these stronger relationships that individuals in the society have. We view this measure of social network size as more comparable to the measure of social group size used in studies of primates, as it is an estimate of the number of partners individuals maintain some kind of social bond with. In our dataset, this measure ranged from individuals maintaining fewer than one relationship on average (in fin whales) to individuals maintaining over 40 relationships on average (as in southern resident killer whales). Interestingly, we find strong evidence for a correlation between the logarithm of social network size and social relationship complexity (*β* ± SE = 0.12 ± 0.06, posterior P(*β* > 0) = 0.98).

What about other features of social structure? Are, for example, multilevel societies truly more complex than other social structures? While more fine-scale analysis would be ideal, we roughly categorized our species as either being primarily solitary (the baleen whales), group living with individualized fission-fusion (beaked whales and most dolphins) or living in multilevel societies (killer whales, pilot whales, sperm whales, and Indo-Pacific bottlenose dolphins). Again fitting our model, we can see clear evidence that both fission-fusion and multilevel societies have higher estimated complexities than the primarily solitary societies (Multilevel vs. Solitary: *β* ± SE = 0.52 ± 0.27, posterior P(*β* > 0) = 0.97; Fission-Fusion vs. Solitary: *β* ± SE = 0.45 ± 0.26, posterior P(*β* > 0) = 0.95). However, we find very little evidence for a difference between fission-fusion and multilevel societies (*β* ± SE = 0.07 ± 0.15, posterior P(*β* > 0) = 0.71).

Finally, we examine whether the “social repertoire score” developed by Fox et al. (2017) correlates with our measure of social complexity. As this was not designed to be a measure of social structure, but rather social behaviour, there is no structural reason why these two measures should be correlated, but there are perhaps evolutionary hypotheses that would propose such a relationship. In our sample, we found very little evidence that this measure correlates with social uncertainty (*β* ± SE = 0.03 ± 0.15, posterior P(*β* > 0) = 0.6).

In summary, it appears that the presence of particular social behaviours is not a useful proxy for the diversity or uncertainty of social relationships. Furthermore, while the contrast between group living and primarily solitary species provides some information about social uncertainty, it does not appear that different types of sociality necessarily correspond to different levels of social complexity as defined here. Rather than multilevel sociality being a form of particularly complex social structure, it may instead be just one way in which a society can be complex.



**Figure 3**. Comparison of our measure of social complexity with other proxies of social complexity in cetaceans.

In contrast, social network size appears to be a very useful correlate of social uncertainty. While it’s unclear the precise reason why this is the case in our dataset, it seems reasonable to suggest that maintaining a large number of social relationships is a necessary pre-requisite for having many different types of social relationships and, ultimately, a strongly varied social environment. This also relates to our finding that solitary baleen whales score lower on this form of social complexity than toothed whales. While these baleen whales may encounter many different individuals at various points, they appear (in the datasets we examined) to maintain very few strong, consistent relationships, resulting in lower estimates of social complexity (for a more detailed discussion of social complexity in baleen whales see Dunlop & Parks, this volume).

*Conclusions and future directions*

Our goal here is to make progress in operationalizing relational social complexity and provide an initial, quantitative overview of social complexity in cetaceans. Our initial survey of this data demonstrates significant variation in social complexity across cetaceans with an apparently strong phylogenetic signal. Interestingly, this variation can’t be fully explained by variation in basic social structure and does not strongly correlate with behavioural repertoires. Social network size, while correlated with relational complexity, also cannot fully explain variation in this measure. An obvious next step is to determine what factors, particularly those related to life history and ecology, predict complex social structure. We also strongly suspect that analyses addressing the social brain and communicative complexity hypotheses using social uncertainty as a predictor may reveal patterns and relationships that have not been clear thus far.

Of particular interest is the within-species variation in killer whales and common bottlenose dolphins. It’s worth considering what this variation might mean for hypotheses about the causes and consequences of social complexity. It seems unlikely that species-level traits, such as morphology and brain size, could be predictably driven by the “social environment” when the social environment itself is so variable between populations of the same species. In contrast, this may point to an important role for habitat and ecology in shaping social systems and their resulting complexity. Well-reasoned socioecological frameworks for delphinids have been proposed (Gowans et al., 2007; Möller, 2012), however, quantitative comparative tests of these frameworks are rarely conducted.

We suggest that future studies expand the taxonomic breadth of the datasets included. Missing from our analysis are any river dolphins, porpoises, or non-rorqual baleen whales. This could be addressed by directly reaching out to field researchers to collate datasets from the numerous individual-level studies currently being conducted on a wide variety of species, or by more raw data being made available along with peer-reviewed publications.

Our method only considers association rates when clustering relationships into types, as this is the primary form of data available to cetacean researchers through photographic identification studies. However, as novel research technologies, especially unoccupied aerial systems and animal-borne tags, make it easier to monitor social interactions (King and Jensen, 2022), it may become possible to incorporate other measures of social relationships into this method. Similar statistical tools could still be used, however, the mixture model would have to be expanded to be multivariate. Furthermore, we are ultimately interested in the uncertainty of social interactions themselves, with relationship types serving as a rough proxy. Observations of direct social interactions and their unpredictability could provide a much richer picture of the complexity of cetaceans’ social worlds.

Another crucial avenue may be to more directly incorporate aspects of communication into our understanding of social complexity in cetaceans. Acoustic playback experiments may help us test whether the different “relationship types” we identify statistically are cognitively relevant to the individuals within the society (King et al., this volume). Furthermore, incorporating acoustic communication may reveal levels of social connectivity not apparent from typical methods for analysing social structure, particularly in baleen whale species that may interact acoustically without being in physical proximity (Dunlop et al., this volume).

While our focus has been firmly on understanding cetacean sociality, our methods and results may help inform studies of social complexity more generally. We’ve highlighted here that the occurrence of particular social behaviours and types of social structure cannot be considered indicative of “social complexity” *a priori*. Instead, we strongly suggest that studies of social complexity focus on well-motivated hypotheses about how sociality may present a challenge to the individuals within them and measure features of social structure that correspond to these hypotheses. There are encouraging signs in primatology that studies of social complexity may move away from simple group size-based analyses and towards quantitative measures of social structure focused on the diversity of relationships individuals maintain (Fischer et al., 2017; Morrison et al., 2020; Ramos-Fernandez et al., 2018). In other taxa, there is a tendency to use very general aspects of social structure, such as the presence and structure of social groups, as measures of “social complexity.” Studies of cetaceans, and our proposed measure of social complexity, emphasize the importance of studying social systems at the level of relationships and individuals, building a bottom-up picture of social complexity. We recommend that future comparative studies of social complexity across taxa make greater attempts to incorporate individual-based studies of social structure; more generally, many taxa would benefit from greater research into their social structure on an individual level.

Understanding the evolutionary causes and consequences of social complexity requires us to operationalize, measure, and compare complexity between societies. We hope that this chapter provides a useful early step towards this goal in cetaceans, a taxon which is inarguably invaluable for studies of social complexity in the wild.

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