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Author for correspondence:

Maurício Cantor

e-mail: m.cantor@gmail.com

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The interplay between social networks and culture: theoretically and among whales and dolphins

Maurício Cantor and Hal Whitehead

Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1

Culture is increasingly being understood as a driver of mammalian phenotypes. Defined as group-specific behaviour transmitted by social learning, culture is shaped by social structure. However, culture can itself affect social structure if individuals preferentially interact with others whose behaviour is similar, or cultural symbols are used to mark groups. Using network formalism, this interplay can be depicted by the coevolution of nodes and edges together with the coevolution of network topology and transmission patterns. We review attempts to model the links between the spread, persistence and diversity of culture and the network topology of non-human societies. We illustrate these processes using cetaceans. The spread of socially learned begging behaviour within a population of bottlenose dolphins followed the topology of the social network, as did the evolution of the song of the humpback whale between breeding areas. In three bottlenose dolphin populations, individuals preferentially associated with animals using the same socially learned foraging behaviour. Homogeneous behaviour within the tight, nearly permanent social structures of the large matrilineal whales seems to result from transmission bias, with cultural symbols marking social structures. We recommend the integration of studies of culture and society in species for which social learning is an important determinant of behaviour.

1. Introduction

Social complexity essentially emerges from individual efforts in creating mutual solutions to maintaining and propagating life. The diversity and flexibility of social behaviour are prominent ingredients of complex mammalian societies. Such plasticity has been carved over evolutionary time by the interaction of ecological, phylogenetic, developmental and genetic factors [1]. But behavioural flexibility can also be an adaptive product of challenges occurring at shorter time scales [2,3].

When the environment varies unpredictably within periods of the order of tens of generations, genetic determination of behaviour may not be optimal. In such cases, environmentally induced phenotypic plasticity [4] through learning [5] may emerge as a more efficient solution [6]. Individuals regulate their behaviour by tracking the environment as it changes and/or by tracking their conspecifics' behaviour [7–9]. The former, individual learning, is an a-social trial-and-error strategy that may be time-consuming, energetically costly or risky; the latter defines social learning, a non-genetic mechanism of information transfer [5,10,11]. When behaviour is socially transmitted and then shared within subsets of a population, it may be called culture [12]. Thus culture, as defined in this way, can have a major role in structuring behavioural diversity within a population [7,13].

As culture is fundamentally built upon social learning [5], social structure and culture are linked (figure 1). If we express the social structure of a community as a network, i.e. nodes depicting individuals linked according to their social relationships ([15]; see the electronic supplementary material, table S1), then we can envisage that social learning occurs along the network edges (i.e. the links between individuals; electronic supplementary material, table S1). In network

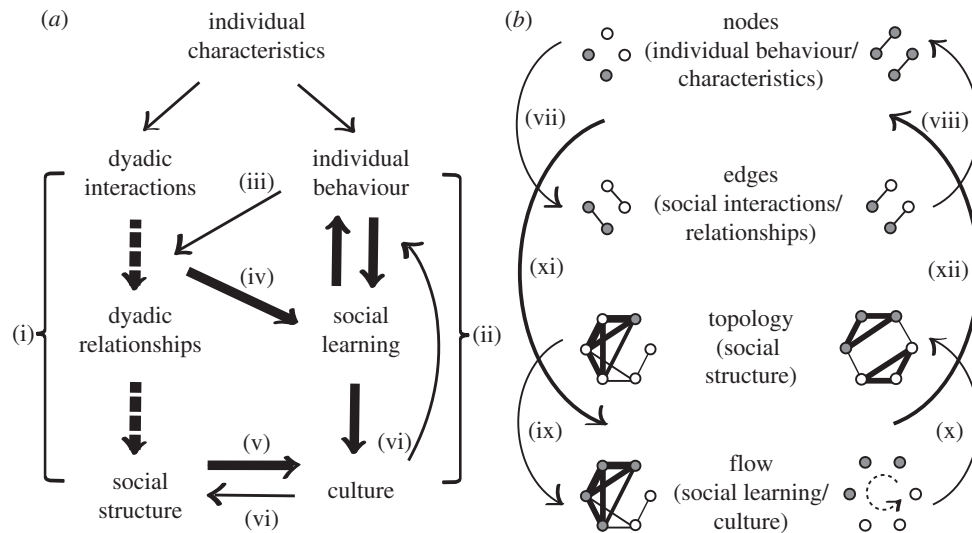


Figure 1. Two representations of the dynamic relationship between social structure and culture. (a) Individual characteristics ultimately influence both social structure, through their effects on social relationships (i), and the cultural context, through variation in both behaviour and the individuals' partialities for social learning (ii). Overall, the interplay between individuals and social relationships influences—and is influenced by—the interplay between social structure and information transmission. (b) This is represented by a coevolutionary social network in which the coevolution of nodes (circles, with different shading representing individuals with different behavioural repertoires) and edges (links, with thickness being proportional to the rate of social interaction) (vii,viii) shapes and is shaped by (xi,xii) the coevolution of network topology and transmission mechanisms (ix,x). Thick dashed arrows illustrate the Hinde's [14] conceptual framework for social structure (i). Thick black arrows illustrate the elements of the concept of culture from Laland & Hoppitt [12] (ii). Thin arrows (iii,vi) represent additional effects hypothesized in this review. For further details on network terminology, see the electronic supplementary material, table S1.

depictions of animal societies, the edge weights usually represent estimates of the proportion of time that each pair of individuals spends together [15], and so may represent the probabilities that individuals learn from one another [16–18]. Thus, as illustrated in figure 1a, we suggest that the process of culture can be placed alongside, and linked to, the process of social structure. Social structure can be conceptualized using Hinde's [14] framework in which social structure is the nature, quality and patterning of the relationships among its members, and where relationships are formed from the content, quality and patterning of dyadic interactions (figure 1a). Then we can think of social learning occurring during interactions, or being governed by relationships (figure 1a(iv)). Network thinking is implicated by another element of the general definition of culture: 'shared' [12]. If some pairs of individuals share behaviour, the implication is that others do not. Thus, we suggest that the network representing the entire population should be modular, i.e. showing strongly connected clusters of individuals with shared behaviour (see [19]; also electronic supplementary material, table S1), for the results of social learning to be called culture. Thus, in figure 1a, we show a second major link (v) from social structure to culture.

But culture can also affect social structure. If individuals preferentially associate with those who behave similarly [20–22] (figure 1a(iii)) and behaviour has a cultural element, then elements of social structure may reflect culture. This may especially be the case when conformism homogenizes behaviour through social learning [23], and/or when cultural symbols are used to mark social entities [24] (figure 1a(vi)).

Although depicted as static diagrams, social networks encode dynamic and coevolutionary systems. Network topology evolves, as changes in node states affect edges, and changes in edges affect node states (reviewed in [25,26]). In a society with social learners and behaviour matching, that means changes in behaviour affecting relationships, and changes in relationships affecting behaviour. Thus, individuals influence and are

influenced by their social network [27–29], owing to behaviour matching (figure 1b(vii)) [21] and social influence (figure 1b(viii)) [20]. Either way, both the network structure and the transmission dynamics can be transformed, subtly or profoundly (figure 1b(xi)). Social structure influences how information flows through the population [16] (figure 1b(ix)), at the same time that the transmission of information can affect the network structure. For instance, stable modules in dynamical systems can emerge when interactions are more likely to form between nodes that have similar states [30], while the dense connections within a module can reinforce the nodes' similar states [31]. In the social context, we get emergent structures if individuals associate primarily with individuals with whom they share behaviour, and learn behaviour primarily from their social associates [22,32,33] (figure 1b(x)). Finally, interplay between social structure and transmission dynamics closes this cycle (figure 1b(xii)), since behaviour defines the cultural context, with its norms and transmission biases, that influences how individuals behave and interact [5,12,23,24].

There are many theoretical studies of the potential relationships between network structure and information flow over human-like social networks [22,26–29,31–34]. However, non-human networks are generally smaller (fewer nodes) and need to be represented with weighted rather than binary edges, because animal social relationships are rarely all-or-nothing [35]. Thus, the human-calibrated models are not necessarily applicable, providing at best a rough starting point for exploring animal societies. However, there have a few theoretical, agent-based models of the relationship between social structure and culture calibrated for non-human societies. We review their results, exploring theoretical facets of the interplay between culture and social structure in animal societies.

We illustrate some of these ideas using results on cetaceans (whales and dolphins). Cetaceans have particularly complex and varied social systems [36], and there is considerable evidence for culture being an important driver of behaviour in these

property	metric	large-scale structure		within-module structure	
		low	high	low	high
network					
proportion of edges	connectance	↑	↓	↑	↓
mean distance of nodes	average path length	↓	↑	↓	↑
cohesive subgroups	modularity	↓	↑	—	—
individual centrality	strength, closeness, betweenness	(↓)	(↑)	↓	↑
transmission					
efficiency	speed	↑	↓	↑	↓
consistency	error chance	↓	↑	(↓)	(↑)
persistence	extinction risk	↓	↑	↓	↑
diversity	SD; diversity index	↓	↑	(↓)	(↑)

Figure 2. How social networks affect information transmission at two structural scales: the large-scale structure of the population and the structure within social modules. In both, the lower the connectance of the network, the longer the path length; thus, more time is required for the information flow, which makes the information more susceptible to loss and transcription errors but more prone to generate diversity. Arrows represent the overall directions of effects of network topology on network properties and on the transmission of information (described by their respective metrics) as indicated by the theoretical literature [16–18,46,49]. Arrows in parentheses represent our own speculations. Up arrows indicate a positive relationship and down arrows a negative relationship. In the hypothetical networks, nodes representing individuals are connected by weighted edges whose thickness is proportional to the rate of social interaction, assumed to be proportional to probability of social learning. Efficiency was measured by the number of steps until all individuals acquired the new information (speed) [16]; consistency was measured by the average path length (minimum number of steps along a chain of relationships from one individual to another), reasonably assuming that longer paths are more likely to be subjected to transcription errors [16]; persistence over time was assessed by simulating the forgetting of acquired information and estimating its extinction risk [16]; and diversity was measured by the standard deviation of continuous behavioural measures or the Shannon diversity index for categorical behaviour [18]. See the electronic supplementary material, table S1 for definitions and interpretation of the network terminology; network metrics formulae can be found elsewhere [15,19,50,51].

species [37]. Among animal groups, cetacean societies have been particularly frequently studied using network methods. Cetacean social relationships are not bounded by defended territories, and individuals usually have large home ranges and more social associates than is typical for terrestrial mammals. These attributes give power and potential to investigations of the relationships between culture and society among cetaceans [38]. However, cetacean cultural behaviour is difficult to study and has rarely been the focus of research. Thus, our examples only illustrate small sections of the rich interplay between society and culture as explained in figure 1, and those imperfectly.

We illustrate these dynamic relationships between culture and social structure using the formalism of coevolutionary networks (also called ‘adaptive networks’) [25], characterized by a feedback loop between the dynamics of the nodes (individuals) and topological evolution (social structure) mediated by transmission processes (social learning; figure 1*b*). Even though disentangling cause and effect in this two-way relationship is not trivial, we first summarize how social structure may affect culture (§2), then how culture may affect social structure (§3). We also consider the potential effects of social learning biases and symbolic marking (§4). We conclude by considering how understanding will advance in this area and by suggesting ways to bridge the gap between theory and real-world cetacean societies (§5).

2. How social structure affects culture

We generally expect the spreading dynamics of information, or other quantities like disease, through a society to be highly

dependent on its network structure [39–45]. Agent-based models that roughly mimic non-human social systems and social learning predict that large-scale structure [16,18,46], within-group hierarchy structure ([17]; see also [47,48]) and the differentiation of individual social roles [49] affect information flow on social networks (figure 2).

Generally, increases in social network structure mean more heterogeneity in the number and intensity of social relationships and longer path lengths (i.e. distance from one node to another; see the electronic supplementary material, table S1) which decrease speed, fidelity and robustness of information flow [16]. Learning errors promote behavioural diversity in the population [18]. In these simulations, as the large-scale structure of the social network increases, behavioural diversity generally increases. As modules become increasingly separate socially, they develop independent behavioural trajectories, leading to higher behavioural diversity in the population. If culture is defined such that socially learned behaviour is consistently different between segments of the population [12], one could conclude that social structure can produce culture when the network is clearly modular [18]. These modules are generally called ‘groups’ by primatologists, and ‘communities’, ‘clusters’ or ‘units’ in cetacean and proboscidean studies. All these terms have contradictory connotations, so here we use ‘social modules’ from the network literature to generalize sets of individuals in which interaction and association rates, as well as social learning opportunities, are consistently greater within social modules than between them. In some societies, different types of social modules can be hierarchically arranged into social tiers [52].

Agent-based models suggest that within small social networks that may be representative of social modules in

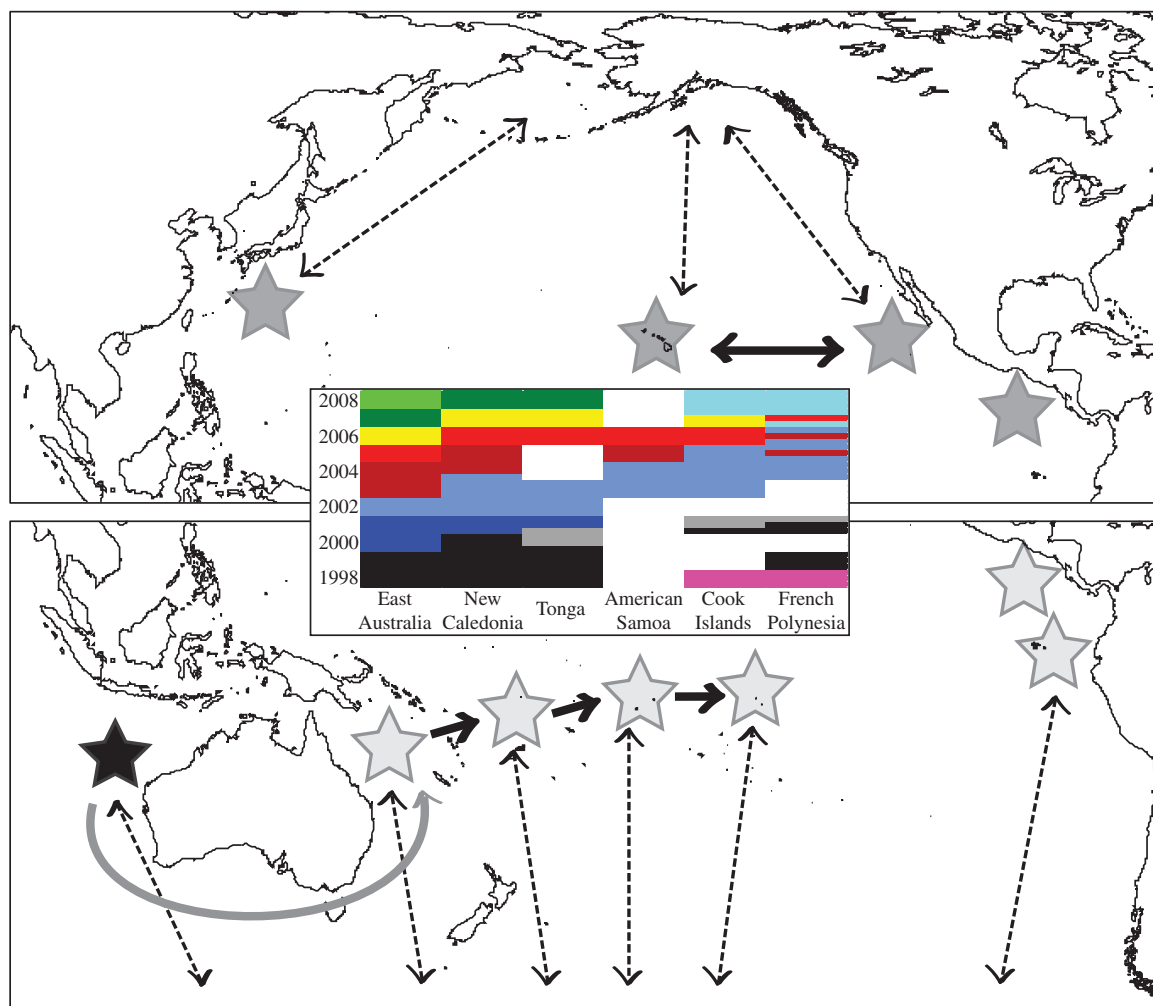


Figure 3. Humpback whale song in the Pacific. Principal breeding grounds are shown by star symbols in the North Pacific (dark grey), South Pacific (light grey) and Indian Ocean (black). Seasonal migration routes are indicated by dashed lines, and routes of information flow by thick arrows. The evolution of the South Pacific song between 1998 and 2008 is shown by the block diagram (adapted from [61]). The different song types are indicated by different colours and missing data by white boxes. The vertical columns of the block diagram are aligned approximately above the study areas where the songs were recorded in the South Pacific map.

non-humans, social structure also determines the spread of socially learned information. Transmission speed and vulnerability of information to extinction vary markedly according to the level of hierarchy among animals within such networks [17]. Social learning homogenizes behaviour in egalitarian networks more quickly and effectively than in despotic ones [17]. Scaling down to the individuals, the social role an animal plays, inferred through the node position in the network, affects the flow of information [53]. For instance, individuals with high centrality, towards the centre of networks (see the electronic supplementary material, table S1), may be key dispersers, funnelling information flow between different social modules, or controlling the access or the quality of information [49]. Thus, even fine-scale social structure influences social learning [47,48,54].

We have summarized these theoretical results on how social structure affects culture in figure 2. What about the real world? There are a few cases where we have been able to trace the spread of information through a reasonably well-mapped social network of whales and dolphins. Sophisticated analytical tools that separate social learning from genetic, environmental, demographic and other factors in the acquisition of behaviour are just beginning to be employed [48,55,56]. Although we recognize a dearth of empirical evidence, we will present current examples suggesting that social learning follows network structure both within and between social modules.

In southwestern Australia, some bottlenose dolphins (*Tursiops aduncus*) beg for food from recreational fishermen [57]. Two factors were strongly implicated in the acquisition and spread of this behaviour through the population: how much time an individual spent in areas of high boat density, and how much it associated with other dolphins that were already begging. So begging behaviour seems to have spread through the population by a combination of individual learning (dolphins spending time with boats) and social learning (spending time with conditioned dolphins) [57].

Our second example is on a much larger scale. Male humpback whales (*Megaptera novaeangliae*) on and near their winter breeding grounds sing long, elaborate songs [58], 'the most elaborate single display known in any animal species' [59, p. 108]. Nearly, all whales on any breeding ground at any time essentially sing the same song, but it evolves over the months of the breeding season. These characteristics are only consistent with social learning, and mean that the humpback song provides 'some of the most compelling evidence for animal cultures' [60, p. 543]. We will consider the humpback whales in the Pacific, with breeding grounds being the network nodes. Migrations and winter breeding grounds are shown in figure 3. Even though the Northern and Southern Hemisphere breeding grounds overlap off Costa Rica [62], they are used at different times of year. The North Pacific and South Pacific songs have different

content. Within the North Pacific, though, the songs on at least two different breeding grounds, those off Mexico and Hawaii, have nearly identical content and evolve synchronously [63,64]. Possible mechanisms for this synchronicity in behaviour on nodes 4800 km apart include information exchange on common feeding grounds or during migration (figure 3), movement of animals between the grounds in successive winters, or the same winter, innate templates of change and song in intermediate parts of the ocean [63,64].

In contrast, song evolution on the South Pacific breeding grounds occurs sequentially, and in a west-to-east direction [61]. A song heard off eastern Australia in one winter might be heard off New Caledonia—2000 km to the east—12 months later, and off French Polynesia after another year (figure 3). In at least one case, a totally new, Indian Ocean, song was injected into the South Pacific system in eastern Australia, perhaps by animals whose autumn migration from Antarctica went up the eastern rather than the western side of the Australian continent [65]. The reasons for the one-way movement of songs across the Pacific are uncertain [61], as are the contrasts with the picture in the North Pacific where songs on breeding grounds more separated than those in the South Pacific evolve in synchrony. Perhaps the constriction of the North Pacific at temperate latitudes (figure 3) connects humpbacks that use well-separated winter breeding grounds—the whales sing on migration [66]—in a manner that does not happen in the Southern Hemisphere, where the high latitude ocean circles the globe.

In summary, the structures of animal social networks over a range of scales reflect the heterogeneous opportunities for individuals, or social modules themselves, to interact and then for cultural traits to emerge, flow and evolve. The topology of social networks generates and moulds culture (figure 2).

3. How culture affects social structure: behaviour matching

While social structure affects culture, the direction of causation can be reversed. In this section, we consider situations in which animals with similar culturally determined behaviour preferentially associate. General models have predicted that such behaviour matching, sometimes called assortativity or homophily, can become an important driver of social network structure [22,29,31,33]. Since behaviour matching breeds relationships, edges between individuals with distinct behaviour tend to dissolve [21] and modules of behavioural homogeneity emerge [22,34,67]. We are not aware of quantitative models of this phenomenon calibrated for non-human societies. However, in figure 4*a*, we illustrate graphically how social network topology might be shaped by variation in individual behaviour and social learning.

Individuals differ in many ways [68], including their social experiences [69] and behavioural repertoires [70], and these characteristics can influence the social network [71]. Natural populations are often composed of individuals displaying different repertoires of behaviour, and/or degrees of specialization [72]. These patterns can partially result from cultural transmission of behaviour [70,73]. If individuals have behavioural repertoires of different central values but similar width, randomly or uniformly distributed through the population's behavioural range, then preferential association between individuals with similar behaviour will not tend to structure the

network (figure 4*a*(i–iii)). However, when individuals have different degrees of specialization (i.e. repertoires differ in their widths) but there is no social learning, then behaviour matching will lead to the 'generalists' becoming central to a 'small-world' type (see the electronic supplementary material, table S1) network as these 'generalists' are more likely to be performing the same act as a randomly chosen individual and so will associate with them more often (figure 4*a*(iv–vi)). Add social learning to the mix, so that individuals converge on similar mean behaviour but with different degrees of specialization, and now the 'specialists' become central to the network (figure 4*a*(vii–ix) (see also [29]). In our final example, specialization is fairly uniform within the population but social learning clusters the individuals' behaviour into several modes, which then through behaviour matching become the characteristic features of semi-discrete social modules (figure 4*a*(x–xii)) (see also [22]).

Two recently published studies suggest that the matching of socially learned behaviour structures the societies of bottlenose dolphins (*Tursiops* spp.) [74,75]. Identifying such processes is difficult as the more parsimonious alternative that social differences explain the behavioural patterns must be eliminated, or at least shown not to be sufficient. However, in these examples, the studies have gone some way towards doing this.

Perhaps most famous among the many foraging specializations of bottlenose dolphins is sponging, a cultural behaviour [76], largely transmitted from mothers to daughters [77]. Bottlenose dolphins of Shark Bay, Australia, place sponges on their rostra, a behaviour that is thought to help them when foraging in rocky substrate [78]. Sponging is performed singly and the sponging dolphins live in the same habitat as non-spongers, but the spongers preferentially associate with other spongers. After accounting for other possible causes of these preferred associations—range overlap, gender and kinship—Mann *et al.* [74] concluded that spongers prefer to associate with other spongers, and hence that behaviour matching is an underlying mechanism driving the social network structure.

This is pretty conclusive evidence, but we would really like an experiment in which we compare the social system with and without the behaviour. This is what happened in Moreton Bay, on the east coast of Australia. In the 1990s, some bottlenose dolphins followed prawn trawlers, feeding on the discards and debris, while others did not [79]. The trawler dolphins associated with one another, and the non-trawler dolphins with one another, but there was very little social interaction between the two social modules even though they lived in the same physical habitat [79]. By 2005, the prawn trawling, which was not sustainable, had been virtually eliminated from the bay by fisheries' managers. When the dolphins' social system was studied again between 2008 and 2010, the social segregation marked by association with trawlers had disappeared. Trawler and non-trawler dolphins that had formed discrete social modules were now well integrated within one social network [75].

Sponging in Shark Bay is almost certainly socially learned [60,76], and it is very likely that exploiting trawlers in Moreton Bay [75] was as well. Thus, these two examples indicate the potential for culture to be a driver of cetacean social structure.

4. Conformism and symbolic marking

In addition to the social context within which the individuals operate, the manner by which behaviour is socially learned

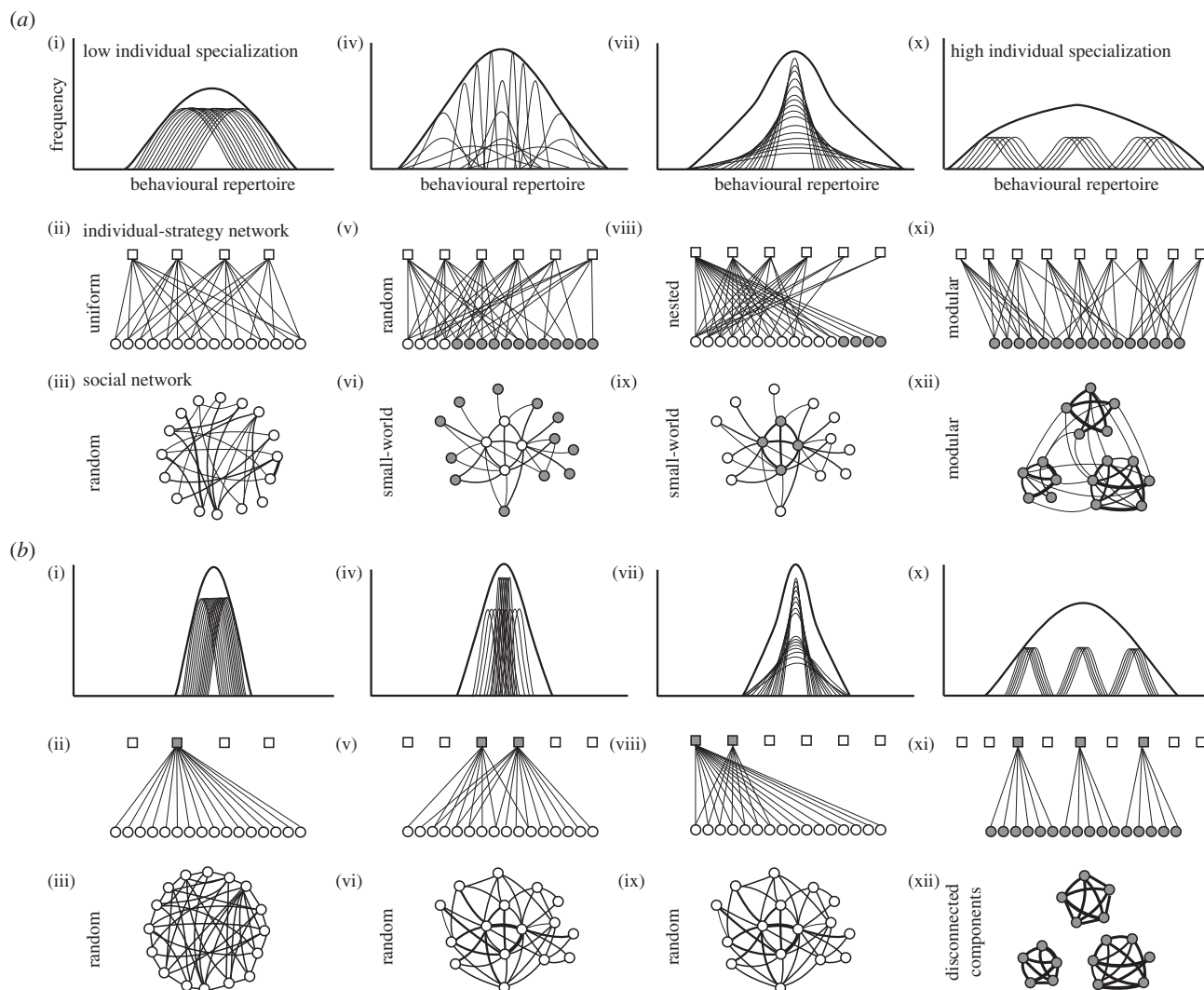


Figure 4. (a) Hypothetical effects of behaviour matching (i.e. when individuals tend to associate with those with similar behaviour) on social structure as influenced by patterns of behavioural specialization. The columns indicate different distributions of individual behaviour within the populations: unspecialized niches with similar widths; individual variation in niche width and location; individual variation in niche width around a common central value; and specializations around several modal values with similar niche widths. The first row represents the distribution of continuous behaviour (thicker lines, population behavioural repertoires; thinner lines, individual repertoires); the second row uses binary two-mode networks to represent equivalent distributions of categorical behaviour types (squares) used by individuals (white circles, 'generalists'; grey circles, 'specialists') and the third row represents the weighted social network that behaviour matching might induce in each case (individuals connect by edges whose thicknesses are proportional to the rate of social interaction). (b) Adding conformism, behavioural repertoires become narrower. With low and moderate individual specialization, the social networks tend to random topologies, but when modules of individuals with specialized behaviour are present, conformism increases their isolation. Definitions and interpretation of network terms are available in the electronic supplementary material, table S1.

can also critically affect the dynamics of cultural transmission [46]. Behaviour can be socially transmitted through several psychological mechanisms [10] that are subjected to biases. Individuals may disproportionately learn from individuals with particular traits (prestige; e.g. [80]) or being increasingly likely to adopt the most frequent behaviour (conformism; e.g. [5,23,81]). Such learning biases affect the probability that information will be transmitted from one individual to another [9], and thus the interplay between behaviour, information flow and network structure. The effect of some of these processes on information flow has been investigated using simulated non-human social networks [46]. In these simulations, prestige or conformism biases had small effects on the transmission of a trait when compared with other demographic or social features.

However, when there is a diversity of behaviour within a population, conformism can strongly affect the manner in

which this diversity influences social structure through behaviour matching. This is illustrated in figure 4b. With conformism at play, individual behavioural repertoires become narrower and more like those of other individuals. In consequence, there is an increase in the likelihood that the behaviour of individuals matches. This can increase connectedness, dismantling small-world-type networks (figure 4b(iv–ix)). However, in an already modular social system, conformism decreases variation in behaviour within the different modules, leading to their increased isolation (figure 4b(x–xii)).

This role of conformism in augmenting and maintaining behavioural homogeneity within modules as well as separation between them is of particular interest to cetologists because of the social structures and behavioural partitioning of the large toothed whales. Sperm whales (*Physeter macrocephalus*), killer whales (*Orcinus orca*), pilot whales (*Globicephala* spp.) and probably some of the other larger Odontoceti, have matrilineal

social systems in which females, and sometimes males as well, usually remain in the same social units as their mothers [36]. However, at least in sperm whales, the units may contain related as well as unrelated animals [82]. The social units may be part of larger, hierarchically organized social tiers, such as 'pods', 'clans', 'communities' and 'ecotypes' [83,84]. In sperm and killer whales at least, members of these social tiers have characteristic behaviour—vocalizations, foraging methods, social and play behaviour—that is thought to be socially learned and so culture [37]. This is despite substantial social connectivity. An individual frequently encounters different units, clans, etc., that have dissimilar behaviour. But it does not adopt this behaviour, and we know that some characteristic behaviour of the elements of the different social tiers varies over time [85,86], so the behavioural repertoire cannot be purely inherited from the mother during ontogeny. There is some horizontal, within-generational learning, and this almost entirely involves transmission within the social module, whether it is a unit, pod, clan or community. To maintain strict homogeneity, it seems that there must be some transmission bias, probably conformism (bias towards 'leader' figures could also have this effect). Then, if behaviour matching is operating, behavioural conformism will feed back into even tighter social modules (figure 4b(x–xii)).

Another mechanism that can increase social cohesion within social modules and social differentiation between them is symbolic marking, when a particular cultural behaviour acts as a marker of a module, and individuals primarily interact only with others who share the marker [24]. Symbolic markers of group identity are sometimes seen as the most fundamental difference between the cultures of humans (which use such markers) and non-humans (which do not) [87]. And, the argument goes, this is an important reason why human societies are tighter, richer and more complex than those of non-humans.

However, there are two indications that cultural symbolic marking may be a factor in the social structures of the large toothed whales. Killer whales use complex sets of stereotypical pulsed calls for communication [88]. Members of the same pod use the same repertoire of calls, different from those of other pods [89]. In the 'resident' ecotype of killer whales, a pod's repertoire may be quite similar to that of other pods within its clan, but completely different from the repertoires of pods from other clans [90]. Specific call types can evolve over time. Over 10 years, the evolution of a specific call (the 'N4' call) occurred in parallel in two neighbouring pods [85]. The call changed in both pods, but in a way that kept the inter-pod difference constant, more constant than if the changes in each pod had been independent. This indicates that the inter-pod differences in the usage of the call were important to the whales, and suggests that the call functioned as a symbolic marker of pod identity.

Sperm whales also have vocalizations that are characteristic of their social entities. But, in the South Pacific, these entities are large. Clans of sperm whales, each containing thousands of animals, have distinctive behaviour, characteristic vocalizations and sympatric distributions [91,92]. So animals will from time to time encounter members of other clans. In the North Atlantic, there is no evidence of sympatric clans [93]. Atlantic sperm whale vocal repertoires vary geographically. However, the level of distinction in sperm whale dialects among areas thousands of kilometres apart in the Atlantic is considerably less than that between

clans that use the same area in the Pacific [93]. The implication is that the sperm whale clans of the Pacific actively differentiate their repertoires to symbolically mark clan membership [84]. This marking is not required in the Atlantic, where there are no sympatric clans.

Conformism and other transmission biases drive culture so that behavioural variation closely reflects the underlying social structure. Then these behavioural contrasts can shape and reinforce network topology. Symbolic marking is a particularly potent link between the realm of culture and the realm of society. It may not be restricted to humans.

5. Conclusions and the way forward

We have outlined conceptual frameworks for how culture and society interact in non-humans. There are also interesting theoretical examinations of this relationship. Most of these are calibrated for the human case, but several agent-based models aligned for non-human societies have produced interesting results [16–18,46]. The primary challenge is in the real world, collecting and analysing empirical data that can illuminate the interplay between these systems (figures 1 and 4). At least for cetaceans, and probably for other mammals such as primates and elephants, it seems that the relationships between society and culture are important drivers of how these animals interact with each other and with their environment. So how should we proceed?

A primary requirement is to describe social structure. Recording associations or interactions among identifying individuals provides the raw data for analyses of social structure [94]. Recent reviews offer guidelines for measuring and quantifying social relationships, testing social features against null models, describing the spatio-temporal structure of a society [94] and examining the multiscale structure of animal social networks [15,19,50,51,95]. The detection and quantification of social learning in animal populations has proved challenging, especially distinguishing between asocial and social processes. To meet this challenge, a number of techniques have been introduced. These include option-bias [96] and network-based [55,97,98] methods of analysing the spread of innovations through populations [48,56]. Regression-type methods, such as multiple regression quadratic assignment procedure, try to tease apart the contributions of social learning, genes, ecology, ontogeny and potentially other factors to the distribution of behaviour among individuals within a population [38,99,100].

The formalism of coevolutionary networks [25], in which the interplay between individual behaviour and social relationships is explicitly coupled with the interplay of social network structure and social learning (figure 1b(xi),(xii)), is an effective way to conceptualize the mutual relationship between social structure and culture. Computer simulations can illuminate these issues. Agent-based models are well-established tools for examining social dynamics that can enlighten the social structure–culture interplay among animals. A recent promising approach is mimicking transmission processes using epidemiological models contextualized in coevolutionary social networks within heterogeneous populations [101,102].

Disentangling the direction of cause and effect between social structure and culture, and investigating the roles of transmission biases, are non-trivial tasks. For instance, consider the case of dolphins that forage with artisanal fishermen off Laguna, Brazil [103]. For at least 100 years, generations of

dolphins have worked cooperatively with generations of human fishermen to catch mullet, using mutually understood communicative symbols [104]. Not all dolphins in the Laguna population take part in the cooperative fishing, even though they use the same habitat. The distribution of this unique foraging is coupled with its social structure—cooperative and non-cooperative dolphins form distinct social modules [103]. While cooperative foraging with humans could have driven this social segregation through behaviour matching, the behaviour could be propagated through social learning within a pre-existing social module [103]. Perhaps, cause and effect between social structure and culture is most directly approached experimentally. Manipulative experiments either in the laboratory or field can examine the effects of social structure and transmission biases on the spread of behaviour [48,54,105]. Although feasible for some taxa, experimental intervention with large-bodied, free-ranging cetaceans is still logistically challenging, aesthetically and ethically questionable, and impractical in many cases. Alternatively, natural experiments in which objects of cultural behaviour are introduced or removed from the environment can be highly revealing, as in the case of the trawler dolphins of Moreton Bay [75]. More generally though, for cetaceans and other large, large-brained and long-lived animals, most progress

is likely to come from large-scale, long-term, systematic studies of social relationships and behaviour, as in the case of the bottlenose dolphins of Shark Bay [74].

In conclusion, when behaviour is learned from conspecifics during social interactions the distribution and dynamics of behavioural phenotypes within the population can be shaped by its social structure. In turn, this behavioural repertoire produces a cultural context for the population that can drive patterns of social interactions and relationships. This feedback can make both societies and cultures structurally and dynamically complex, strongly affecting the ecology of a species, and thus should be considered when studying species in which social learning is an important determinant of behaviour. Combining network formalism with meticulous observational studies, experimental intervention and computer simulations will allow us to look at both directions of the relationship between social structure and culture.

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