ON THE INTERPLAY BETWEEN SOCIETY AND CULTURE: CAUSES, CONSEQUENCES AND STABILITY OF SPERM WHALE CLANS

by

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I dedicate my work to:

The circle of life—Leonilda Cantor Magnani (*in memoriam*), Edite Abicalaf Neves (*in memoriam*), Alcilena de Souza Magnani (*in memoriam*), and Lucas Aiden Prince;

The birds—for teaching what really matters;

The whales—for not caring about the ideas, intentions, or conclusions herein presented.

"Ê lá no mar
Eu vi uma maravilha
Vi o rosto de uma ilha
Numa noite de luar

Êta luar
Lumiou meu navio,
Quem vai lá no mar bravio
Não sabe o que vai achar"

Lenine, 'Miragem do porto'

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ABSTRACT

The overarching goal of my thesis is to formalize the interplay between animal society and culture, using sperm whales as a model. Sperm whales live in multilevel societies, characterized by cooperation and social learning. Females form nearly-permanent social units and communicate using codas, stereotyped patterns of clicks. Units temporarily group with other units that use similar codas, forming vocal clans—whales of the same population with distinct coda dialects. I investigate the causes, consequences and temporal stability of the sympatric sperm whale clans in the Pacific Ocean. First, I explore the relationship between social structure and social learning as a phenomenon non-exclusive of human societies. Social relationships demarcate how information flows among individuals, as well as its content, while social learning affects who interacts with whom. Second, I show that culture affects sperm whale society by creating clans. With computer models mimicking the dynamics of empirical populations, I test multiple mechanisms of coda transmission—individual learning, genetic inheritance, pure and biased social learning. Clans with different dialects emerge only when whales learn codas from each other, conforming to the most similar individuals around them. Third, I evaluate the consequences of clan membership. Using a long-term dataset, I show differences in social behaviour among clans: members of one clan dived more synchronously and had more homogeneous, briefer relationships than the other. Cultural drift may explain such divergence, with whales replicating within-clan social norms. Finally, I investigate temporal stability of clans by studying the Galápagos population over 30 years. I document a complete population turnover leading to cultural shift: sperm whales studied in 2013-2014 do not belong to two clans that used the area between 1985-1995; instead they are members of clans previously found in other areas of the Pacific. In conclusion, culture gave rise to sperm whale clans, which in turn drives social behaviour, in a two-way relationship that is stable over time but dynamic over space. These findings strengthen the evidence for culture among sperm whales, highlighting that processes driving behavioural flexibility in humans—information transmission through biased social learning and cultural drift—also operate in non-human animal populations.

LIST OF ABBREVIATIONS AND SYMBOLS USED

ABM	Agent-based model
AIC	Akaike information criterion
b_{emp}	Empirical birth rate
c	Probability of migrating to another social unit
C	conformism
CCC	Cophenetic correlation coefficient
CI	Confidence intervals
CV	Coefficient of variation
d	day
dB	decibel
DF	Degrees of freedom
DGDD	Different groups, different days
DNA	Deoxyribonucleic acid
ΔQAIC	Delta quasi-likelihood Akaike information criterion
ENSO	El Niño Southern Oscillation
ETP	Eastern tropical Pacific Ocean
ξ	Maximum reachability distance
g	group size
GI	Genetic inheritance
h	hour
H	Homophily
Hz	Hertz
HWI	Half-weight index
I	Increasing click intervals along the coda
ICI	Inter-click interval
IL	Individual learning
$ilearn$	Individual learning rate
KHz	Kilohertz
km	kilometer

LDA	Linear discriminant analysis
N	Noise
N_0	Initial population size
m	meter
min	Minute
minpts	Minimum number of coda samples
m_t	Mortality rate
P	p-value
Q	Quality of photograph
PC	Principal component
PCA	Principal component analysis
QAIC	quasi-likelihood Akaike information criterion
R	Regularly spaced clicks
S	Social differentiation
SD	Standard deviation
SE	Standard error
SGDD	Same group, different days
SL	Social learning
SLAR	Standardized lagged association rates
SLR	Single-lens reflex camera
SM	Symbolic marking
t	Time step
+	Extended interval between clicks

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CHAPTER 1

INTRODUCTION

"I to be nature looking into nature with such easy sympathy as the blue-eyed grass in the meadow looks in the face of the sky"

~H.D. Thoreau, 1841

Behaviour pervades Life. Simply put, behaviour is everything an individual—be it Procaryota or Eucaryota—does from the moment it comes into life until the moment it dies (Lehner 1998). It is inside and all around us, on the interface between individuals and their environments (Kapeller *et al.* 2013). Behaviour is one of Nature's essential ingredients. Any system in Nature—be it simple, complicate or complex—can be fleshed out by studying two fundamental characteristics: the elements composing the system, and the rules of their interactions (Amaral & Ottino 2004); expressly, how these elements behave and interact with each other. Societies are one of such complex biological systems—an organized complexity (Weaver 1948) within which we and other animals are inserted. As biological complex systems, societies intrigue the attentive observer with their self-organizing and dynamic elements (Camazine *et al.* 2001): individuals with adaptive behaviour.

1.1 SOCIETIES: EMERGENT PATTERNS FROM ADAPTIVE SOCIAL BEHAVIOUR

A society is a collection of individuals of the same species, and the nature, quality and patterning of their social relationships, which are themselves a synthesis of the behavioural interactions between individuals (Hinde 1976). While the individuals' behaviours are usually intricate, the emergent behavioural rules in a society are often simple. So how do complex patterns arise in a society from simple behavioural rules (Hemelrijk 2005)?

The basics of sociality are dictated by the interactions among individuals and with their environment in the search for individual or collective solutions to the challenges of reproducing and staying alive (*e.g.* Wilson 1975, Krause & Ruxton 2002). Thus sociality evolves where there is tension between cooperation and conflict (Tinbergen 1953, Hamilton 1964, Frank 1998). The spatiotemporal predictability of resources, together with predation risks, regulate the trade-offs of group-living; they are the general underlying mechanisms of social structure (*e.g.* Connor 2000, Krause & Ruxton 2002, Gowans *et al.* 2007). However, the big picture is more complex—and fascinating.

Social behaviour is diverse, flexible and adaptive among highly cognitive animals, which is one of the reasons why their societies are dynamic (*e.g.* Lott 1984). A wide range of animal social structures emerges in response to varied ecological pressures, constrained by historic phylogenetic signals (Clutton-Brock 1989, Mann *et al.* 2000, Smuts *et al.* 2008). But such social plasticity is also a product of proximate mechanisms operating at the individual level—physiological, hormonal, developmental, genetic factors (*e.g.* Oliveira 2005, Crossin *et al.* 2013, Schradin 2013, Kappeler *et al.* 2013).

Therefore, individual characteristics can have major effects on social structure, especially at small spatial and temporal scales.

We now have evidence that social behaviour flexibility can also be a product of processes occurring over shorter scales than evolutionary time—one or few generations (see Laland & O'Brien 2012, Perreault 2012). Individuals adjust their behaviour by observing the changing environment and/or the behaviour of conspecifics (*e.g.* Heyes 1994, Laland 2004, Lefebvre *et al.* 2004, Rendell *et al.* 2011). Both, individual and social learning, can be efficient solutions to track varying environments (Richerson & Boyd 2005, Perreault *et al.* 2012). When socially learned behaviours are shared within subsets of a population, they are considered culture (Boyd & Richerson 1985, Laland & Hoppitt 2003), which has been increasingly understood as an important driver of mammalian phenotypes (*e.g.* Rendell & Whitehead 2001, Whiten & Whiten 2011).

1.2 Culture: The way we do it, they way they do it

Culture is pervasive in human societies. It has propelled recent human evolution and transformed our lives in unprecedented ways, by broadening niches (*e.g.* Laland *et al.* 2001, 2014), improving individual fitness (*e.g.* Boyd *et al.* 2011) and, likely, cognition (Ji & Yap 2016). Via social learning, information flows within and between generations at a faster pace than via genetic transmission (Cavalli-Sforza & Feldman 1981). Thus culture allows for a rapid spread of (generally) adaptive behaviours (Boyd & Richerson 2004). Culture is not an exclusively human feature. The fundamentals of culture extend to societies of other taxa (*e.g.* Laland & Hoppitt 2003, Laland & Janik 2006), though human cultures are arguably different than those of other animals (Laland & Galef 2009).

The key distinctions between the two cultural realms seem to be that human cultures are more cumulative and symbolic. Human cultural evolution is clearly incremental: achievements are improved in successive generations. Perhaps because human learning is more process-oriented whereas animal social learning is more product-oriented (Tennie *et al.* 2009), the evidence for cumulative culture among animals remains embryonic, and contentious (*e.g.* Marshall-Pescini & Whiten 2008). Human culture is also clearly based on a symbolic system for thinking and communicating (Ernst 1944). Symbols—as shared conventions, socially-agreed and self-referential signs—are part of everyday lives of humans in any corner of the world. They seem to be lacking in animal cultures (*e.g.* Perry 2009, Jablonka & Lamb 2014), at least in the rich forms observed across human societies.

While accumulation and symbolism primarily define the divergence between human and animal cultures, there is much debate about how to define culture. Some definitions are very specific and anthropocentric, occasionally only including humans (*e.g.* Braidwood 1975), while others are more inclusive (*e.g.* Boyd & Richerson 2004). Here I consider the working definition of culture as behaviour that is socially transmitted and shared within subsets of a population (*e.g.* Rendell & Whitehead 2001, Laland & Hoppitt 2003). This is permissive enough to be measurable across species, while retaining two main underlying properties of the more restrictive definitions of culture: 1) a behavioural trait distinguishable between groups; and 2) a transmission process involving social learning (acquiring behaviour via observation of conspecifics). This broader concept of culture facilitates interdisciplinary research ultimately interested in tracking its evolutionary origins and trajectories.

As such, the chasm between human and other animal cultures has been slowly bridged by data painstakingly collected during long-term field studies (*e.g.* Whiten *et al.* 1999) and carefully-designed controlled experiments (*e.g.* Whiten *et al.* 2005). We can now appreciate that culture also pervades animal societies—birds, fishes, terrestrial and aquatic mammals to name but a few (Laland & Hoppitt 2003, Laland & Janik 2006). Semantic disputes aside (*e.g.* Laland & Galef 2009), the point is culture evolves shaped by population-dynamic processes both among humans and other animals (Mesoudi 2011, Perreault *et al.* 2012).

The cultural inheritance system can act together with genetic transmission driving phenotypes (Boyd & Richerson 1985, Laland *et al.* 2010) and shaping the behavioural repertoire (Rendell & Whitehead 2001, Laland & O'Brien 2012). Cultural transmission of information is one of the determinants of behavioural syndromes and intrapopulational behavioural variation (see Araújo *et al.* 2011, Sih *et al.* 2012, Wolf & Weissing 2012). Although many social and biological theories are built upon the assumption that individuals are ecologically equivalent, individual heterogeneity is no longer being neglected as insignificant noise. It has profound implications for individual survival and fitness (*e.g.* Curio *et al.* 1978) and population (*e.g.* Whitehead & Richerson 2009), community (Bolnick *et al.* 2011, Sih *et al.* 2012) and social dynamics (*e.g.* Krause *et al.* 2010, Castellano *et al.* 2009). In consequence, the resultant heterogeneity in individual behavioural repertoire influences the structure of a society, and how information spreads over it. In turn, information transmission via learning processes can also influence social structure (Timbergen 1953, Nunn *et al.* 2009, Whitehead & Lusseau 2012).

1.3 SOCIETY AND CULTURE: A TWO-WAY RELATIONSHIP

The way individuals behave can affect, and be affected by their social ties. Essentially, this is how culture and society influence each other. Culture is founded on the transmission of behaviour through social learning among individuals (Boyd & Richerson 1985, Franz & Nunn 2009). Social learning can occur through a variety of psychological mechanisms (Heyes 1994, Laland 2004, Hoppitt & Laland 2008), such as emulation, teaching, social facilitation, local enhancement, product imitation and others (for a recent review and definitions, see Rendell *et al.* 2011). Thus, with learning clearly taking place during individual interactions, social structure—who interacts with whom—affects the transmission of learned behaviours (*e.g.* Voelkl & Noë 2008, 2010, Whitehead & Lusseau 2012). In fact, social structure influences the efficiency, consistency and persistence of behavioural transmission through social learning (Cantor & Whitehead 2013). Moreover, social structure can define the content of information being socially transmitted, and thus becomes a cause of cultural diversity (Norenzayan 2011, Whitehead & Lusseau 2012).

For example, consider two hypothetical populations, one in which all individuals interact with each other on a regular basis (a highly connected society), and another structured into two groups whose members tend interact more often with themselves than with the rest of the population (a socially segregated society). Now consider that a novel, more efficient way of finding a food resource was introduced in both populations by individual learning, i.e. by an individual creating the new technique by itself. If individuals learn from each other (for example by observing, copying the behaviours of their social contacts), the new foraging technique is likely to spread more quickly in the first population because there all individuals will have a chance to interact with the innovator or with the innovator's close friends. In the first population, the innovation would also be learned more accurately, since individuals are more likely to learn from the source (the innovator) than through a long chain of social connections. In contrast, in the second, socially segregated population the foraging technique may change faster over time, due to learning errors or deliberate introduced modifications. Thus, in general, the higher the structure of the society, the lower the speed, fidelity and robustness of the information being transmitted (e.g. Cantor & Whitehead 2013, Duboscq *et al*. 2016). All of these illustrate how social structure can affect culture when behavioural traits flows among individuals via learning.

In turn, culture can shape social structure by influencing the opportunities for social interactions (see Boyd & Richerson 2004, Morgan & Laland 2012). In humans, for example, culture affects higher-level social attributes (*e.g.* Boyd & Richerson 1985) directly—for instance individuals learning that they must accept and live in a monarchical society—as well as indirectly—a socially-learned deference to elders or members of one sex will drive the social structure into particular forms. Through either, or both, of these routes, populations may possess different social structures. In other species for which culture is important, social learning can enhance social cohesion—through activity synchronization and behavioural homogenization within groups (Coussi-

Korbel & Fragaszy 1995)—and sometimes split the population into subsets of individuals with distinct behavioural repertoires. Individuals may prefer to interact with individuals who perform similar behaviours; and during these interactions, they can learn other behaviours from one another. Thus, through social influence (social relationships leading to behavioural similarity) and behaviour matching (vice-versa), a population of social learners can be structured into distinct cultural groups (Axelrod 1997, Centola *et al.* 2007). For example, socially-learned foraging techniques and communication signals among animals can lead to the coexistence of sympatric groups with distinct behavioural repertoires.

Some examples come from populations of whales and dolphins. Cetaceans have diverse and flexible behavioural repertoires, and even subsets of individuals from the same population may be split into groups according to behavioural repertoires. In south Brazil, for example, this is clear in a small population of bottlenose dolphins, in which nearly half of the individuals cooperate with artisanal fishermen when hunting mullet fish schools. The dolphins that perform the foraging technique are more socially connected with each other than with those who do not, dividing the population into distinct social modules (Daura-Jorge *et al.* 2012). Among whales that live in multilevel societies, learned acoustic communication signals are also important in defining who interacts with whom. For example, pods of killer whales form vocal clans with distinct repertoires of calls (Ford 1991, Filatova & Miller 20015), and sperm whales form clans with distinct repertoires of sequences of clicks used for communication (Rendell & Whitehead 2003, Gero *et al.* 2016a). In both cases, individual whales primarily interact with—and so learn from—their clan members, reinforcing behavioural boundaries within the same population.

Neither these cultural behaviours nor these cultural groups are static. Rather, they are evolving products of individual and collective experiences. Over time, cultural groups may change their composition, and cultural repertoires may change as cultural traits are fixed and selected, lost and changed due to innovations, founder effects, transmission errors and biases (Koerper & Stickel 1980, Cavalli-Sforza & Feldman 1981).

1.4 EVERYTHING CHANGES: ADDING TIME TO THE MIX

Culture and society are closely linked by dynamic ties. They coevolve as social learning is based upon association, and association may be biased by shared learned behaviours. Add time to the mix and who interacts with whom and what they learn from one another may change, influencing the outcomes of the culture-society interplay. Individuals change as they grow, and so do their behaviour and social affiliates (*e.g.* Biro *et al.* 2006, Matsuzawa *et al.* 2006, White *et al.* 2012, Patterson *et al.* 2015). Populations change in composition as individuals enter and leave via birth/immigration and death/emigration, and so do the social relationships within the society (*e.g.* Cantor *et al.* 2012). Culture changes over time, as both individual traits and the groups bearing them spread and decline (Cavalli-Sforza & Feldman 1981, Richerson & Boyd 2005), and so a population's behavioural repertoire changes (*e.g.* Avital & Jablonka 2000).

Cultural change is now recognized as one pillar of evolution, along with genetic and epigenetic (non-DNA cellular transmission of traits) inheritance systems (*e.g.*

Jablonka & Lamb 2014). Culture evolves with analogous ingredients of Darwinian evolution: variation ("mutations" by transmission errors or deliberate innovations), heredity (transmission of information via vertical, horizontal, oblique social learning), differential survival and multiplication (cultural selection) and drift (see Cavalli-Sforza & Feldman 1981, Richerson & Boyd 1985, Boyd & Richerson 2005). Here, I illustrate cultural changes in acoustic communication systems, since they are strongly linked to social structure (see Freeberg *et al.* 2012) and change over time, at least partially, through cultural processes.

While communication systems adapt over the time scales of genetic evolution, significant changes can also happen during few generations time (*e.g.* Podos & Warren 2007, Nelson *et al.* 2004), and even much more rapidly, within the same generation (Deecke *et al.* 2000, Noad *et al.* 2000, Garland *et al.* 2011) due to cultural processes. Cultural selection may guide changes stabilizing specific behavioural variants that perform better in a given context. For instance, culturally-transmitted bird songs can be well adapted to a habitat (*e.g.* Tobias *et al.* 2010) thus stable over time (*e.g.* Byers *et al.* 2010); or show directional change in parallel to shifts in the acoustic environment (*e.g.* Slabbekoorn & Boer-Visser 2006). Similarly, the structure and meaning of human acoustic signals can be shaped by cultural pressures to become compressible and maintain distinctions (*e.g.* Kirby *et al.* 2015, Tamariz & Kirby 2016). Alternatively, neutral cultural processes can alter learned repertoires but with no apparent fitness benefits (Koerper & Stickel 1980). An example is random-copying, which can induce rapid shifts in frequency of cultural variants, as observed in the high turnover of popularity in several human behaviours (Hahn & Bentley 2003, Bentley *et al.* 2004, 2007, Rendell *et al.* 2010). Simultaneously, behavioural repertoires can change as individuals, while learning from one another (Janik & Slater 2000), introduce errors and innovations that can be selected or fixed by cultural drift (*e.g.* Williams *et al.* 2013, Filatova & Miller 2015).

Demographic mechanisms can significantly affect the dynamics of communication systems with socially learned vocal signals. In allopatric groups or populations, variation becomes evident (*e.g.* songbirds: Krebs & Kroodsma 1980, Podos & Warren 2007; primates: Tanaka *et al.* 2006; cetaceans: Filatova *et al.* 2015), as spatial segregation generally promotes cultural diversity and reinforces divergences (Whiten *et al.* 1999, van Schaik *et al.* 2003). In sympatric groups or populations connected by movement of individuals, repertoires tend to either maintain their differences or homogenize, depending on the strength of opposite cultural forces. As behaviourally distinct groups meet, or individuals leave and enter populations, behavioural differences could be used to label group identities and so reinforcing cultural boundaries (*e.g.* Boyd & Richerson 1987). On the other hand, differences can be successfully introduced and diffuse through the population (*e.g.* Fayet *et al.* 2014, Whiten *et al.* 2016), causing immigrant and local cultures to merge (*e.g.* Mesoudi *et al.* 2016). In acoustic cultural repertoires, such changes are usually gradual (*e.g.* Slater & Ince 1979, Nelson *et al.* 2004); but a local cultural revolution may be triggered when an injected foreign trait is adopted rapidly and collectively (*e.g.* Noad *et al.* 2000, Garland *et al.* 2011).

For the social animal, a communication system is of paramount importance. It tends to increase in complexity with higher social demands (*e.g.* Freeberg *et al.* 2012), as more diverse communication helps one to navigate through multiple social relationships (*e.g.* Dunbar & Shultz 2007). Arguably, vocal communication may have peaked in complexity in human languages—a symbolic system with unrestricted range of meanings (Jablonka & Lamb 2014, Tamariz & Kirby 2016). Yet, acoustic communication is imperative for many non-human animals (*e.g.* Horn & Leonard 2005, McGregor 2005, McGregor & Horn 2015), particularly in the aquatic environment where light is usually limited but sounds travel farther and more effectively (Tyack 1998, Janik 2005).

Vocal communication in whales and dolphins is sophisticated (*e.g.* Tyack 1998, Janik 2014), in line with their complex sociality (May-Collado *et al.* 2007). The sounds they produce are crucial to every aspect of their lives, including a range of social skills such as grouping cohesively (*e.g.* King *et al.* 2014), maintaining long-term relationships (Bruck 2013), addressing and remembering affiliates (King & Janik 2013, King *et al.* 2013), coordinating foraging strategies (*e.g.* King & Janik 2015), attracting mates (Smith *et al.* 2008) and marking multiple social tiers (Gero *et al.* 2016a). Partially in consequence, cetaceans have particularly complex and varied social systems (Connor *et al.* 1998) based on evolving acoustic communication systems, which gives considerable evidence for culture being an important driver of behaviour in these species (Rendell & Whitehead 2001, Whitehead & Rendell 2014).

1.5: OCEANIC CULTURAL SOCIETIES: WHALES AND DOLPHINS

I begin with a caveat. Logistics may constrain studies on the interplay between social structure and cultural transmission in cetaceans. There are many challenges in studying long-lived, deep-diving animals that range over thousands of kilometers in offshore waters. But as data accumulate in long-term multidisciplinary efforts, we begin to accurately depict the social systems (*e.g.* Mann *et al.* 2000). Cetacean cognitive capacities are highly developed (Marino *et al.* 2007) and confer behavioural plasticity and diversity to their social systems (*e.g.* Connor *et al.* 1998), which inspired a number of conceptual models and empirical analyses of cetacean socioecology (*e.g.* Mann *et al.* 2000, Whitehead 2003, Gowans *et al.* 2007).

These outcomes from the sea counterbalance the theoretical expectations of socioecological theory build upon animals from the terrestrial environment (*e.g.* Wilson 1975). Cetaceans live in a tridimensional, mobile environment characterized by red noise (Whitehead 2008a), where risk and resources are more unpredictable in space and time (Gowans *et al.* 2007). Consequently, cetacean societies are not bounded by defended territories, and are generally larger than those of primates and other terrestrial animals. All of these attributes give power and potential to the dynamic relationships between culture and society (see Gero & Rendell 2015).

Cetacean societies are diverse. While ephemeral associations may be the general pattern among baleen whales (Mysticeti), the social relationships of toothed whales (Odontoceti) contain both labile and stable features (Connor *et al.* 2000). A variety of ecological (*e.g.* Gowans *et al.* 2007), biological (*e.g.* Lusseau *et al.* 2006) and spatiotemporal mechanisms (*e.g.* Cantor *et al.* 2012) underpin the variation in cetacean social structures. It is becoming clear that social learning is an important part of how individual whales and dolphins cope with their ecological and social environments, especially in foraging, communication and social behaviours (*e.g.* Boran & Heimlich

1999). In other words, culture adds another layer of social complexity in cetacean societies (Rendell & Whitehead 2001, Whitehead & Rendell 2014).

The evidence for culture among whales and dolphins grows as we refine our understanding on their social complexity, geographical distribution, life history, memory and learning abilities (reviewed in Whitehead & Rendell 20014). Captivity experiments show that cetaceans do learn from their peers (*e.g.* Janik 2014), supporting that social learning can underlie sympatric behavioural divergence, fast spread of innovations within populations, and rapid evolution and long-term maintenance of behavioural variants observed in the wild. For instance, the rapid evolution and spread of complex songs (Noad *et al.* 2000, Garland *et al.* 2011) and rapid spread of innovative foraging tactics (Allen *et al.* 2013) of humpback whales can only be explained by individuals learning from those whom they interact with. Similarly, the vocal tradition (Ford 1991) and dietary differences (Ford *et al.* 1998) among killer whale ecotypes are compelling examples of the influence of social learning in sympatry and over large spatial scales. Finally, the role of learning is clear in the emergence and maintenance of highly specialized foraging techniques among cetaceans—some of which lasting for many generations (*e.g.* Simões-Lopes *et al.* 1998). Examples include the spontaneous stranding (Lopez & Lopez 1985) and (potentially) the cooperating hunting (Pitman & Durban 2012) of pods of mammal-eating killer whales, as well as the long list of feeding tactics of bottlenose dolphins, such as sponging, mud-ring, barrier and trawler feeding (reviewed in Whitehead & Rendell 2014). In some of these cases, it seems that the spread of a local foraging variant via social learning can shape the structure of the society (*e.g.* Daura-Jorge *et al.* 2012, Ansmann *et al.* 2012, Mann *et al.* 2012).

The effect of culture on cetacean societies is not restricted to localized and small populations. We also find impressive examples at a vast, oceanic scale. Sperm whales (*Physeter macrocephalus*) have one of the most complex social structures among all sea creatures (*sensu* Bergman & Beehner 2015) as they form multilevel societies (Whitehead *et al.* 2012), in which cooperation, social communication, and culture are important underlying mechanisms (Whitehead 2003). These traits make sperm whale societies a very good model to address cultural processes (Rendell and Whitehead 2001, Whitehead & Rendell 2014), social structure (Whitehead 2008b) and their interdependence—along with the many particularities of their natural history that make such studies challenging and exciting.

1.6 STUDY SYSTEM: SOCIETY AND CULTURE IN SPERM WHALES

Sperm whales are circumglobally distributed in offshore, deep waters (Jaquet 1996). There they perform deep (~200-2000m) and long (~40min) dives to forage, mainly, for squids (Rice 1989). Sperm whales have two distinctive behavioural states: 75% of the time foraging at depth, and the rest resting/socializing at the surface (Whitehead 1989, Whitehead & Weilgart 1991). For both, acoustic communication is essential. Sperm whales possess a sonar-like apparatus—the spermaceti organ—with which they produce series of broad-band clicks to echolocate prey. During social contexts, they use the same system to produce a range of stereotyped patterns of clicks, called codas (Watkins & Schevill 1977), used for communication (*e.g.* Schulz *et al.* 2008, Frantzis & Alexiadou 2008).

The social patterns of sperm whales reflect their sexual divergences in life styles. Males depart from their natal groups to live quasi-solitary lives near the poles and return to tropical waters to breed (Whitehead 2003). On the other hand, females and immatures spend their lives in the tropics, living together in stable, nearly-matrilineal social units of about 11 related, as well as unrelated, individuals (Richard *et al.* 1996, Christal *et al.* 1998, Lyrholm *et al.* 1999). The social lives of females are cooperative. There is evidence for communal care of the young (Gero *et al.* 2009, 2013), as well as for defending against predators (Arnbom *et al.* 1987), and suggestions that females might finding food together (by sharing, or eavesdropping on, information about ephemeral but somewhat predictable food patches) (Whitehead 1989). In addition, the absence of territoriality and within-unit mating suggest reduced competition among unit members (Christal & Whitehead 2001). These cooperative activities take place within and between social units of females.

Sperm whale societies are multilevel: individuals living in nearly-permanent social units that form temporary groups within a larger vocal clan (Figure 1.1, Whitehead *et al.* 2012). Members from different social units form temporary groups (travelling together for periods from hours to few days; Whitehead *et al.* 1991), within which they preferentially associate in close spatial proximity (Whitehead & Arnbom 1987) with members of their own unit (Christal & Whitehead 2001). But more strikingly, these temporary groups are formed by social units that share a similar repertoire of codas. Thus a higher level of social organization is recognized: the vocal clans (Rendell & Whitehead 2003, Gero *et al.* 2016a,b). Vocal clans span large areas, are sympatric and genetically indistinct (in the nuclear genome), which strongly supports the hypothesis of culture driving their social structure (Rendell & Whitehead 2003, Rendell *et al.* 2012, Whitehead *et al.* 2012, Gero *et al.* 2016b).

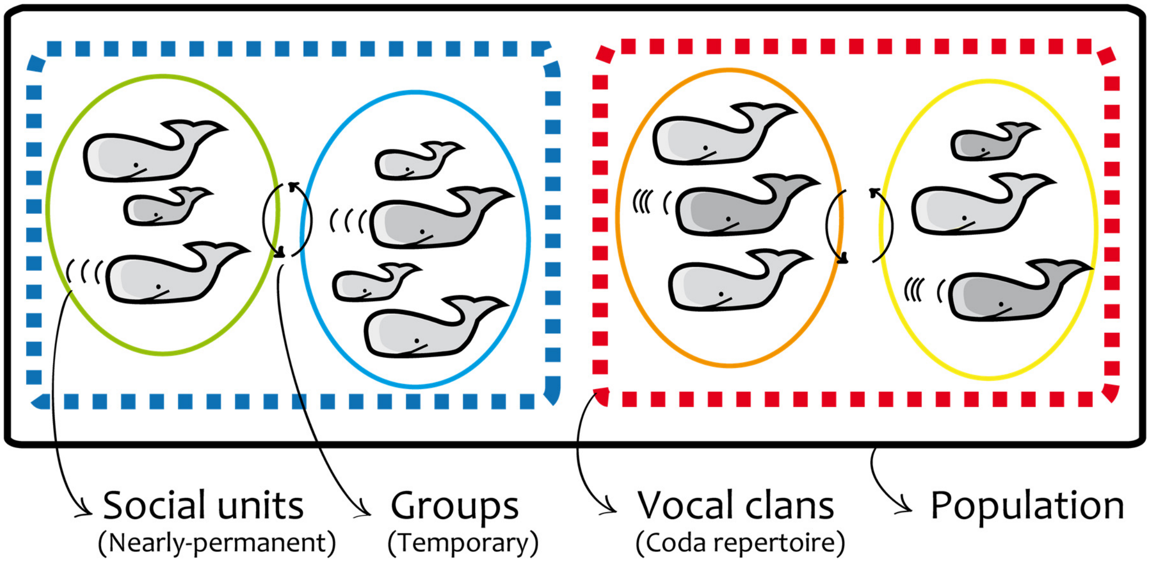

Figure 1.1. Schematic representation of the fundamental social levels of a female sperm whale society from the Pacific Ocean (see Whitehead *et al.* 2012). In a *population*, individual females and their young live in nearly-permanent *social units* for several years (presumably their entire lives). Social units form temporary *groups* (from hours to few days) with other units, but tend to do so with units with which they have high similarity in the repertoire of codas (stereotyped patterns of click sounds used in social communication), forming a *vocal clan*. A clan of sperm whales is identified as such collections of social units that share an identifiable part of their coda repertoire, where that part of the repertoire both forms a large portion of the coda production of those social units and is readily distinguishable from the coda repertoires of social units from other clans (see Rendell & Whitehead 2003). This multilevel structure applies only to the

females and immature individuals; males disperse from their natal groups to live nearly-solitary lives near the poles, returning to tropical waters to mate (Whitehead 2003).

Clans of sperm whales are different from most other animals' social structures (but see orca acoustic clans; Ford 1991). They may be the largest cooperative social entity outside of humans (Whitehead & Rendell 2014). But what are the drivers of clan structure in sperm whale societies? What are the consequences of a cultural population structure for the individuals? How stable is this structure over time? In my research, I describe and explain these three aspects of the interplay between social structure and culture in sperm whales.

1.7 THESIS OBJECTIVES AND ORGANIZATION

The overarching goal of my thesis is to investigate the interplay between society and culture and infer its behavioural mechanisms, behavioural consequences and temporal stability, using the multilevel sperm whale society as a model. To accomplish that, I employed an array of analytical methods to combine fieldwork, simulations and a long-term empirical database, representing a multidisciplinary study that spans over nearly 30 years.

In the second chapter, I delineate how social structure and learned behaviour are mutually dependent, putting forth a conceptual framework for the interplay between animal culture and society. I further explore theoretical expectations of this two-way relationship, and back them up with recent advances in empirical studies with cetaceans.

This chapter is a review essay that sets the theoretical ground for the thesis. I have reviewed the relevant literature on the theory and methods to propose the formalism of adaptive networks as a feasible tool to explore the society-culture interplay. This chapter was published in 2013 in the theme issue of *Philosophical Transactions of the Royal Society B* entitled “Flexibility and constraint in the evolution of mammalian social behaviour”.

In the third chapter, I explore the mechanisms that give rise to the cultural segregation that structures sperm whale populations. Here I focus on one side of the culture-society interplay: whether cultural transmission can shape social structure. The aim is to backtrack the empirically-observed social pattern (sperm whales organized in sympatric clans with distinct repertoires of communicative signals) to infer on its causes. By building mechanistic agent-based models informed by 18 years of empirical data, I tested competing mechanisms—namely genetic inheritance, individual learning, pure or biased social learning—that could give rise to vocal clans, the social level that crowns the sperm whale multilevel society. I show that clans are unlikely products of stochastic processes such as genetic or cultural drift but likely originate from cultural transmission via biased social learning of acoustic communicative signals. I then suggest cultural transmission as a key ingredient in the emergence of sympatric clans of sperm whales, which increases the similarities between human and non-human societies. This chapter was published open-access in 2015 in the journal *Nature Communications* and has received considerable attention in the media (featured in over 200 news outlets from 18 countries).

In the fourth chapter, I switch gears to the other side of the culture-society equation, and test whether the known social structure into vocal clans could have consequences for their members. Using a long-term database from 1985 to 2003, I quantify the fine-scale social behavioural differences of the members of the two main vocal clans of sperm whales off the Galápagos Islands. I show the clans differed consistently in diving synchrony, heterogeneity, and temporal stability of social relationships, and suggest that disparities in surface-time coordination and quality of social relationships are byproducts of clan segregation, with potential effects in alloparental care giving and calf survival rates. This chapter was published in 2015 the journal *Marine Mammal Science.*

In the fifth chapter, I add time to the mix and evaluate the temporal stability of the clan structure in the sperm whales off the Galápagos Islands over the last thirty years. Populations are dynamic, and so are societies and culture. I updated the long-term database on population structure acoustic behaviour with new data I collected off Galápagos in 2013 and 2014 to compare acoustic repertoires that defines the vocal clans and clan membership through individual identification. I present the curious case of the bimodal cultural makeup of this population, in which the two original sympatric cultures may have been replaced by two different culturally-defined groups. Previous data indicate members of two clans using the Galápagos waters until about 1995, whereas new data indicate that two different clans, formerly common elsewhere across the South Pacific, are now using this area. In brief, I document a local cultural turnover triggered by a complete population turnover using the area. While these findings suggest some temporal stability in clan structure (long-lasting clan membership), it also points to low spatial stability (clans with large and dynamic ranges). This chapter is in review in the journal *Royal Society Open Science.*

In the final chapter, I conclude my "sympathetic look" in the face of the nature of animal societies and cultures. I discuss the combined relevance of my research by reviewing the four key highlights of the thesis. Here I argue that information transmission through biased social learning and cultural drift—key drivers of human behaviour—can also be at play in wild animal populations structuring their social relationships. Finally, I suggest the future steps for advancing the field on the relationship between cultures and societies of animals. This chapter is followed by four appendices containing supplementary material for the chapters 2 to 5.

CHAPTER 2

ON THE INTERPLAY BETWEEN SOCIAL NETWORKS AND CULTURE: THEORETICALLY AND AMONG WHALES AND DOLPHINS [1,2,3]

> *"The universe is wider than our views of it"*
>
> *~ H.D. Thoreau, 1854*

2.1 ABSTRACT

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

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[1] *This chapter has been published in the theme issue of the Philosophical Transactions of the Royal Society Series B "Flexibility and constraint in the evolution of mammalian social behaviour" compiled and edited by Peter M. Kappeler, Louise Barrett, Daniel T. Blumstein and Tim H. Clutton-Brock. The full reference is: Cantor M. & Whitehead H. 2013. The interplay between social networks and culture: theoretically and among whales and dolphins. Philosophical Transactions of the Royal Society B. 368. 1618, 20120340. doi:10.1098/rstb.2012.0340*

[2] *Authors' contributions: Mauricio Cantor (MC), Hal Whitehead (HW): Developed the conceptual framework; MC: reviewed literature; MC: created the figures; MC: drafted the manuscript; HW contributed several ideas, comments, edits in the figures and manuscript; MC reviewed the manuscript during the peer-review process.*

[3] *Publication history: Manuscript First Submission: 14 SEP 2012; Reviewed Manuscript Received: 21 NOV 2012; Manuscript Accepted: 26 NOV 2012; Manuscript Published: 08 ABR 2013.*

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.

2.2 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 [see 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 [*e.g.* 6]. Individuals regulate their behaviour by tracking the environment as it changes and/or by tracking their conspecifics' behaviour [*e.g.* 7-9]. The former, individual learning, is an asocial trial-and-error strategy that may be time-consuming, energetically costly or risky; the latter defines social learning, a nongenetic 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 [*e.g.* 5], social structure and culture are linked (Figure 2.1). If we express the social structure of a community as a network, i.e. nodes depicting individuals linked according to their social relationships [*e.g.* 14; see Appendix A2.1, Table S2.1], then we can envisage that social learning occurs along the network edges (i.e. the links between individuals; Table S2.1). In network depictions of animal societies the edge weights usually represent estimates of the proportion of time that each pair of individuals spends together [14], and so may represent the probabilities that individuals learn from one another [*e.g.* 15-17]. Thus, as illustrated in Figure 2.1A, 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 [18] 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 2.1A). Then we can think of social learning occurring during interactions, or being governed by relationships (Figure 2.1A, d). Network thinking is implicated by another element of the general definition of culture: “shared” [see 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; see also Table S2.1], for the results of social learning to be called culture. Thus, in Figure 2.1A we show a second major link (e) from social structure to culture.

But culture can also affect social structure. If individuals preferentially associate with those who behave similarly [*e.g.* 20-22] (Figure 2.1A, c) and behaviour has a cultural element, then elements of social structure may reflect culture. This may especially be the case when conformism homogenizes behaviour though social learning [*e.g.* 23], and/or when cultural symbols are used to mark social entities [24] (Figure 2.1A, f).

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 [*e.g.* 27-29], due to behaviour matching (Figure 2.1B, g) [21] and social influence (Figure 2.1B, h) [20]. Either way, both the network structure and the transmission dynamics can be transformed, subtly or profoundly (Figure 2.1B, k). Social structure influences how information flows through the population [*e.g.* 15] (Figure 2.1B, i), 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 [*e.g.* 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 [see 22,32,33] (Figure 2.1B, j). Finally, interplay between social structure and transmission dynamics closes this cycle (Figure 2.1B, l), since behaviour defines the cultural context, with its norms and transmission biases, that influences how individuals behave and interact [see 5,12,23,24].

There are many theoretical studies of the potential relationships between network structure and information flow over human-like social networks [*e.g.* 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 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 [see 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 illustrated in Figure 2.1, and those imperfectly.

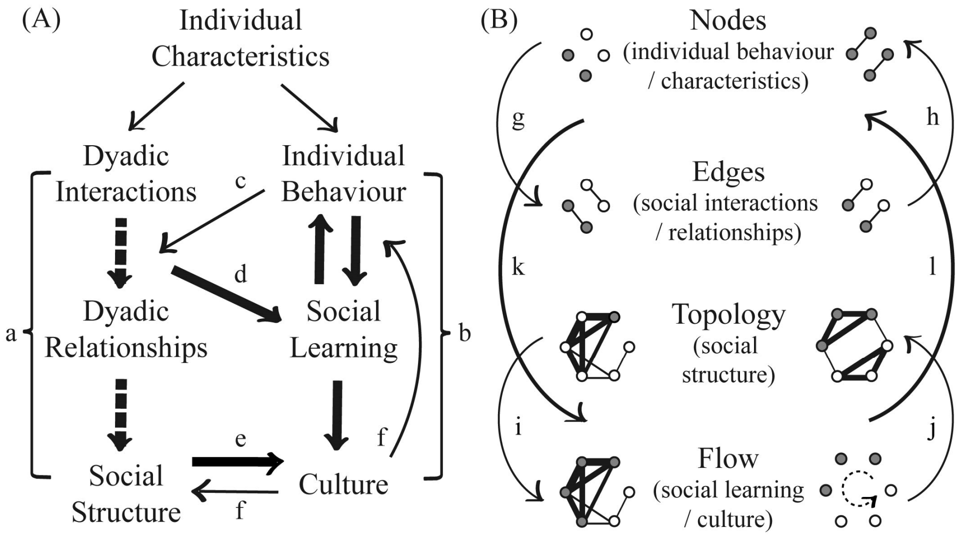


Figure 2.1. Two representations of the dynamic relationship between social structure and culture. (A) Individual characteristics ultimately influence both social structure, through their effects on social relationships (a), and the cultural context, through variation in both behaviour and the individuals' partialities for social learning (b). 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 representing individuals) and edges (links representing relationships) (g, h) shapes and is

shaped by (k, l) the coevolution of network topology and transmission mechanisms (i, j). Thick dashed arrows illustrate the Hinde's [18] conceptual framework for social structure (a). Thick black arrows illustrate the elements of the concept of culture from Laland & Hoppitt [12] (b). Thin arrows (c-f) represent additional effects hypothesized in this review. For further details on network terminology please see the Appendix A2.1, Table S2.1.

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 2.1B). Even though disentangling cause and effect in this two-way relationship is not trivial, we first summarize how social structure may affect culture (section 2), then how culture may affect social structure (section 3). We also consider the potential effects of social learning biases and symbolic marking (section 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 (section 5).

2.3 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 [*e.g.* 39-45]. Agent-based models that roughly mimic non-human social systems and social learning predict that large-scale structure [15,17,46], within-group hierarchy structure

[16; see also 47,48] and the differentiation of individual social roles [49] affect information flow on social networks (Figure 2.2).

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 Table S2.1) which decrease speed, fidelity and robustness of information flow [15]. Learning errors promote behavioural diversity in the population [17]. 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 [*e.g.* 12], one could conclude that social structure can produce culture when the network is clearly modular [17]. 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 [*e.g.* 50].

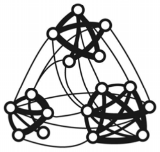
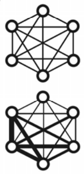
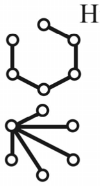
		Large-scale structure		Within-module structure	
Property	Metric	Low 	High 	Low 	High 
Network					
Proportion of edges	Connectance	↑	↓	↑	↓
Mean distance of nodes	Average path length	↓	↑	↓	↑
Cohesive subgroups	Modularity	↓	↑	–	–
Individual centrality	Strength, Closeness, Betweenness	(↓)	(↑)	↓	↑
Transmission					
Efficiency	Speed	↑	↓	↑	↓
Consistency	Error chance	↓	↑	(↓)	(↑)
Persistence	Extinction risk	↓	↑	↓	↑
Diversity	SD; Diversity index	↓	↑	(↓)	(↑)

Figure 2.2. 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 [15-17,46,49]. Arrows in parentheses represent our own speculations. Up arrows indicate a positive relationship and down-arrows a negative relationship. 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. 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) [15]; 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 [15]; persistence over time was assessed by simulating the forgetting of acquired information and estimating its extinction risk [15]; and diversity was measured by the standard deviation of continuous behavioural measures or the Shannon diversity index for categorical behaviour [17]. See Table S2.1 (Appendix A2) for definitions and interpretation of the network terminology; network metrics formulae can be found in elsewhere [*e.g.* 14,19,93,94].

Agent-based models suggest that within small social networks that may be representative of social modules in 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 [16]. Social learning homogenizes behaviour in egalitarian networks more quickly and effectively than in despotic ones [16]. Scaling down to the individuals, the social role an animal plays, inferred through the node position in the network, affects the flow of information [see 51]. For instance, individuals with high centrality, towards the centre of networks, (see Table S2.1) may be key dispersers, funnelling information flow between different social modules, or controlling the access or the quality of information [see 49]. Thus, even fine-scale social structure influences social learning [47,48,52].

We have summarized these theoretical results on how social structure affects culture in Figure 2.2. 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 [*e.g.* 48,53,54]. 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 [55]. 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) [55].

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 [56], "the most elaborate single display known in any animal species" [57, 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" [58, 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 2.3. Even though the northern and southern hemisphere breeding grounds overlap off Costa Rica [59], 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 [60,61]. Possible mechanisms for this synchronicity in behaviour on nodes 4,800 km apart include information exchange on common feeding grounds or during migration (Figure 2.3), 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 [see 60,61].

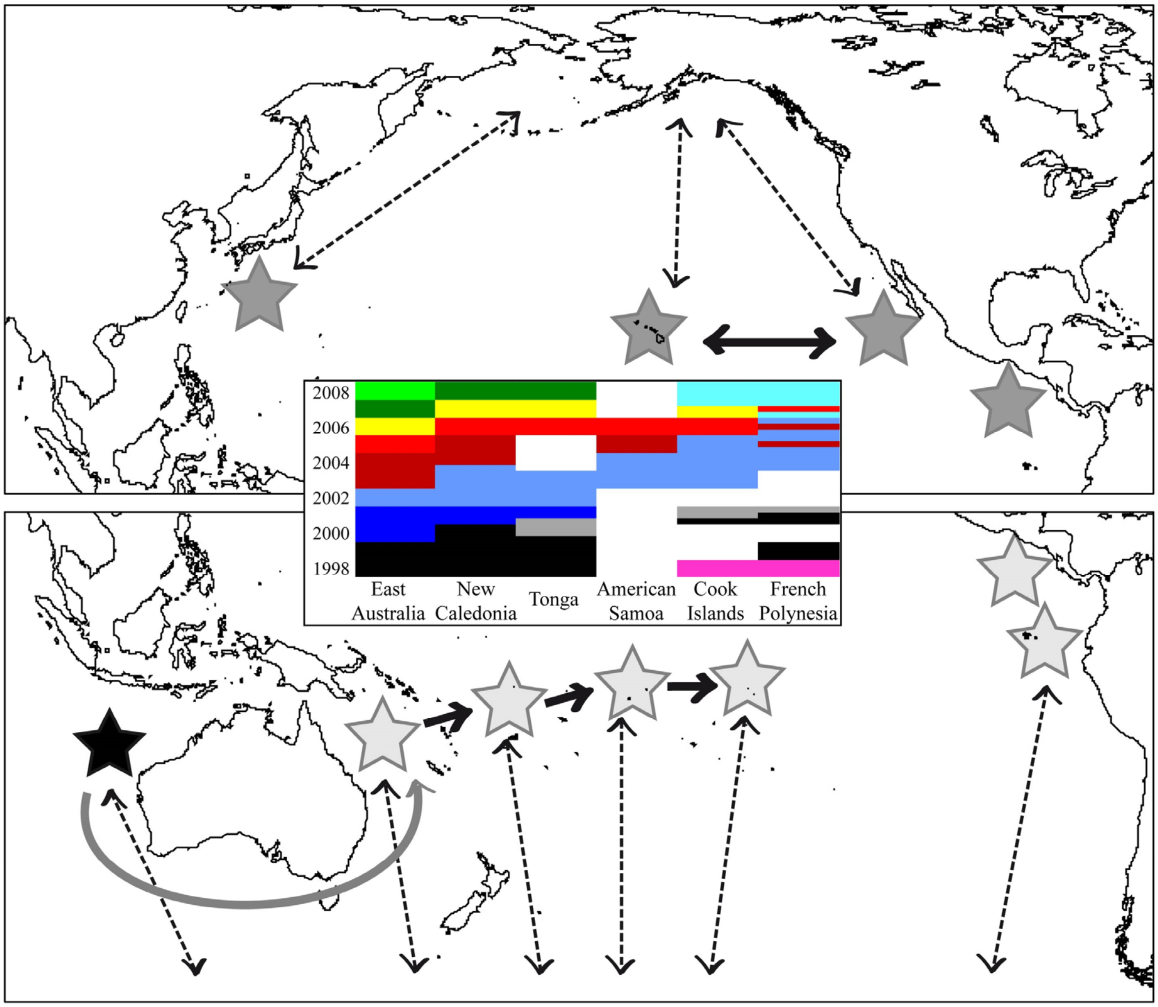


Figure 2.3. Humpback whale song in the Pacific. Principal breeding grounds are shown by star symbols in the North Pacific (dark grey), South Pacific (light grey) and Indian Ocean (black). Seasonal migration routes are indicated by dashed lines, and routes of information flow by thick arrows. The evolution of the South Pacific song between 1998 and 2008 is shown by the block diagram [adapted from 62]. 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.

In contrast, song evolution on the South Pacific breeding grounds occurs sequentially, and in a west-to-east direction [62]. A song heard off eastern Australia in one winter might be heard off New Caledonia—2,000km to the east—12 months later, and off French Polynesia after another year (Figure 2.3). 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 [63]. The reasons for the one-way movement of songs across the Pacific are uncertain [62], 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 2.3) connects humpbacks that use well-separated winter breeding grounds—the whales sing on migration [see 64]—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 2.2).

2.4 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 [*e.g.* 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 [*e.g.* 22,34,65]. We are not aware of quantitative models of this phenomenon calibrated for non-human societies. However, in Figure 2.4A we illustrate graphically how social network topology might be shaped by variation in individual behaviour and social learning.

Individuals differ in many ways [*e.g.* 66], including their social experiences [67], and behavioural repertoires [*e.g.* 68], and these characteristics can influence the social network [69]. Natural populations are often composed of individuals displaying different repertoires of behaviour, and/or degrees of specialization [see 70]. These patterns can partially result from cultural transmission of behaviour [*e.g.* 68,71]. 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 2.4A a-c). 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 Appendix A2.1, Table S2.1) 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 2.4A d-f). 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 2.4A g-i) [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 2.4A j-l) [see also 22].

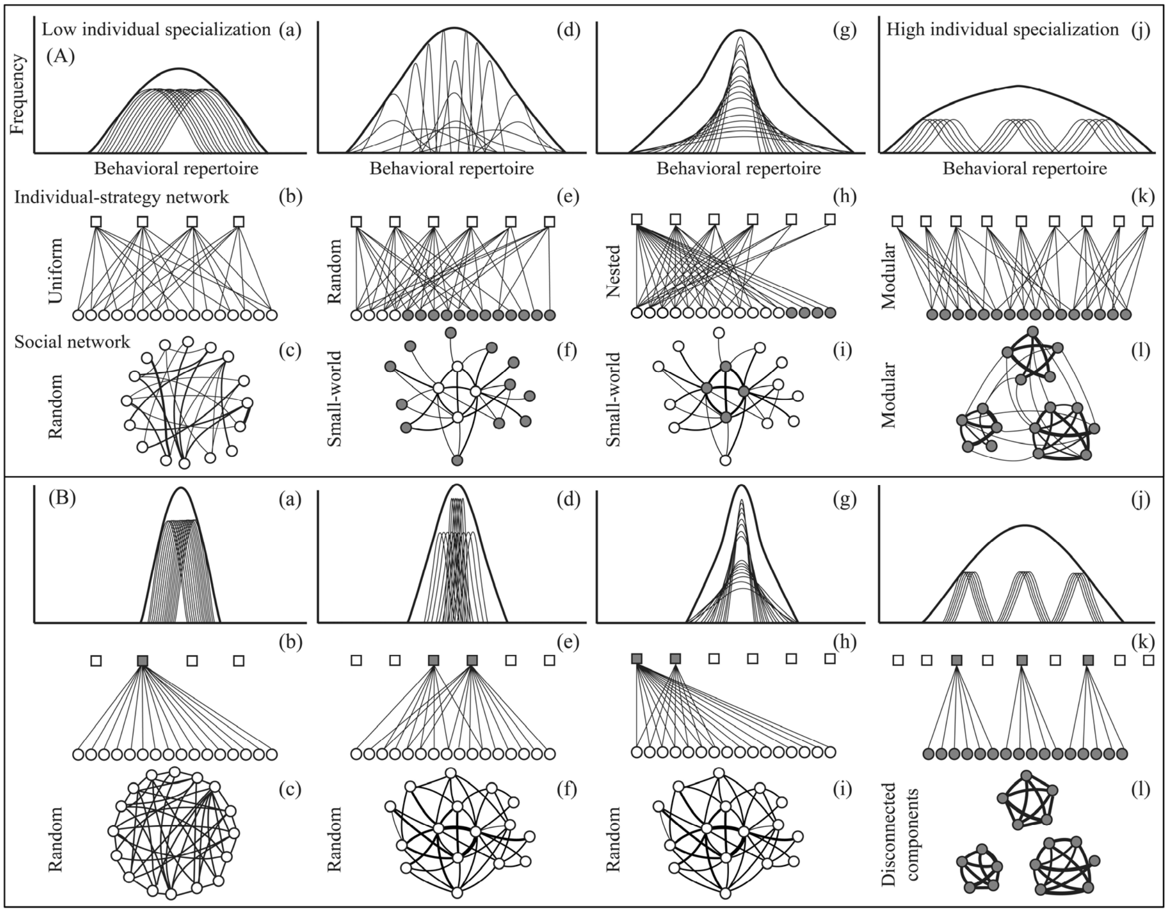


Figure 2.4. (A) Hypothetical effects of behaviour matching (i.e. when individuals tend to associate with those with similar behaviour) on social structure as influenced by patterns of behavioural specialization. The columns indicate different distributions of individual behaviour within the populations: 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 Appendix A2 (Table S2.1).

Two recently-published studies suggest that the matching of socially-learned behaviour structures the societies of bottlenose dolphins (*Tursiops* spp.) [72,73]. 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 [74], largely transmitted from mothers to daughters [75]. Bottlenose dolphins of Shark Bay, Australia, place sponges on their rostra, a behaviour that is thought to help them when foraging in rocky substrate [76]. 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.* concluded that spongers prefer to associate with other spongers, and hence that behaviour matching is an underlying mechanism driving the social network structure [72].

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 1990's some bottlenose dolphins followed prawn trawlers feeding on the discards and debris, while others did not [77]. 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 [77]. 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 2008-2010 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 [73].

Sponging in Shark Bay is almost certainly socially learned [58,74] and it is very likely that exploiting trawlers in Moreton Bay [73] was as well. Thus these two examples indicate the potential for culture to be a driver of cetacean social structure.

2.5 CONFORMISM AND SYMBOLIC MARKING

In addition to the social context within which the individuals operate, the manner by which behaviour is socially learned can also critically affect the dynamics of cultural transmission [*e.g.* 46]. Behaviour can be socially transmitted through several psychological mechanisms [*e.g.* 10] that are subjected to biases. Individuals may disproportionately learn from individuals with particular traits [prestige; *e.g.* 78] or being increasingly likely to adopt the most frequent behaviour [conformism; *e.g.* 5,23,79]. 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 to 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 2.4B. 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 2.4B d-i). However, in an already modular social system, conformism decreases variation in behaviour within the different modules, leading to their increased isolation (Figure 2.4B j-l).

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 [80]. The social units may be part of larger, hierarchically-organized social tiers, such as “pods”, “clans”, “communities” and “ecotypes” [81,82]. 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 [*e.g.* 83,84], 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 toward “leader” figures could also have this effect). Then, if behaviour matching is operating, behavioural conformism will feed back into even tighter social modules (Figure 2.4B j-l).

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 [85]. 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 [86]. Members of the same pod use the same repertoire of calls, different from those of other pods [87]. 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 [88]. 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 [83]. 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 [89,90]. So animals will from time to time encounter members of other clans. In the North Atlantic, there is no evidence of sympatric clans [91]. 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 [91]. The implication is that the sperm whale clans of the Pacific actively differentiate their repertoires to symbolically mark clan membership [82]. 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.

2.6 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 [*e.g.* 15-17,46]. The primary challenge is in the real world, collecting and analyzing empirical data that can illuminate the interplay between these systems (Figures 2.1 and 2.4). 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 [92]. Recent reviews offer guidelines for measuring and quantifying social relationships, testing social features against null models, describing the spatiotemporal structure of a society [92] and examining the multiscale structure of animal social networks [*e.g.* 14,19,93-95]. 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 [see 53,97,98] methods of analyzing the spread of innovations through populations [*e.g.* 48,54]. 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 [see 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 2.1B k,l), 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 [*e.g.* 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 one hundred 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 [*e.g.* 48,52,105]. 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 [73]. 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 [72].

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.

2.7 ACKNOWLEDGEMENTS

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CHAPTER 3

MULTILEVEL ANIMAL SOCIETIES CAN EMERGE FROM CULTURAL TRANSMISSION [4,5,6]

"Life can only be understood backwards; but it must be lived forwards"

~ S. Kierkegaard, 1844

3.1 ABSTRACT

Multilevel societies, containing hierarchically nested social levels, are remarkable social structures whose origins are unclear. The social relationships of sperm whales are organized in a multilevel society with an upper level composed of clans of individuals communicating using similar patterns of clicks (*codas*). Using agent-based models informed by an 18-year empirical study, we show that clans are unlikely products of

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[5] *Authors' contributions: Mauricio Cantor (MC), Hal Whitehead (HW) conceived the research idea; MC, Lauren Shoemaker (LS) wrote the models; HW contributed empirical data; MC analyzed the data with several contributions of LS, Reniel Cabral (RC), Cesar Flores (CF), Melinda Varga (MV), HW; MC wrote the manuscript; LS, RC, CF, MV, HW contributed several ideas, comments, edits in the models and manuscript; MC reviewed the manuscript during the peer-review process.*

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stochastic processes (genetic or cultural drift) but likely originate from cultural transmission via biased social learning of codas. Distinct clusters of individuals with similar acoustic repertoires, mirroring the empirical clans, emerge when whales learn preferentially the most common codas (*conformism*) from behaviourally similar individuals (*homophily*). Cultural transmission seems key in the partitioning of sperm whales into sympatric clans. These findings suggest that processes similar to those that generate complex human cultures could not only be at play in non-human societies but also create multilevel social structures in the wild.

3.2 INTRODUCTION

Selection for effective reproduction, foraging, and survival shapes social interactions and relationships—both in current ecological conditions and historic evolutionary pathways—and produces a variety of animal social structures [1-3]. Multilevel societies, consisting of hierarchically-nested social levels, are particularly interesting as they suggest multi-level selection. Such societies are found in human [4-5] and non-human primates [6,7], African elephants [7,8], and orca whales [7,9]. The origins of multilevel social structures remain unclear, and are likely to be complex [4-7]. They likely include general drivers of social patterns—the ecological, evolutionary and social contexts regulating group-living trade-offs [10,11]—as well as individual variation in behaviour [3] and the time and cognitive constraints involved in managing multiple social relationships [12,13].

A frequently neglected potential driver of animal sociality is culture—socially learned behaviour shared within subsets of a population [14]. Experiments in captivity and the wild, as well as long-term observational studies and computer simulations, all suggest that culture can be important drivers of phenotypic variation in several animal taxa [14,15] and shape social structures [16]. One hypothesized effect occurs when individuals who behave similarly preferentially interact (*homophily*) [17] and thus learn from each other, resulting in groups or sub-populations with increasingly homogenous behaviour [18]. Particularly strong homogenization may occur when individuals disproportionately learn the most common behavioural variant from their social contacts (*conformism*) to assist group integration or because a well-spread behavioural trait may generally be adaptive [19]. Since social relationships are cognitively and energetically costly, particular cultural behaviours can be used to mark the identity of a social group (*symbolic marking*) [20,21], which facilitate interactions among individuals who behave similarly. Therefore, biases such as conformism, homophily and symbolic marking affect the learning of behaviours among individuals [22,23] segregating them into groups with increasingly distinctive behavioural patterns [16,24-26]. Examples include the cultural boundaries delineated by specialized foraging techniques and traditions [27,28] and distinct dialects and communication signals [29,30] observed in primates, birds, and cetaceans.

Cultural segregation can naturally follow geographic segregation [31,32]. With little or no contact between sets of individuals, behavioural repertoires tend to diverge over time. Therefore, pure spatial and/or demographic factors can lead to the accumulation of behavioural variations, with drift over time generating behavioural heterogeneity between sets of individuals [33]. Typically, the more distant these sets of individuals are [31], and the lower the levels of dispersal, migration and population mixing among them [34], the more divergent their cultural traits [32,35]. Among allopatric cultural groups, large distances or limited movement of individuals can complicate the understanding of true drivers of behavioural divergence, since environmental and genetic differences make it difficult to isolate cultural determinants of behavioural variation [15]. We know little about how behaviourally-distinct animal groups evolve and are maintained in sympatry, but in a common environment the effects of culture can be clearer (for human examples, see [23, 26, 36]).

Long-term observational studies have unveiled social complexity [37] and cultural diversity among cetaceans using the same waters at the same time [38]. For instance, female sperm whales (*Physeter macrocephalus*) form matrilineally-based social units with about twelve members each [39]. These units are organized into clans with distinctive behaviour in several realms, including vocal repertoires [30], creating a multilevel society [39]. Social units have characteristic repertoires of *codas* [40]—patterns of clicks used for communication—and unit members are observed to only group with other social units from their own clan, with whom they have similar coda repertoires [30]. In sperm whales, as in other cetaceans, information flow through social learning is a key driver of behaviour [38]. As learned acoustic signals can be important in social relationship mediation [41], they could also possibly shape social structure [16]; for instance, learned vocalizations are hypothesized to underlay the partition of sperm whales into clans [30,39]. The sperm whale clans in the Pacific are sympatric [30,42] and include genetically-similar individuals of all ages [43], thus systematic differences between them are likely to be cultural, representing a good model for investigating how sympatric animal cultural groups form in the wild.

Here, we investigate the mechanisms giving rise to the nested social levels of sperm whale society observed empirically. We build mechanistic agent-based models, using empirical data collected over 18 years in offshore waters of the eastern Pacific Ocean, to test whether clans could emerge in sympatry solely via cultural or genetic drift of communication signals over time, or if social learning is required. We also consider more sophisticate scenarios in which social learning is biased by homophily, conformism, and/or symbolic marking. With homophily, communication similarity drives social relationships so coda learning is preferentially from individuals with similar vocal repertoires [17]. With conformism, the most common coda types that an individual is exposed to are learned disproportionately more often [18]. In symbolic marking, particular codas are used by all members of a social entity [20]. We accounted for different degrees of population mixing by allowing coda transmission processes to operate in the entire population, within social units or within pre-existent allopatric clans, such as the geographically-based clans observed in the North Atlantic [39,44]. Our investigation of the social patterns that emerge from animal collective behaviour is the first formal effort to our knowledge to relate the formation of multilevel societies to cultural evolution. We show that the higher social level of sperm whale societies unlikely originates from stochastic processes but rather from biased cultural transmission of acoustic communication signals.

3.3 RESULTS

3.3.1 Empirical Social Patterns

Over our 18-year study of sperm whales in the Eastern Pacific, the sperm whale society showed a hierarchical structure with three conspicuous nested levels: individuals in social units forming vocal clans (Figure 3.1). The social network of photo-identified individuals (nodes) connected by their social relationships (weighted links estimated by half-weight association indices) displayed a modular topology (Q = 0.886), in which modules of highly connected nodes delineated social units of individuals that live and move together for several years or more [45]. These modules representing social units formed larger modules in an overlapped acoustic network of social units (nodes) connected by acoustic behaviour similarity (weighted links estimated by multivariate similarity of coda repertoires). The acoustic network also displayed a modular topology (Q = 0.154, 95% CI = 0-0.124): here modules of social units with shared coda repertoires depicted the vocal clans [30]. The multilevel sperm whale society exhibited high within-clan acoustic similarity but very low between-clan acoustic similarity, and no between-clan social interactions (Figure 3.1).

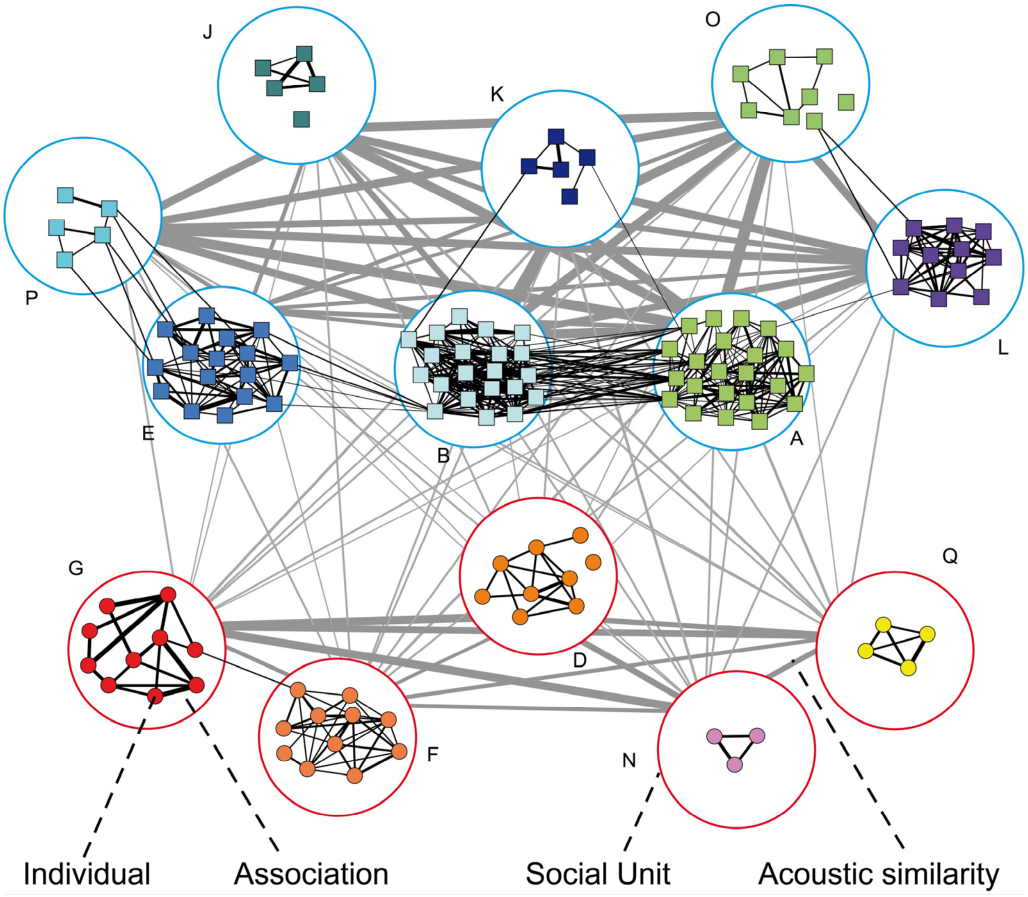

Figure 3.1. Empirical multilevel network depicting the three nested levels in the sperm whale society off the Galápagos Islands: individuals within social units within vocal clans. In the social network, modules of individual whales (coloured small nodes) connected by their social relationships (black lines with thicknesses proportional to the time individuals were identified in the same group) define the social units (letter-labeled large nodes). In the overlapped acoustic network, modules of social units connected by the similarity in acoustic behaviour (grey lines whose thicknesses are proportional to multivariate similarity of coda repertoires) represent the vocal clans (blue: *Regular* clan, characterized by codas with regularly-spaced clicks; red: *Plus-One* clan, characterized by

codas with extended pause before the final click [30]). Social relationships and acoustic similarities are re-plotted results from [52] and [30], respectively.

3.3.2 Emergent Social Patterns in Simulations

With agent-based models (ABMs) grounded on empirical evidence (Figure 3.2, Appendices B3.8, B3.9: Supplementary Methods 3.1, 3.2), we simulated 20 scenarios (Figure 3.3A) to test which transmission processes of coda types between individuals—individual learning, genetic inheritance, pure and biased oblique social learning—could split individuals into sympatric clans with similar acoustic behaviour, as observed empirically (Figure 3.1). We focused on two high-level attributes of the simulated data: similarity of coda repertoires among social units, and the emergence of modules of social units with distinct repertoires.

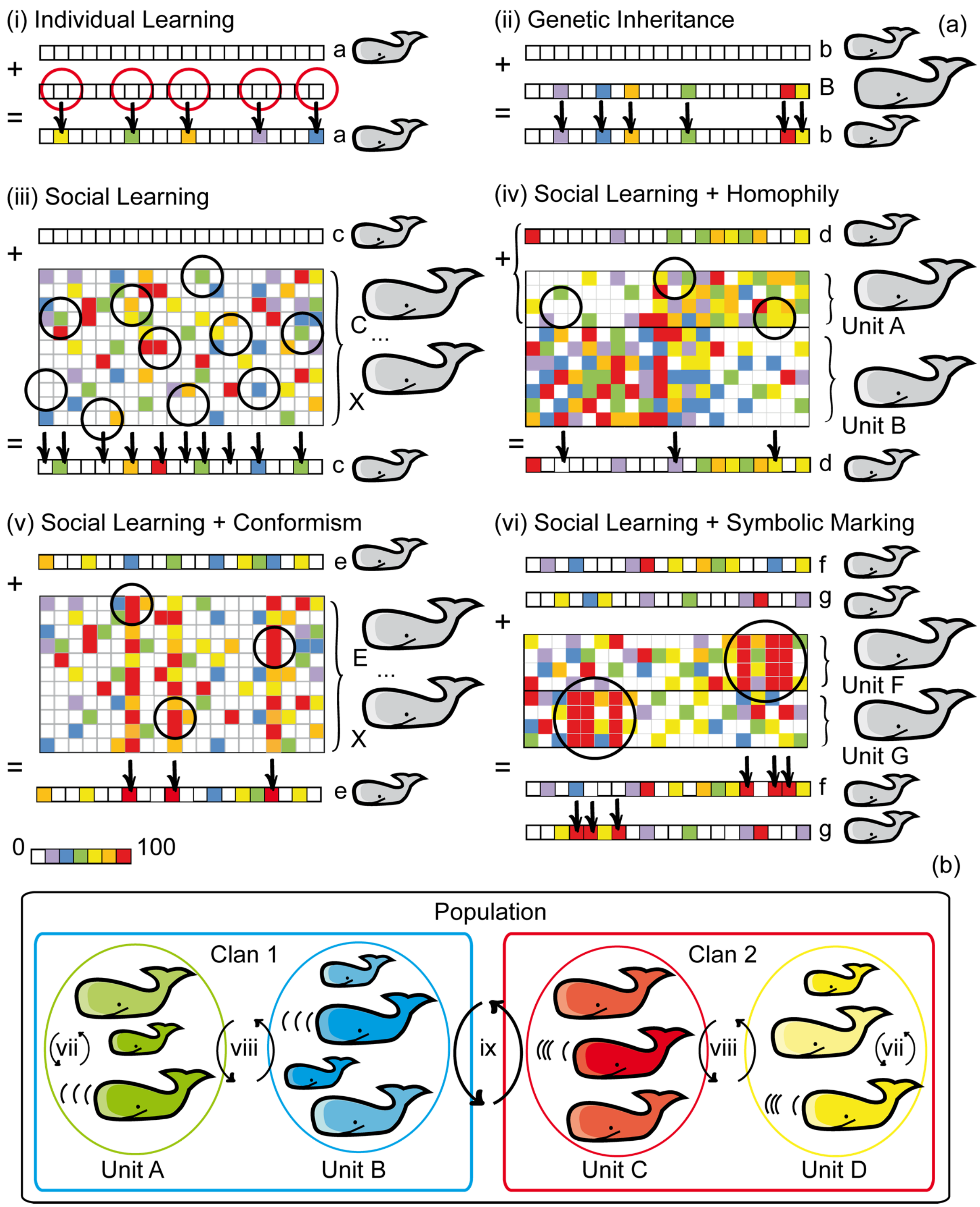

Figure 3.2. Schematic representation of the agent-based models. (a) Coda transmission mechanisms are represented as changes in the coda repertoires vector (squares: coda types; colors: frequency of usage: absent=0, always=100%). Calf agents change

repertoires three times (between 0-2 years old) under one of following mechanisms. (i) Individual learning: newborn agent *a* starts with an empty coda vector; half of the elements are randomly selected to receive absolute frequencies of usage from a uniform distribution ϵ[0,100]. (ii) Genetic inheritance: newborn agent *b* starts with an empty coda vector, which is filled with the same coda types and frequencies of its mother *B.* (iii) Oblique social learning: newborn agent *c* starts with an empty coda vector; at the age 0 it randomly samples 62 elements from the coda vector of other adult agents, kin-related or not (including zeroed elements); at ages 1 and 2 the calf repeats the process, replacing sampled elements. For iv-vi, calves gain an initial repertoire via oblique social learning, then at ages 1 and 2 the following effects were included. (iv) Homophily: calf *d* copies from adult agents of the social unit *A,* which has the highest coda repertoire similarity with its own social unit. (v) Conformism: calf *e* preferentially copies the coda types with higher frequencies of usage, here the three codas commonly performed by the adults. (vi) Symbolic marking: calves *f* and *g* were born in different social units, which have a specific subset of codas ("symbol") that all members always perform to mark the identity of the unit (the sequences of red codas). Both calves copy codas from other adults, but also deliberately copy their units' "symbols". (b) Oblique social learning (iii) and the additional effects (iv-iv) occurred at three social levels. (vii) Social unit: calf agents copy only from agents of their own social unit. (viii) Predefined clans: simulation started with predefined clan labels and calves copy from any agent inside of its predefined clan. (ix) Population: calves copy from any agent in the population. In all scenarios, calves had a low individual learning probability (replacing 1 random coda type by a random frequency) per year.

The similarity of coda repertoires of social units varied considerably across the 20 simulated scenarios (Figure 3.3B), which only differed in how and at which social level the codas were transmitted (Figure 3.3A). Scenarios with individual learning (ABM1), genetic inheritance (ABM2), and pure oblique social learning (ABM3) yielded the lowest acoustic similarities. Neither vertical transmission (when agents received the same codas from their mothers mimicking genetic transmission and/or mother-to-offspring learning) nor pure social learning of codas (when agents copied coda types from each other) were sufficient for coda repertoires to diverge between social units. Instead, differences among individuals propagated over time and did not significantly deviate from the structure seen with the null agent-based model with just individual learning of codas (when coda types and frequencies of use were randomly assigned to agents) (ABM1).

However, the coda repertoires of social units tended to become more similar and less variable when social learning was biased via two distinct effects: homophily (agents copying preferentially from adults of those social units with similar repertoires to their own) (ABM6-8) or conformism (agents copying preferentially the most common coda types) (ABM9-11). By introducing symbolic marking (when agents of different social units were assigned to specific subsets of codas) (ABM12-14), simulations had more distinct starting points which were maintained over time reducing similarity among social units' repertoires. While the combination of symbolic marking with homophily pushed all agents to a homogeneous repertoire (ABM18-20), the combined effect of homophily and conformism led to an overall high similarity, but specially more variability among repertoires than other scenarios (ABM15-17) (Figure 3.3B).

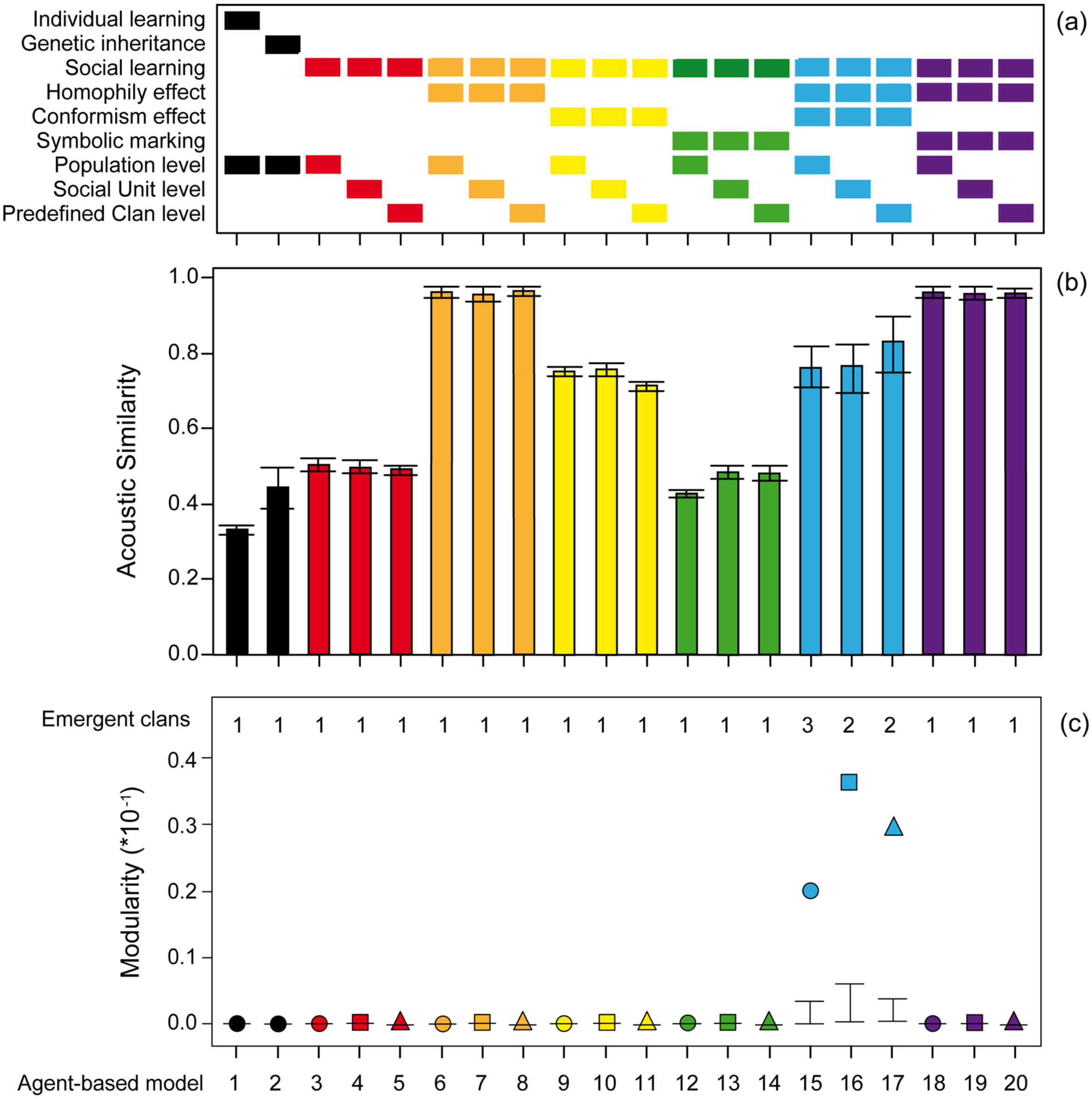

Figure 3.3. Coda repertoire similarities and clan partitioning across simulated scenarios. (a) Agent-based models (ABMs) differed in how a coda was transmitted (individual learning, genetic inheritance, social learning), if there was any transmission biases (homophily, conformism, symbolic marking), and the social level at which the

transmission operated (population, social units, and predefined clans). Columns represent ABMs and filled cells represent the presence of the model features (transmission mechanisms, biases, social levels) indicated in the rows. Color code denotes similar transmission mechanisms operating at different social levels. (b) Average coda repertoire similarity of all emergent social units. Whiskers represent standard deviation (SD). (c) Modularity (*Q*-values) of the resultant acoustic networks from each ABM. Significantly high modularity values ($P < 0.001$) fall outside of the 95% confidence intervals (whiskers) generated by a theoretical model (1000 replicates) and indicate the emergence of vocal clans, i.e. modules of highly connected social units due to high coda repertoire similarity in the acoustic network. Number of emergent vocal clans is listed on the top of the plot; symbol shapes denote the social level where the transmission mechanisms operated (circle: population; square: social unit; triangle: pre-defined clans).

Sperm whale clans exhibit distinct coda repertoires in the wild. This pattern was evident in only three simulated acoustic networks, all of which included biased learning (Figure 3.3C). Modules of highly connected social units representing clans emerged only when codas were socially learned with homophily and conformism in tandem, regardless of the social level they operated (ABM15-17) (Figure 3.4). In these three scenarios, the measure of clan partitioning (modularity) was significantly higher than the theoretical expectation and four orders of magnitude higher than the remaining scenarios (Figure 3.3C, Appendix B3.4, Table S3.1). The more complex scenarios—with combinations of social learning, symbolic marking, and homophily even starting with predefined geographically-segregated clans (ABM18-20)—performed similarly to the simpler scenarios (ABM3-11) with almost zeroed modularity values. In consequence, the topology of the acoustic networks produced by these remaining scenarios was almost completely connected, with no emergent clans (Figures 3.3C, 3.4), resembling the networks produced by the null models, with no social learning (ABM1-2). While clans did not emerge in the complex scenarios due to the convergence of the repertoires into a single and homogeneous one, in the simpler scenarios clans did not emerge due to the overall low similarity among social unit repertoires.

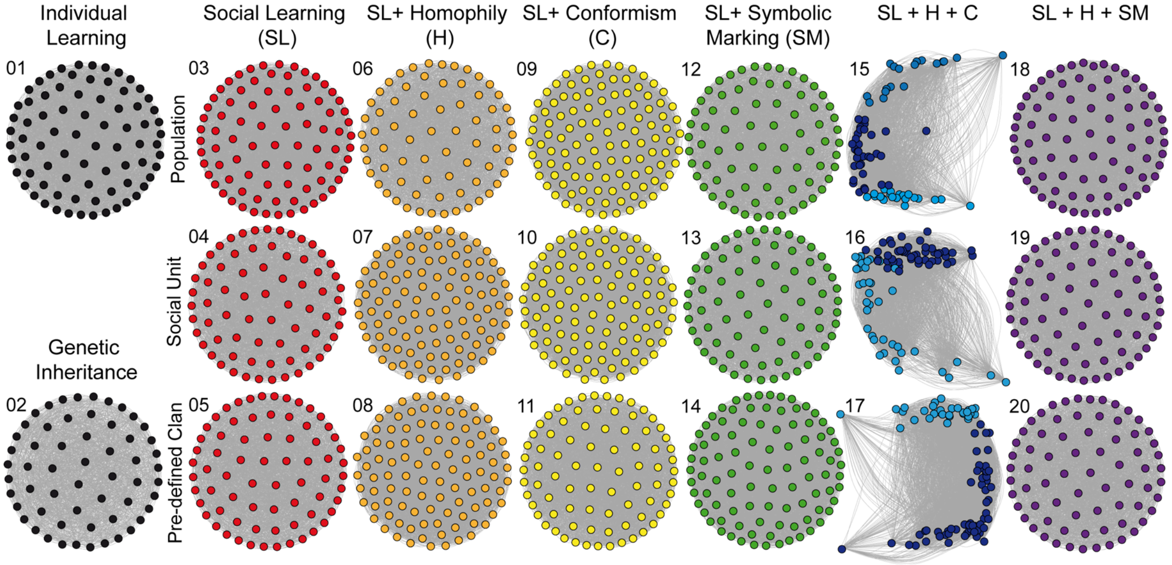

Figure 3.4. Acoustic networks simulated by the 20 agent-based models (ABMs). Nodes representing social units are connected by links representing coda repertoire similarity. Colour code indicates similar transmission mechanisms operating at different social levels across the ABMs, which differed in the coda transmission process (individual learning, genetic inheritance, social learning), in the presence, type and combination of transmission biases (columns: homophily, conformism, symbolic marking), and in the

social level at which the transmission operated (rows: population, social units, and predefined geographically-segregated clans). ABMs 01 and 02 represent the null agent-based models with no social learning, but individual learning and genetic inheritance of codas, respectively. From ABM03 to 20, all models contain social learning of codas, with and without biases. Distinct clans (modules in blue shades) emerged only when codas were transmitted by social learning (SL) biased by conformism (C) and homophily (H) operating in tandem at the population (ABM15), social unit (ABM16) and pre-defined clan levels (ABM17). In all remaining scenarios, the acoustic network resembled the null models (ABM1-2), with no distinct clans.

3.3.3 Robustness of the Emergence of Clans

Our findings emphasize the importance of transmission mechanisms, particularly biased social learning, on similarity and divergence of acoustic behaviour of sperm whales, showing that behavioural learning can create social hierarchies in sympatry. We accounted for the effect of movements of individuals—while respecting the structure of the sperm whale societies with nearly-permanent social units—in coda transmission by replicating the transmission mechanisms in the three social levels relevant for the sperm whales (social units, predefined geographically-segregated clans, and population). Similarity and modularity patterns were consistent across the different social levels where the transmission mechanisms operated (Figures 3.3B,C) indicating that different degrees of population mixing had negligible effects on the emergence of clans.

Furthermore, clan emergence was robust regardless of initial conditions and across varying parameterizations (Appendix B3.10: Supplementary Methods 3.3). A sensitivity analysis yielded similar outputs (Appendix B3.1, Figure S3.1): only the very same three scenarios with biased social learning of coda types (ABMs 15-17) yielded significant modules in the acoustic networks, regardless of model parameterization. Therefore, the proportion and dispersal of potential tutors (adult agents) and learners (calf agents), and copying errors or innovations as source of cultural traits (coda types) are shown to have a minor effect on the diversity of cultural traits (coda types) and thus the emergence distinct cultural clans of whales (Appendix B3.6, Supplementary Note 3.1). Moreover, the metric of clan emergence was robust to variation in the sampling of acoustic similarity among social units (Appendix B3.11, Supplementary Methods 3.4). For all of the 20 ABMs, modularity was high, stable, and consistent across the range of possible weights for a link (coda repertoire similarity) between nodes (social units) in the simulated networks (Appendix B3.2: Supplementary Figure 3.2, Appendix B3.7: Supplementary Note 3.2).

3.4 DISCUSSION

Our empirical findings and simulations combined reveal how the social levels of sperm whales are nested and point out cultural transmission as the most likely candidate mechanism giving rise to the upper social level of their multilevel society. Whale clans are based on learning of communication signals, and biased learning may be necessary to generate sympatric culturally-driven social tiers. By modelling the processes that give rise to the complex yet highly structured social system of sperm whales, we show that key processes attributed to human culture may not only be present in non-human societies, but also likely created the social structure we observe in sperm whales. While ecological, cognitive, and time constraints and benefits [11,12,13] may delineate the lower sperm whale social level (social units) as in other multilevel societies [7], we suggest that the process that has produced the higher level (clans) is information flow.

In small multilevel human societies, the flow of information, materials, energy, genes and/or culture among individuals plays an important role in regulating the quantity and quality of social relationships [5,46]. Would the flow principles of a two-dimensional terrestrial world create similar additional selective forces for sociality in the three-dimensional marine environment [7]? While predation and resource availability are thought to be basal for sociality in both environments, marine resources generally tend to be more dispersed and less predictable in space and time [47,48], making it logistically impossible for marine mammals to defend or transfer resources among individuals (though they are sometimes shared). We hypothesized that, in this situation, information is the primary resource that can be stored and transferred among selected companions; the way such information flows can subsequently shape the structure of their society [16]. Take for example the knowledge of how to manipulate a certain food resource: it can certainly flow within a population through social learning among individuals, but sometimes not among all of them, which demarcates subsets of the society with distinct behavioural repertoires [28,49]. In addition to foraging and movement behaviours [50], sperm whales, and other cetaceans, can learn acoustic communication signals from each other [41]. In the aquatic environment, where sounds spread particularly well, acoustic communication—the likely function of codas [51]—may help maintain group cohesion, reinforce bonds, aid negotiations and collective decision-making [52,53]. Since vocal learning in cetaceans is an output of complex social behaviour and may assist the maintenance of multiple social relationships [41], we asked if it could trigger the formation of the vocal clans.

This question is logistically unable to be answered using experimental manipulations or observational studies (which would not provide a mechanism), making an agent-based simulation an ideal approach. Our simulations suggest that clans are unlikely products of stochastic processes, such as genetic or cultural drift. The simulated acoustic behavioural segregation seems not to be a collection of individual innovations diverging over time, or an artefact of genetic transmission. Whereas vertical, mother-offspring, social learning can establish and maintain behavioural traits in some cetacean populations (*e.g.* tool use and foraging tactics in bottlenose dolphins) [49,54], our models suggest that oblique social learning is necessary to promote clan-like vocal repertoires among sperm whales.

Still, social learning alone was not enough to segregate social units into clans, and our vocal clan recipe needed additional ingredients. Social learning is susceptible to biases [22], which affect flow of information and potentially the emergence of cultural patterns. The theoretical expectation is that unbiased transmission can only lead to marked cultural differences among allopatric, strictly isolated groups of individuals [55]. Yet, how are different coda repertoires maintained in the same Pacific waters? Our results suggest that the answer may be in biased transmission, which can maintain similarities within, and disparities between, sympatric cultural groups through time [55,56]. By means of feedback between homophily and social influence [17,18], individuals who behave similarly preferentially associate and learn from one another, increasing their behavioural similarity. This process breeds relationships among like-minded individuals, and simultaneously tends to dissolve relationships between individuals with distinct behaviour. As seen in our simulations, this effect is leveraged when individuals are conformists and disproportionately learn the most common behavioural traits [19,57]. Combined, behavioural matching and majority-biased transmission can promote a segregation of individuals into behaviourally distinct groups [16,26].

This is the case in our simulations: when the whales were more prone to learn the most common coda types from those who already had similar coda repertoires, clans of social units with distinct acoustic repertoires emerged and matched the pattern observed empirically. Increasing behavioural homogeneity with some peers, and so reinforcing social differentiation and cultural boundaries between subsets of the population, can be particularly striking in sympatric large toothed whale societies. As with Pacific sperm whales, killer whales (*Orcinus orca*) can display remarkable intrapopulation behavioural segregation, seemingly marked by an intricate system of pulsed calls for communication [9,58]. These calls can change over space and time, but tend to do so in a way that preserves the differences between pods [59], suggesting that acoustic signals can allow pods to distinguish themselves.

Our findings highlight the contribution of behavioural transmission mechanisms, as opposed to purely demographic or spatial factors, in the emergence of the sympatric cultural groups. Other factors, such as population size and proportion of tutors as source of cultural traits, age distributions, dispersal rates, or copying errors/innovations [34,35,60,61] played a minor role and have had no substantial impact in the emergence of clans of sperm whales. Additionally, the complete spatial isolation into predefined geographically-segregated clans [44], with members learning only within their clans, did not produce the acoustic divergence required to split the population into distinct dialects. This show that multilevel social structures can arise even in the absence of spatial and temporal heterogeneity, implying that learning mechanisms may have more influence in driving social structure than previously thought.

In conclusion, sperm whales are distinctive among multilevel animal societies with the higher social level produced by biased cultural transmission. By modelling the evolution of the repertoire of acoustic communication signals, we were able to overcome the logistical impossibilities of field experiments in the vast spatio-temporal scales that are relevant for sperm whales, and show that the sympatric behavioural segregation that delineates the sperm whale clans is not controlled by genes, neither by genetic or cultural drift. Our empirically-founded models incorporating population dynamics and multiple transmission mechanisms indicate that learning coda types plays a crucial role in promoting similarity in acoustic behaviour, and, more strikingly, that biases in social learning are required to split the sperm whales into sympatric clans with distinct dialects observed in the wild. We suggest therefore that empirical clans have emerged like the simulated ones: as a cultural segregation. While transmission biases drive culture and social structure in humans [56], there is much debate about whether or not they are exclusive features of human culture [62]. Providing evidence that the processes generating the complex and diverse cultures in human populations could also be at play in non-human societies is a crucial step towards evaluating the contrasts and convergences between human and non-human cultures.

3.5 METHODS

3.5.1 Empirical Data and Social Levels Definition

Sperm whale groups were tracked visually and acoustically, day and night, during 2 to 4 week research trips between 1985 and 2003 in the Eastern Pacific Ocean, mainly off the Galápagos Islands (summarized in [39]). Three nested social levels were evident within the Pacific sperm whale society: individuals, social units, and vocal clans. Individuals were identified by photographic records, comparing the natural markings on the trailing edge of tail flukes [63]. Social units were sets of about 12 individuals [39] that live and move together for years, delineated using association indices on long-term photo-identification data [45]. Clans were sets of social units with high similarity in their coda repertoires, the stereotyped patterns of clicks used for communication [40]. Codas were recorded with hydrophones and repertoires were assigned to the social units whose members were photo-identified within 2h of the recording and had at least 25 codas recorded [30]. The social units' repertoires were compared to define the best partition of social units with distinct repertoires into clans [30]. Clans are estimated to contain many social units and several thousands of members, based on the estimated abundance of sperm whales in the Pacific and number of clans [30]. Social units are typically found in behaviourally-coherent groups with other units from their own clan, but never with units from different clans even though sperm whales from several clans may use the same waters [30].

3.5.2 Agent-Based Modeling

We simulated the interactions of multiple individual whales using an agent-based modelling framework (ABM) to test whether the clan structure observed in the sperm whale society could arise from evolving vocal behaviour. The ABMs were built in R [64] based on empirical parameters (Appendix B3.8, B3.9: Supplementary Methods 3.1, 3.2), and are described according to the Overview, Design concepts and Details protocol [65] as follows:

a) *Purpose*. The models test which transmission mechanisms for acoustic behaviour, if any, can give rise to clans of social units of sperm whales with distinct acoustic repertoires, and explain the multilevel social structure observed empirically.

b) *Entities, state variables and scales*. The models have one kind of agent, which behaves under realistic life-history parameters (empirical support for model parameters available in the Appendix 3.9, Supplementary Methods 3.2): female whales that learn coda types at ages of 0 up to 3 years old. Because male sperm whales lead quasi-solitary lives and rarely produce codas [63,66] they were not represented in the models. The agents are characterized by their age (years), their coda repertoire (a vector of frequencies of use of different coda types), and which social unit and vocal clan they belong to (nested categorical variables). The models were explicitly temporally-structured and implicitly spatially-structured. However, we accounted for different levels of population mixing (and so implicitly for individual movements), with coda transmission operating among individuals of three different social levels (see 'd'). Simulations lasted for 700 time steps (years).

c) *Process overview and scheduling*: During each time step, biological processes occurred in the following order: birth, coda repertoire composition and changes (at ages up to 3 years old), social unit membership change (or not), and death. Calves have high probability of staying with their natal group, and migration of individuals among social units is rare [45]; thus nearly-permanent and nearly-matrilineal social units are an emergent property. In these respects, the models mimic several transmission processes characteristic of some socially complex species. We started with two null models without social learning: in one the agents only learn their codas individually; in the other they receive their mothers' coda repertoire, representative of genetic inheritance (as well as stable vertical cultural transmission). We then simulated a total of 20 complementary scenarios with combinations of oblique social learning of coda types and transmission biases operating at the three different social levels (see 'g').

d) *Design concepts*. There are two emergent properties of the interactions among agents: social units (sets of females and their offspring who stay together along the simulated time) and vocal clans (sets of social units with highly similar vocal repertoires). Social units emerge in all models and vocal clans can be predefined (see 'g'), or may emerge. All demographic processes were modeled with demographic stochasticity and parameterized from empirical studies (see Appendix B3.9, Supplementary Methods 2). Birth rates were age-specific, and mortality rates were density- and age-dependent (calf agents had higher probability of dying than adult agents [67]), and migration rates of individuals between units were low and decreased with age. The main process of interest modeled is changes in individual coda repertoires, i.e. in frequencies of use of coda types. Each agent has a repertoire represented by a vector with 62 elements denoting continuous absolute frequencies of different coda types from 0 (absent) to 100 (always performed coda type) (Figure 3.2A) (details in Appendices B3.12, B3.13: Supplementary Methods 3.5, 3.6). Calves compose repertoires at early ages (although precise age is inherently difficult to estimate empirically; Appendix B3.9, Supplementary Methods 3.2). Repertoire composition was represented by calf agents replacing some coda types and frequencies once a year, while at ages of 0, 1 and 2. After age 3, all agents' repertoires were fixed. Depending on the sub model (see 'g'), the repertoire change occurred according to one of the three main transmission processes (see Figure 3.2A): (i) Individual learning—calf agents compose their own coda repertoires, i.e. are assigned to random coda types and frequencies drawn from uniform distribution $\epsilon[0,100]$; (ii) Genetic inheritance (which also represent vertical social learning)—calf agents receive their mothers' coda repertoires; and (iii) Oblique social learning—calf agents copy coda types and frequencies from adult agents, of different generations, kin-related or not. To the models with oblique social learning, the three following effects were included: (iv) Homophily—calf agents preferentially copy codas from adult agents of social units with the highest repertoire similarity with the calf's social unit's repertoire. (The homophily effect posits that behaviourally-similar individuals tend to interact more often [17]; since social learning occurs during social interaction, the homophily effect on learning can be represented as individuals with similar behaviour learning preferentially from each other.); (v) Conformism—calf agents disproportionately copy the most common coda types; and (vi) Symbolic marking—all agents of a given social unit are assigned to a random sequence of 6 coda types with frequency of usage 100 (a "symbol") at time t=1, to mark the identity of their units; all calf agents from t=1 deliberately copy the "symbol" of the unit they belong to. To account for different degrees of population mixing, we replicated the models with oblique social learning and additional effects (iii-iv) across the three levels of the sperm whale society: social unit, predefined clans and population (Figure 3.2B): (vii) Social units—calf agents randomly copy codas from agents of their own social unit; (viii) Predefined clan—agents were arbitrarily assigned to three clans and calf agents learned only from adult agents of their own clan. (Since clan partition could be driven by non-learning mechanisms, we simulated the pre-existence of clans representing geographically-segregated clans such as those that seem to occur in the Atlantic where acoustic variation is driven by spatial isolation [44]. We refer to these as 'predefined clans' as opposed to the 'emergent clans' that may arise in the simulations due to acoustic similarity.); (ix) Population—calf agents learn from any agent in the population. We combined transmission mechanisms, effects, and social levels in a total set of 20 ABMs (see 'g', Figure 3.3A). At the end of each simulation, we observed the number and size of social units and vocal clans and how similar their coda repertoires were (methods below).

e) *Initialization*. Simulations were initialized with the following parameters based on empirical data (details, justification, and references in Appendix B3.9, Supplementary Methods 3.2). At the first time step, year t=1, all simulations started with a population of N_0=1000 agents, to which ages were randomly assigned from a negative exponential distribution (so the initial population was mostly young, with ages typically varying from 0 to about 70 years old), and social unit membership labels were assigned with equal probabilities. Each agent received an empty vector of 62 elements (i.e. coda types) representing their coda repertoire. For each agent, half of the elements in its coda repertoire vector were randomly selected to receive an absolute frequency of usage from a uniform distribution ϵ[0,100] (absent coda type=0; always performed=100). Agents are considered calves when they are 0, 1, and 2 years old, during which changes in the coda repertoire occurred. Adult female agents became sexually mature after 9 years old, stopped reproducing after 41 years old, and lived 70 years on average. Population was modeled density-dependent, with age-dependent reproduction, mortality and migration rates, such that the population fluctuated around the carrying capacity (N_0) over time. The initial number of social units was based on the initial population size (N_0) and empirical average unit size in the Pacific (about 12 members). Social units split in half when double the maximum initial unit size. Calf agents remained in the mother's social unit since they highly depend on their mothers; and adult agents had low probability of randomly migrating to other social units during their lives (c=0.05). Repertoire changes were represented by replacement of frequencies of coda types and occurred three times for each agent (repertoires were fixed after the age of 3). Newborn agents started the simulation with empty coda repertoires; each simulated year, all calf agents changed their coda repertoires under one of the three main mechanisms—with additional effects or not—operating at one of three social levels (see 'g', Figure 3.2B). In all models calf agents also had low individual learning rate (*ilearn* = 0.02), i.e., each year replacing the frequency of one coda type (62 codas*0.02≈1) chosen at random by a frequency drawn from a uniform distribution ϵ[0,100], which accounted for random learning errors or deliberate innovations [61]. Supplementary Figure S3.3 (Appendix B3.3) illustrates the population output measures of a typical simulation.

f) *Input*. The models have no external input data, but initial parameters differed in sub models.

g) *Sub models*. We created a total of 20 sub models (Figure 3.3A), all of which have the same structure but differ in the way calves compose their coda repertoires (Figure 3.2). In the first null model (ABM01), calf agents learn their coda repertoire only through individual learning. In the second null, model (ABM02), calves receive the exact repertoire of their mothers, mimicking the genetic or vertical-cultural transmission of coda repertoires. In all the following models (ABM03-20), calves change repertoires with oblique social learning, some with combinations of the three transmission biases: homophily (ABM06-08, 15-10); conformism (ABM09-11, 15-17); and symbolic marking (ABM12-14, 18-20). Oblique social learning and its biases occurred within social units (ABM04, 07, 11, 13, 16, 19), across social units of the same predefined clans (ABM05, 10, 14, 17, 20); and in the entire population (ABM03, 06, 09, 12, 15, 18).

3.5.3 Coda Repertoire Similarity

The empirical repertoires of the social units were compared based on the inter-click intervals of each coda using an averaged multivariate similarity metric [30]. Because in the agent-based models we simulated frequencies of usage of coda type—and not the inter-click intervals of each coda—we compared repertoires of each pair of simulated social unit with the weighted Bray-Curtis index between the average frequency of usage of codas of all agents of these units. We adjusted the index to represent similarity, which ranged from 0 (completely different) to 1 (exactly the same repertoire).

We detail the differences between empirical and simulated codas and repertoire comparison in the Appendix B3.14 (Supplementary Methods 3.7).

3.5.4 Clan Partition in Empirical and Simulated Data

Clan partitioning in the simulated data was adapted from the original methods for vocal clan definition: the social units' coda repertoires were compared and the best partition into clans was based on the repertoire similarity [30]. While the original approach included hierarchical clustering, we used the network formalism to depict social units (nodes) connected by similarity of coda repertoires (links) and modularity to define the emergence of clans (see below). To allow direct comparisons, we reanalyzed the empirical social and acoustic data [30,45] with the same network framework. First, we built a social network of photo-identified individuals (nodes) connected by the strength of social relationships (links), i.e. the proportion of time individuals were seen together [45] estimated by the half-weight association index. We then overlapped the empirical acoustic network, in which the social units (nodes) were connected by the similarity in their averaged coda repertoires (links).

For both empirical and simulated data, vocal clans were defined by modules in the acoustic networks, i.e. subsets of nodes (social units) that are highly and strongly linked within each other (by acoustic similarity) and weakly linked with the rest of the network. We searched for the best module partition using the *Walktrap* algorithm [68], which is based in the assumption that random walks in a network will tend to get "trapped" inside strong connected modules. More specifically, this algorithm uses an agglomerative approach to form modules, using a distance metric based on the probability of a random walk go from node i to node j. Hence, nodes belonging to a given module will share similar probabilities of going to nodes outside their module. To the resultant hierarchy of modules, the largest increase ratio of the total distance is used to infer the best partition into modules. Subsequently, we assigned a value to this partition using the weighted version of modularity metric Q [69]:

$$Q = \frac{1}{2m}\sum_{ij}\left(A_{ij} - k_i k_j/2m\right)\delta(g_i, g_j) \qquad (1)$$

where A is a weighted adjacency matrix, with elements representing the acoustic similarity between social units, $m = \frac{1}{2}\sum_{ij} A_{ij}$ is the weighted number of links, k_i is the weighted degree of node i, $\sum_j A_{ij}$ and g_i gives the label of the module (herein clan) the node (herein social unit) i belongs to.

The significance of clan emergence, both in empirical and simulated data sets, was assessed comparing the modularity Q-values to a benchmark distribution generated from 1000 theoretical networks. We created theoretical networks with same size (number of nodes, i.e. social units), same link weight distribution (i.e. acoustic similarity) and connectance (proportion of realized links) using a model that randomizes the link weights among nodes [70]. Clan emergence was considered significant whenever the modularity Q-values of the observed acoustic networks lied outside of the 95% confidence intervals of the benchmark distribution.

3.5.5 Sensitivity Analysis and Robustness of Clan Emergence

The parameters and initial conditions of the agent-based models (ABMs) were grounded on empirical evidence (Appendix B3.9, Supplementary Methods 3.2) and fixed across scenarios to allow directly comparison of learning strategies without any confounding influence of other changing parameter values. To evaluate whether the observed partition of social units into clans was robust to varying the initial conditions in the models, we performed a sensitivity analysis of the 6 initial demographic and 2 learning parameters that were common to all of the 20 ABMs (population size and carrying capacity, reproductive age, migration rate, mortality rates, age distribution, initial average social unit size, individual learning rate, coda repertoire size) (full description in Appendix B3.10, Supplementary Methods 3.3). We ran each ABM changing a single parameter value at a time to two extreme parameter estimates of a biologically-meaningful range (Appendix B3.5, Table S3.2) and calculated modularity and 95% confidence intervals with the theoretical model described above. Specifically, we tested whether changing the ABMs initial setup would still yield emergence of clans in the scenarios with biased social learning (ABMs 15-17); and conversely, whether clans would emerge in the rest of the scenarios in which they originally have not emerged (ABMs 1-14, 18-20) (see Figures 3.3C, 3.4).

In addition, we evaluated the robustness of the metric for clan partition (modularity) by bootstrapping the links of the 20 simulated acoustic networks (Appendix B3.11, Supplementary Methods 3.4). The simulation of coda repertoires by the ABMs represented a complete sampling, in the sense that all codas of all agents of all social units were recorded and compared. This is clearly not the case for the empirical data, in which field logistics inherently yield incomplete sampling of the social units' coda repertoires. To make empirical and simulated data more comparable and assess whether the modularity patterns in the simulated data were consistent in subsets of the simulated data, we re-sampled the acoustic network weighted links (i.e. coda repertoire similarity between social units) with replacement (bootstrap, 1000 iterations) and calculated the weighted modularity with increasing sampling, from 5% to 100% with increment of 5% of the links at a time.

3.5.6 Code and Data Availability

Agent-based models and data are available in the R package *balabm* v.1.1 (Appendix B3.8, Supplementary Methods 3.1).

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CHAPTER 4

HOW DOES SOCIAL BEHAVIOUR DIFFER AMONG SPERM WHALE CLANS? [7,8,9]

"Four snakes gliding up and down for no purpose that I could see. Not to eat. Not for love. But only gliding"

~ R.W. Emerson, 1834

4.1 ABSTRACT

When individuals primarily associate with and learn from those who behave similarly, society and culture become closely tied. Sperm whales (*Physeter macrocephalus*) exhibit multilevel social structure, the levels of which are differentiated in part by characteristic cultural behaviours. Sperm whales are organized into sympatric clans, with distinctive vocal repertoires that are socially learned. Other behaviours, such as movement patterns and foraging, also differ among clans. Here we ask whether the clan partition also

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[8] *Authors' contributions: Hal Whitehead (HW), Mauricio Cantor (MC) conceived the research idea; HW contributed empirical data; MC analyzed the data with contributions of HW; MC wrote the manuscript; HW contributed several ideas, comments and edits in the manuscript. MC reviewed the manuscript during the peer-review process.*

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includes divergences in social behaviour. Off the Galápagos Islands, members of two clans differed consistently in diving synchrony, heterogeneity, and temporal stability of social relationships. While number of associates (indicated by social unit, group, and cluster sizes) was similar between clans, *Regular* clan members dived more synchronously and had more homogeneous relationships than the *Plus-One* clan members. *Plus-One* social units had generally longer associations than those of the *Regular* clan. Differences in surface-time coordination and quality of social relationships are likely byproducts of the clan segregation, which could affect alloparental care giving, therefore scaling up to differential calf survival rates between clans. This new dimension of behavioural divergence between sperm whale clans indicates that sympatric, socio-cultural entities of nonhumans can also display characteristic social behaviour.

4.2 INTRODUCTION

Culture, defined as socially-learned and group-specific behaviour, is increasingly being recognized in primates, cetaceans, and some other nonhuman species (*e.g.,* Laland and Hoppitt 2003, Laland and Galef 2009). Culturally-recognized behaviours in these species include food preferences, foraging techniques, migratory and movement behaviour, vocalizations, play, and social conventions (Laland and Hoppitt 2003). Because cultural behaviour is socially learned, social structure drives and moulds cultural behavioural diversity, but it is important to consider that cultural diversity can in turn influence social structure (Cantor and Whitehead 2013).

Social learning of behaviour among peers—the foundation of culture (*e.g.,* Boyd and Richerson 1985)—can affect the patterns of social relationships, thus shaping social structure. This could be direct, for instance, if individuals directly learn social norms from one another. It could also be indirect if socially learned behaviour sets up conditions in which different social structures emerge. For instance the social structures of bottlenose dolphins (*Tursiops* spp.) may be structured by individually-characteristic solitary or communal foraging methods, at least some of which are socially learned, as individuals preferentially associate with others using the same methods (*e.g.,* Ansmann *et al.* 2012, Daura-Jorge *et al.* 2012, Mann *et al.* 2012). Furthermore, cultural tendencies to engage in individual *vs*. communal foraging will affect attributes and measures of social structure. Even more indirectly, culturally-learned foraging behaviour may set up conditions, *e.g.,* a particular spatial or temporal distribution of the selected resources, in which different social structures are expected to be favoured (*e.g.,* Krause and Ruxton 2002).

In some cases, social learning can promote the emergence of sympatric, behaviourally-distinct groups (*e.g.,* Centola *et al.* 2007). Social behaviour within such groups may tend to diverge over time due to behavioural innovations, founder effects, as well as transmission errors and biases (Koerper and Stickel 1980, Whitehead and Lusseau 2012). Alternatively, conformism and symbolic marking can homogenize behaviour within social groups and accentuate differences between them (Cantor and Whitehead 2013). These processes could be operating on social behaviour, or in other kinds of socially-learned behaviour such as foraging, that directly or indirectly impacts social structure, as in the case of the bottlenose dolphins mentioned above (Cantor and Whitehead 2103). Thus culture can augment and interact with the most-generally invoked factors driving interspecific and intraspecific variation in social organization: the spatiotemporal availability and predictability of resources, predation risk, and individual differences in social behaviour (*e.g.,* Lott 1984, Kappeler *et al.* 2013, Schradin 2013, Sacher *et al.* 2013, Wolf and Krause 2014).

Here we investigate whether two sympatric clans of sperm whales in the eastern tropical Pacific that possess distinct foraging, movement, and vocalization (Whitehead 2003, Rendell and Whitehead 2003, Whitehead and Rendell 2004) also show differences in their social behaviour. While male sperm whales lead quasi-solitary lives, females and immatures live in nearly-permanent social units (see Whitehead 2003), within which social relationships tend to be fairly homogenous. Social units form temporary groups, but only with other units from their own clan. These clans can overlap spatially and have minimal genetic differences between them, especially in the nuclear genome (Rendell *et al.* 2012, Whitehead *et al.* 2012). Thus differences in their social behaviour are likely due directly or indirectly to culture. Individuals may be learning from each other ways of organizing social relationships, or, probably more likely, cultural behaviour leads indirectly to differences in social structure between clans. In the latter, the candidate processes are different foraging behaviours, differences in microhabitat use, or simple stochasticity within socially isolated sets of animals.

4.3 MATERIAL AND METHODS

4.3.1 Photographic and Acoustic Sampling Effort

Groups of sperm whales were tracked visually and acoustically with a directional hydrophone, day and night (Whitehead 2003) during 2- to 4-week research trips between 1985 and 2003 off the Galápagos Islands, Ecuador (Figure 4.1). Recordings of sperm whale codas (stereotypical patterns of clicks used for communication) were made using a variety of hydrophones (frequency responses: 6 Hz–10 kHz, ±3 dB; 1–10 kHz, ±3 dB), recorders and amplifiers (details in Rendell and Whitehead 2003). Females and immature individuals were identified from photographs of natural markings on the trailing edge of tail flukes with the assistance of a computer program (Whitehead 2003). Black and white photographs were taken with 35 mm film SLR cameras until 2001, when we switched to equivalent digital equipment. The quality of each photograph was rated (from Q=1, very poor, to Q=5, very high quality) based on focus, exposure, orientation of the fluke in the frame, percent cover and tilt of the fluke in relation to the water surface (see Whitehead 2003). We excluded from the analyses photographs with Q<3, calves (distinctively small individuals, likely less than 2 year old) and mature males (distinctively large animals). Our long-term data set comprised 3,943 coda recordings, 6,193 high-quality $Q\geq3$ photographs, and social behaviour data of photo-identified individuals collected during 12,550 d of group follows (that varied from hours to a maximum of 12 consecutive days and nights) over a period of 18 years (Figure 4.1).

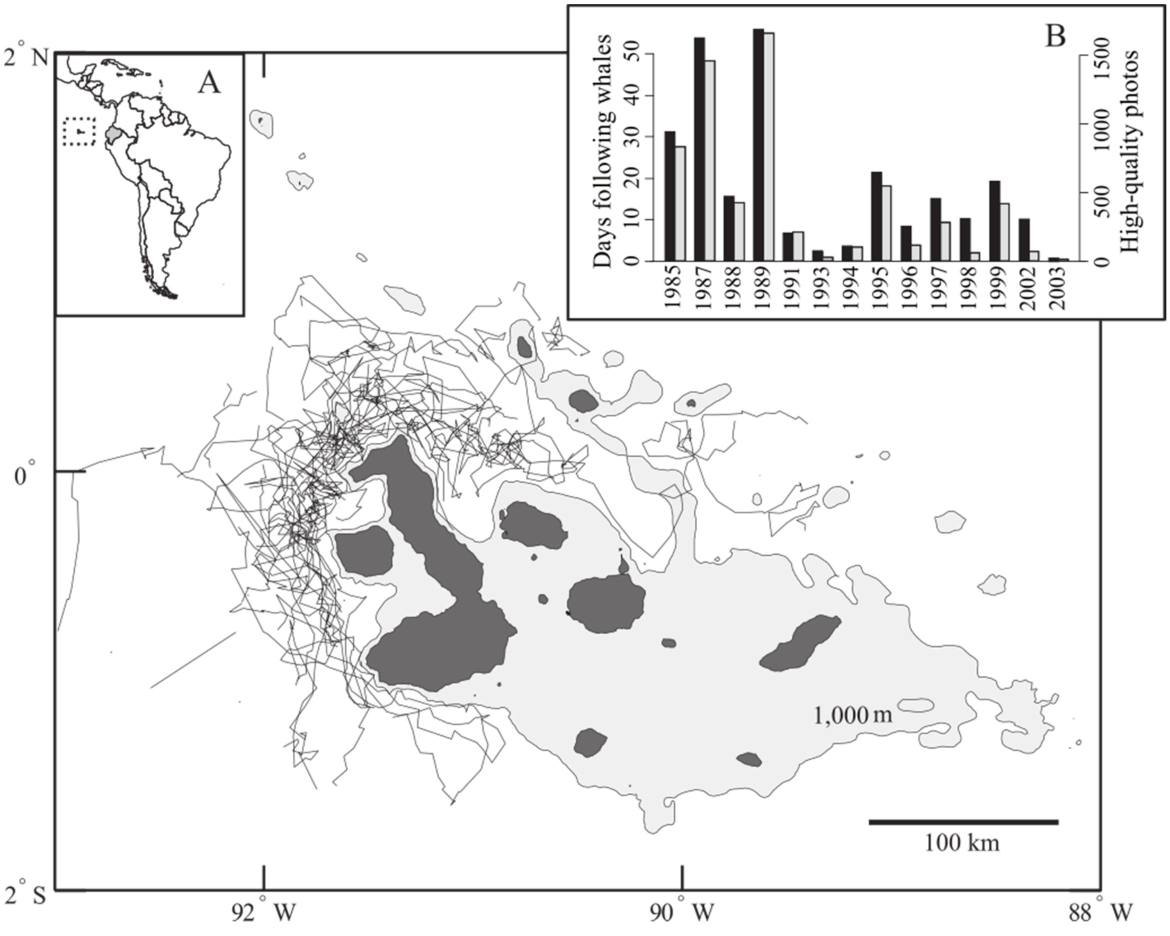

Figure 4.1. Spatio-temporal sampling effort off the Galápagos Islands, Ecuador, in the South Pacific Ocean. (a) The islands (dashed box) have darker shading, lighter shading represents waters less than 1,000 m deep (rarely used by sperm whales) and black lines represent the tracks of followed whales. (b) Black bars represent days following whales per year (of both clans); and gray bars represent the number of high-quality pictures (*Q*≥3) used for photo-identification.

4.3.2 Sperm Whale Clans

Vocal clans were defined as sets of social units of sperm whales (see Table 4.1) with high similarity in the repertoires of their coda vocalizations (Rendell and Whitehead

2003). In the South Pacific clans span ranges of several thousand kilometers and in all well-studied areas two or more clans are present. Social units were assigned to clans as in Rendell and Whitehead (2003), so we will summarize the methodology. The vocal repertoires of social units were identified based on inter-click intervals of the codas. Codas were assigned to social units whose members were photo-identified within 2 h of the recording. We analyzed repertoires of social units that had at least 25 codas recorded. Coda repertoires were compared with an averaged multivariate similarity method and hierarchical cluster analyses were used to define the best partition of social units into vocal clans (see Rendell and Whitehead 2003). We examined social variation between the two principal clans found off the Galápagos Islands: '*Plus-One* clan' (predominantly codas with the final inter-click-interval extended), and '*Regular* clan' (predominantly codas with 4-8 regularly-spaced clicks).

4.3.3 Social metrics

We compared clans using seven social metrics, all direct measures of the extent to which individuals were photo-identified together: three estimates of the number of individuals in different social levels (1: social unit size, 2: group size, and 3: cluster size), and four measures of interindividual association (4: dive synchrony within groups, 5: social differentiation, *S*, among all pairs of individuals within social units, 6: half-weight association indices, *HWI*, among all pairs of individuals within social units, 7: standardized lagged association rates, SLAR, among all pairs of individuals within clans). We chose the first three because they indicate the number of associates that individuals experience with different definitions of association; the remainder are good proxies for, and inform different aspects of, the quality of relationships (4: behavioural coordination within groups; 5: heterogeneity of relationships within social units, 6: strength of relationships within social units, and 7: temporal stability of relationships among members of different units within the same clan). Definitions of social metrics and methods of estimation are presented in Table 4.1.

Table 4.1. Definition and estimation methods for the seven social metrics.

Social metric	**Definition**	**Estimates based on**	**Method**	**Units of analysis**
1. Social unit size[1,2,3]	Number of individuals in a social unit, which is a set of adult females and immature individuals that live and move together over periods of years, generally of one or more matrilines.	Individuals associated with at least two other individuals during at least two 12h-identification periods spaced out by at least 30 d.	We considered the number of individuals assigned to the same social unit as in Christal *et al.* (1998).	Social unit
2. Mean group size[3,4,5]	Number of individuals in a group, which is a set of individuals moving together in a coordinated manner over periods of few hours to few days.	The number of photo-identified individuals for each day.	Two-occasion closed-population Lincoln-Petersen mark-recapture estimator: $g = \left[\frac{(x_1+1)\cdot(x_2+1)}{x_{12}+1}\right] - 1$, where x_1 are the number of individuals identified in the first half of the photo-identifications on that day, x_2 in the second half, and x_{12} in both.	Days (estimated group size on day)
3. Cluster size[4,6,7]	Temporary subsets of a group, composed of the individuals at the surface swimming in the same direction and speed, side by side in a coordinated manner a few body lengths or less apart usually for a matter of minutes.	Observations of number of individuals in clusters within 500m of boat only when whales were engaged in foraging. Clusters of socializing whales were not considered because they are very variable in size and can sometimes include all group members.	Mean cluster size for all records of cluster size for a social unit	Social unit

Social metric	**Definition**	**Estimates based on**	**Method**	**Units of analysis**
4. Dive synchrony[4,6,7,]	Expression of behavioural coordination among group members when foraging.	The maximum interval (in min) between the starts of consecutive deep dives of grouped individuals during each hour, minus its expected value, as predicted by group size and the presence of calves, averaged first over hours of each day, and then over those days in which a particular clan was sampled with at least 5 of such hours.	Expected intervals for any hour are given by the regression model $d = const + \frac{b}{n} - \beta \cdot c$, where d is the longest interval between consecutive dives for each hour, n is the number of dives made by the group during the hour, c is presence (1) or absence (0) of calves during the hour, and b and β are regression coefficients.	Days with groups of different clans
5. Social differentiation [4,8]	Variability in social relationships (homogeneous *S*=0; heterogeneous *S*>>0), here used to estimate the variation in dyadic probabilities of association within social units.	The estimated coefficient of variation (CV) of the true association indices (*S*). Higher S-values indicate more heterogeneity within-social unit relationships.	S was estimated from the photo-identification data with association defined as for metric 6, using the maximum likelihood method described in the appendix of Whitehead (2008b), with standard errors estimated by bootstrap resampling technique.	Mean *S*-values within social units
6. Strength of social relationships [3]	Proportion of time a pair of individuals was observed together in relation to the number of times that they were observed.	Associations among pairs of individuals diving within 10-min intervals. Within this period individuals are usually in well-synchronized diving cycles, at close spatial proximity (<600 m).	Half-weight association index: $HWI = \frac{x}{x+yab+\left(\frac{ya+yb}{2}\right)}$, where, x is the number of 10-min sampling intervals that individuals a and b were observed together; yab is the number of intervals with a and b identified but not together; ya and yb are the number of intervals with only individual *a,* or *b,* were identified.	Mean HWI among pairs of members of a social unit
7.Temporal stability [4,9]	Temporal stability of association between two individuals is given by the average probability of re-association after a given time lag.	The rate of association over time, for instance if individuals *A* and *B* were identified as associates, then a randomly chosen associate of *A* after lag t was *B*.	Plotting of the Standardized lagged association rates (SLAR) over increasing time lags and fitting exponential decay models to the observed SLARs (Table 4.3).	SLAR for all members of each clan

[1]Christal *et al.* 1998, [2]Christal and Whitehead 2001, [3]Whitehead 2003, [4] Whitehead 2008*a*, [5]Otis *et al.* 1978, [6]Whitehead 1996, [7]Whitehead 1999, [8] Whitehead 2008*b*, [9]Whitehead 1995.

4.3.4 Clan Comparison

We primarily asked whether there are differences in the social metrics between the social units from the two main vocal clans. As a cross-validation, we further asked the reversed question: how can we best separate the two clans using these metrics? To answer the former, we used Student's *t*-tests (two-sample unequal variance) to test the null hypothesis of no mean difference between the *Regular* and *Plus-One* clan, for all social metrics other than SLAR (see below). We also measured the magnitude of the differences with Cohen's *d* effect size (difference in means divided by combined standard deviation, SD), which informs how many SDs difference there is between the means of the two groups on a given social metric. In these tests, the unit of analysis was the mean value of the social metric for each available social unit. However, group size data typically involved individuals from two or more social units at the same time, so we used days spent following sperm whale groups as the units of analyses (Table 4.1).

To answer the latter, we applied a linear discriminant analysis (LDA). We aimed to express how different were the two clans as a linear function, evaluating which of the social metrics were important in quantifying their differences. We further aimed to predict the classification of a new unknown social unit into a clan, given the descriptors of its social behaviour. Here, the mean value of a metric for each social unit was also used as the unit of analysis, thus standardized lagged association rates (SLAR) and group sizes were not considered. We started by building the saturated LDA model with all the five remaining social metrics; then used forward and backward stepwise leave one out cross-validation to test whether models with fewer variables would have higher prediction accuracy. At each step, a new LDA model was created—by including variables not in the model (forward) or excluding those already in the model (backward)—and its prediction accuracy was estimated. The processes stopped when the accuracy did not improve, indicating that the resultant model was more efficient than other formulations.

Finally, we compared how social relationships changed over time in each clan by fitting four exponential decay models (SLAR1-4) with different possibilities for the decay of relationships over time to the lagged association rate data within clans (Table 4.3). Because members of a social unit are, by definition, permanent associates, in this context the lagged association rate primarily summarizes the dynamics of the associations among social units as they form groups. The first model, SLAR1, is constant, with no decay, representing permanent associations; in SLAR2, the association rate decays down to zero, representing associations that occurred for a given time lag and then never again; in SLAR3 the rate decays down to a lower level after a given time lag and then levels off, representing a mix of long-lasting and more temporary associations; the last model, SLAR4, is a sum of two exponential decay processes down to zero, representing two levels of disassociation, at a shorter and a longer time lag (the full description of the models and their parameter interpretation are available elsewhere: Whitehead 1995, 2008*a*). The SLAR models were fitted by iterative convergence to the original association data. We selected the most parsimonious model for each clan with the lowest quasi-Akaike Information Criterion (QAIC) (Burnham and Anderson 2002), to account for the overdispersion of the association data. The degree of support for the models was given by differences in the QAIC with the best fit model (ΔQAIC) and standardized relative QAIC weights ($e^{(-0.5\cdot\Delta\text{QAIC})}$) (Burnham and Anderson 2002). We obtained standard errors for the model parameters using the temporal jackknife procedure (omitting 30 day periods of data each time) (Whitehead 2008*a*). SLAR and related analyses were performed in SOCPROG (Whitehead 2009), while the remaining analyses were done in R environment (R 2014).

4.4 RESULTS

There was generally greater variation in the social level sizes between units in the same clan than between the clans (Figure 4.2A-C, Appendix C4.1 Table S4.1). The *Plus-One* clan appeared to contain smaller social units (mean unit size: *Regular* 13.6; *Plus-One* 10.7 individuals), that formed larger groups (mean group size: *Regular* 16.7; *Plus-One* 22.9 individuals), and larger clusters (mean cluster size: *Regular* 1.6; *Plus-One* 1.8 individuals) but such differences were not statistically significant at the 5% level (Table 4.2).

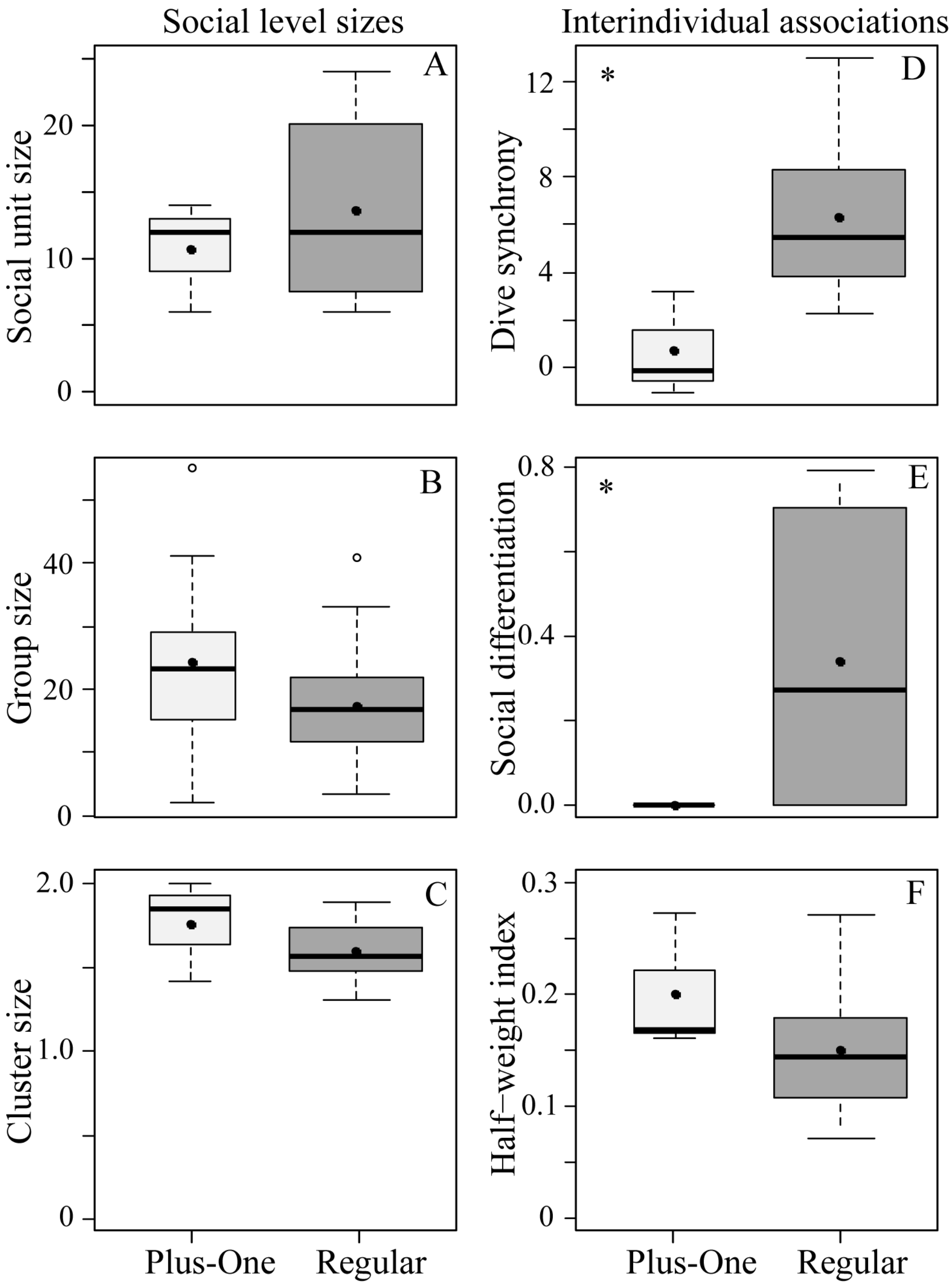

Figure 4.2. Social behaviour variation among sperm whale vocal clans (*Plus-One*, *Regular*): (a) Social unit size (number of photo-identified individuals); (b) Group size (number of individuals in temporary association); (c) Mean cluster size while foraging (number of individuals seen together at the surface); (d) Dive synchrony (residuals of no-

dive gap in minutes, from the dive synchrony regression model); (e) Social differentiation (*S*, estimated CV of the actual rate of association); (f) Half-weight association indices (mean HWI within units, estimated proportion of times pairs of individuals were seen together). Boxplots show mean values (black dots), median (horizontal bar), 1st and 3rd quartiles (box, which widths are proportional to sample sizes), minimum and maximum values (whiskers). Asterisks represent Student's *t*-test statistical significance at $P<0.05$ (Table 4.2).

Table 4.2. Mean values of social metrics for units of the *Regular* and *Plus-One* clans off the Galápagos Islands. Only social units to which we have data for all social metrics (except group sizes; see text) were included in the tests. SD: standard deviation; *t*: Student's t statistic; DF: degrees of freedom; *P*-values significant at $P<0.05$ are italicized; Cohen's *d*: effect size and 95% confidence intervals (CI). HWI: half-weight association index; *S*: social differentiation (estimated coefficient of variation of the true HWIs).

Social metric	*Regular* clan ($\bar{x}$ ± SD)	*Plus-One* clan ($\bar{x}$ ± SD)	*t*	DF	*P*-value	Cohen's *d* (95% CI)
Social unit size (individuals)	13.6 ± 7.0	10.7 ± 4.2	-0.9	6.41	0.42	0.46 (-0.89, 1.79)
Group size (individuals)	16.7 ± 6.6	22.9 ± 14.6	-1.4	12.74	0.18	0.66 (-0.03, 1.33)
Cluster size (individuals)	1.6 ± 0.2	1.8 ± 0.3	0.9	2.62	0.45	0.74 (-0.65, 2.08)
Dive synchrony (residual no-dive gap in minutes)	6.3 ±3.5	0.7 ± 2.3	-3.2	5.84	*0.02*	1.74 (0.16, 3.25)
Social differentiation *S*	0.35 ± 0.34	0.00 ± 0.00	-2.8	7.00	*0.03*	1.13 (-.032, 2.52)
Dyadic relationships (mean within-unit HWI)	0.15 ± 0.06	0.20 ± 0.06	1.2	3.64	0.31	0.80 (-0.60, 2.16)

In contrast, between-clan variation was clearer for interindividual association measures (Figure 4.2 D-F). Average association indices were not statistically different between clans (mean HWI: *Regular* 0.15; *Plus-One* 0.20). Social units that were members of the *Plus-One* clan dived less synchronously (mean residual no-dive gap: *Regular* 6.3; *Plus-One* 0.7 min). They were also more homogeneously associated, with less variable association indices (mean *S*: *Regular* 0.4; *Plus-One* 0.0) (Table 4.2). Moreover, the SLAR plots (Figure 4.3) and the most parsimonious models for temporal stability of within-clan relationships (Table 4.3) suggest that the *Regular* clan units were engaged in briefer associations: mean of 1.0 d (1/1.00) for the *Regular* clan *vs*. 2.0 d (1/0.491) for the *Plus-One* clan. The higher SLAR rates for the *Regular* compared with the *Plus-One* clan can be explained by the greater degree of social differentiation (individuals keep associating preferentially with the same small set of preferred companions).

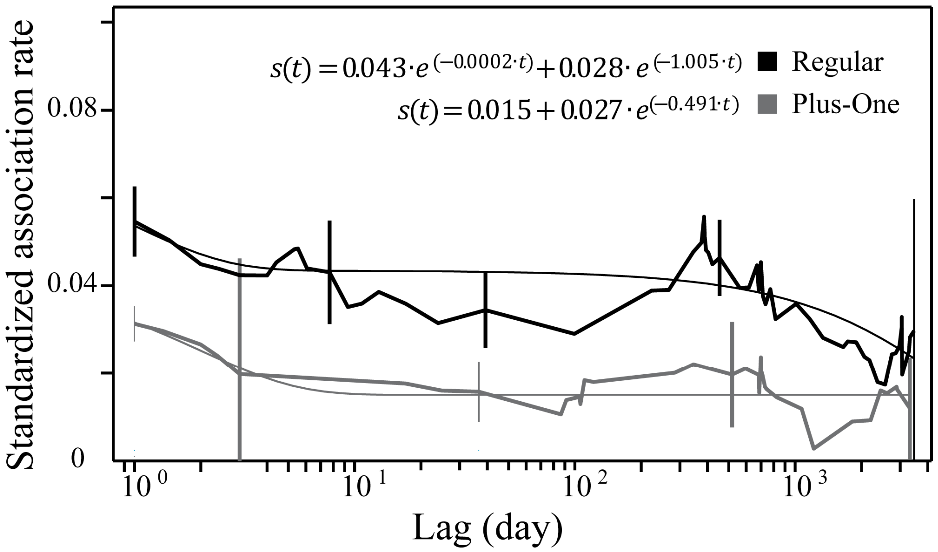

Figure 4.3. Standardized lagged association rates (thicker lines) and best fit models (thinner lines; Table 4.3) among whales within each vocal clan (black: *Regular*; gray: *Plus-One*). Low overlapping of the standard errors (vertical bars, from a jackknife procedure) suggests significant differences.

In the linear discriminant analysis, the prior probability (*i.e.,* the observed proportion) of social units being from the *Plus-One* clan was 0.27, and 0.73 from the *Regular* clan. The saturated LDA model ($Clan = 0.12 \cdot Unit\ size - 1.12 \cdot Cluster\ size + 0.35 \cdot dive\ synchrony + 0.36 \cdot S - 1.64 \cdot HWI$) had only moderate prediction accuracy: 63% of correctly *a posteriori* assignment of social units to clans. By removing variables from the saturated model, the resultant reduced models were more efficient. Both forward and backward stepwise procedures yielded predictive models (forward: $Clan = 0.15 \cdot Unit\ size + 0.38 \cdot dive\ synchrony$; backward: $Clan = 0.14 \cdot Unit\ size + 0.38 \cdot dive\ synchrony + 0.28 \cdot S$) that were equally accurate (correctness rates of 91% for both). Along the linear discriminant, the *Plus-One* social units clustered towards the negative, and the *Regular*'s clustered towards the positive values. The reduced models endorsed *t*-test results, which indicated that dive synchrony and S were significantly different between clans. Dive synchrony seemed to be the most divergent social metric between the two clans (see also Cohen's *d* in Table 4.2).

Table 4.3. Models fit to Standardized Lagged Association Rates (SLAR) ranked by the lowest quasi-Akaike Information Criteria (QAIC) for each of the two clans of sperm whales off the Galápagos (*Plus-One*, *Regular*). ΔQAIC, QAIC weights and likelihood

indicates the relative support for each model. Details on the interpretation of the model parameters are available elsewhere (Whitehead 1995, 2008*a*).

SLAR Model		QAIC	ΔQAIC	QAIC weight	Likelihood
	Plus-One Clan				
SLAR3	$s(t) = 0.015 + 0.027 \cdot e^{(-0.491 \cdot t)}$	1,232.06	0	0.68	1.00
SLAR4	$s(t) = 0.069 \cdot e^{(-1.038 \cdot t)} + 0.088 \cdot e^{(-0.454 \cdot t)}$	1,233.98	1.92	0.26	0.38
SLAR2	$s(t) = 0.025 \cdot e^{(-0.0002 \cdot t)}$	1,237.44	5.38	0.05	0.07
SLAR1	$s(t) = 0.023$	1,240.95	8.89	0.01	0.01
	Regular Clan				
SLAR4	$s(t) = 0.043 \cdot e^{(-0.0002 \cdot t)} + 0.028 \cdot e^{(-1.005 \cdot t)}$	8,011.47	0.00	0.65	1.00
SLAR2	$s(t) = 0.046 \cdot e^{(-0.0002 \cdot t)}$	8,012.73	1.26	0.35	0.53
SLAR3	$s(t) = 0.038 + 0.061 \cdot e^{(-1.218 \cdot t)}$	8,036.69	25.22	0.00	0.00
SLAR1	$s(t) = 0.041$	8,052.07	40.60	0.00	0.00

In summary, the two clans principally differed in behavioural coordination (dive synchrony), heterogeneity of relationships within units (*S*) and the temporal stability of social relationships among units (SLAR). We should, however, bear in mind a few caveats regarding the nature of our comparison. We reported social differences between two, out of five, known vocal clans (Rendell and Whitehead 2003). There are substantial logistical challenges in collecting long-term data on deep-diving cetaceans in offshore waters over large spatial scales. Thus at the moment we can only speculate whether the social contrasts would extend to other clans.

4.5 DISCUSSION

In addition to vocal, movement and foraging behaviours (Rendell and Whitehead 2003, Whitehead and Rendell 2004, Marcoux *et al.* 2007*a*), our long-term study adds social behaviour to the distinctions among the sperm whale clans inhabiting the Pacific waters. While clan partitioning is likely driven by cultural processes at a broad scale (Rendell and Whitehead 2003, Whitehead *et al.* 2012), we suggest that fine-scale social variation was shaped by a pre-defined clan partition, and therefore is a by-product—rather than a cause—of cultural segregation.

Overall, our findings indicate variation in the social behaviour of sperm whales from different clans. Most obviously, clan memberships imply differences in diving synchrony, heterogeneity and temporal stability of social relationships, with members from *Regular* clan diving more synchronously but with associations that are relatively more heterogeneous and briefer than the *Plus-One* clan. However, the clans showed no statistically significant variation in the sizes of lower social level, such as social units, groups, clusters. Taken together, our results suggest that social life is more unit-oriented for members of the *Regular* clan. Compared with a member of the *Plus-One* clan, a *Regular*-clan sperm whale has relatively more equivalent relationships with its co-members. Grouping with other units is less frequent and less prolonged for these *Regular* units. In the *Plus-One* clan the emphasis seems more on dyadic individual relationships, expressed by larger social differentiation, as well as associating with other units in the clan, rather than the unit itself.

Such fine-scale social variation may ultimately propagate into fitness differences between members of different clans (see also Marcoux *et al.* 2007*b*). Dive synchrony is an expression of social affiliation and behavioural coordination among group members. Primarily, it is an inverse measure of the quality of calf-protection at the surface: the more synchronous their characteristic 40 min dives are, the less reliably there will be babysitters at the surface for calves (Whitehead 1996). Because the provision of alloparental care seems to be a key function of the social units (Gero *et al.* 2013), differences in diving and surface-time synchrony, along with variation in quality and duration of social relationships among females, could lead to different rates of calf survival between clans. Additionally, diving synchrony serves as a proxy for foraging coordination and perhaps cooperation at depths, where more echolocating individuals might be more likely to find a food patch and could potentially assist one another in prey capture. Thus, differences in diving coordination could lead to differences in feeding success between clans (see also Marcoux *et al.* 2007*a*). Fitness differences between clans could also arise indirectly, through learning of other behavioural patterns exclusively within a clan. Social patterns affect the flow of behaviours through social learning (*e.g.,* Voelkl and Nöe 2010, Cantor and Whitehead 2013), thus the between-clan variation in social relationships could indicate different paths by which innovations and predominant behaviours are transmitted within the clans over time. For instance, as is the case for some other species in which variation in fine-scale social interactions can affect foraging strategies (*e.g.,* Aplin *et al.* 2012, Atton *et al.* 2014), movement patterns and micro-habitat use of sperm whales can be socially learned within the clan (Whitehead and Rendell 2004) and determine diet composition (see Marcoux *et al.* 2007*a*) as well as potentially feeding success of clan members.

There are a few explanatory mechanisms for the emergence of behaviourally-distinct clusters in a population, such as the sperm whale vocal clans. Intrapopulation variations in social behaviour are usually assigned to genetic, ontogenetic, ecological, and/or cultural factors (*e.g.,* Schradin 2013, Cantor and Whitehead 2013, Cronin *et al.* 2014). Pinning down the principal mechanism can be challenging (*e.g.,* Whitehead 2009, Allen *et al.* 2013, Mace 2014). In our case, sperm whale vocal clans are sympatric, span large areas (Whitehead *et al.* 1998, Rendell and Whitehead 2003), are not genetically distinguishable (Whitehead *et al.* 1998, Rendell *et al.* 2012), and contain individuals from all age classes (Rendell and Whitehead 2003). Therefore behavioural differences between clans are unlikely to be environmental, genetic, or ontogenetically-driven; they are more parsimoniously ascribed to social learning (Rendell and Whitehead 2003, Whitehead *et al.* 2012, Whitehead and Rendell 2014). More specifically, behavioural distinctions between clans can emerge when: a) individuals with similar behaviour preferentially associate (also called assortment, homophily), and b) associations reinforce behavioural similarity (social influence) through social learning (see Centola *et al.* 2007, Cantor and Whitehead 2013). In this way, the population would segregate into clans if sperm whales with similar social behaviour tend to associate more often—either actively by preferential association among like-minded individuals; or passively by differences in habitat use strategies (see Croft *et al.* 2009, Farine 2014). However, it is much more likely that matching of acoustic behaviour structures the associations among sperm whales (see Rendell and Whitehead 2003, Schulz *et al.* 2008): coda types are used for communication, are learned socially and only individuals with highly similar vocal repertoires tend to associate. Indeed vocal similarity is how the clans were initially recognized (Rendell and Whitehead 2003).

Once the sperm whale population is structured into vocal clans, other behavioural variations, which may be functionally neutral (*e.g.,* Hahn and Bentley 2003) such as the social behaviour we report here, may emerge and disappear through drift over time (Cavalli-Sforza and Feldman 1981). Analogously to phylogenetic processes (Koerper and

Stickel 1980, Boyd and Richerson 1985), such changes in frequencies of socially-learned behaviours occurring by neutral processes involving no selection or preference would amplify the differences between the behavioural repertoires of the segregated clans. Therefore, it may be parsimonious to view the social variation between clans as a consequence of a predefined partition in the whales' social network, with individuals and social units replicating the patterns in dive synchrony and social behaviour of their clan members, and drift leading to distinctive variation among clans in either the social behaviour itself or other behaviour that directly or indirectly affects social structure (*e.g.,* Whitehead and Lusseau 2012).

Behavioural segregation within populations adds another layer of complexity to intraspecific variation in social structure (Kappeler *et al.* 2013). We showed that some elements of the sociality of sperm whales are mapped onto the upper level divisions of their society. These findings are among the few showing that culturally-marked groups of nonhumans living in the same area have characteristic social behaviour (see also Cronin *et al.* 2014). In perhaps the closest known parallel, sympatric killer whale (*Orcinus orca*) ecotypes in the eastern North Pacific have distinctive social structures (Baird 2000), and the evolution of these ecotypes may have been driven by cultural differences (Riesch *et al.* 2012). However the ecotypes are now so different that there have been calls to recognize them as distinct species (Morin *et al.* 2010). Social variation between sperm whale clans further shows that their behavioural segregation is not limited to communicative signals. The presence of sympatric clans with rich, divergent, culturally-initiated behavioural norms suggest that sperm whale populations could carry multiple traditions. Multiple traditions within populations are considered a rare trait for nonhuman societies (*e.g.,* Whiten *et al.* 1999, Allen *et al.* 2013), but they might remain unrecognized either because behavioural ecologists have failed to look for them, or because intrapopulation behavioural variation is fully, but incorrectly, attributed to ecological or genetic differences. Sorting out the contribution of culture from other factors in driving intraspecific variation remains a timely challenge (Kappeler *et al.* 2013, Mace 2014).

4.6 ACKNOWLEDGMENTS

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CHAPTER 5

CULTURAL TURNOVER AMONG GALÁPAGOS SPERM WHALES [10,11,12]

> *“All change is a miracle to contemplate, but it is a miracle which is taking place every instant.”*
>
> *~ H.D. Thoreau, 1854*

5.1 ABSTRACT

While populations may wax and wane, it is rare for an entire population to be replaced by a completely different set of individuals. We document the large-scale relocation of cultural groups of sperm whale off the Galápagos Islands, in which two sympatric vocal clans were entirely replaced by two different ones. Between 1985-1999, whales from two clans (called *Regular* and *Plus-One*) defined by cultural dialects in coda vocalizations were repeatedly photo-identified off Galápagos. Their occurrence in the area declined

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[11] *Authors’ contributions: Hal Whitehead (HW), Mauricio Cantor (MC) conceived the study idea; HW, Luke Rendell (LR) designed the study; HW, LR, MC collected data; LR, MC processed data; MC, Shane Gero (SG) performed statistical analyses; SG, LR, HW, MC programmed computer analyses; MC drafted manuscript and HW, SG, LR edited and contributed to writing. All authors gave final approval for publication.*

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through the 1990's; by 2000 none remained. We reassessed Galápagos sperm whales in 2013-2014, identifying 463 new females. However, re-sighting rates were low, with no matches with the Galápagos 1985-1999 population, suggesting an eastward shift to coastal areas. Their vocal repertoires matched those of two other clans (called *Short* and *Four-Plus*) found across the Pacific but previously rare or absent around Galápagos. The mechanisms behind this cultural turnover may include large-scale environmental regime shifts, and cascading responses to heavy whaling in the region. The fall and rise of sperm whale cultures off Galápagos reflect the structuring of the Pacific population into large, enduring clans with dynamic ranges. Long-lasting clan membership illustrates how culture can be bound up in the structure and dynamics of animal populations and how tracking cultural traits can reveal large-scale population shifts

5.2 INTRODUCTION

Behavioural repertoires of animal populations change over time. Changes may result from adaptive genetic evolution and genetic drift, phenotypic plasticity, individual or social learning [*e.g.* 1,2]. Changes can take many generations (typical for genetic evolution) or occur over a small part of the life cycle (*e.g.* phenotypic plasticity in the face of rapid environmental change). When behaviour is socially learned and shared, hence culture, evolutionary processes influence these dynamics at various scales [2,3]. When cultural behaviour changes rapidly relative to generation time, it can do so in two distinct ways. First, by replacement of behaviours: individuals learn new behaviours and those spread through the standing population. Second, by replacement of the individuals themselves: the population using that area dramatically changes in composition such that entire cultural trait groups are replaced by others.

There are multiple non-human examples of the first case—replacement of behaviours. Take humpback whales (*Megaptera novaeangliae*) for example. Male humpbacks sing a continuously evolving population-specific song [4], but in the South Pacific populations regularly discard entire songs in favor of a new song from a neighboring population in a revolutionary transition that takes less than a year [5,6]. Similarly, humpback populations can rapidly diffuse foraging innovations in response to ecological shifts [7]. As for the second case—replacement of individuals—there are examples from human history of cultural groups replacing each other in a given territory. One is the history of the Sahel, the sub-Saharan semiarid vegetation belt that was once home for different cultural groups with two distinct feeding strategies—nomadic pastoralism and sedentary farming [8]. Following large-scale environmental changes after the French colonial rule—a combination of natural and anthropogenic desertification—groups whose feeding strategies no longer fit the habitat were forced to move [8,9], resulting in a cultural turnover caused by the replacement of individuals by those from different culturally-defined groups. However, examples outside humans are much rarer. Here, we document rapid cultural turnover in an animal population caused by the replacement of cultural groups on an oceanic scale: the sperm whales (*Physeter macrocephalus*) off the Galápagos Islands.

Female sperm whales live in multilevel societies [10]. The fundamental social level is the nearly-permanent social units of about 11 females and their young [10-12]. The largest level is the vocal clan, that we distinguish using characteristic repertoires of codas—stereotyped patterns of broad-band clicks used in social communication [13]. Vocal clans are sympatric (groups from multiple clans are found around the Galápagos and off the coasts of Chile and mainland Ecuador [14]) but socially segregated such that social units only form temporary groups (about 2-3 social units typically over periods of days) with other units that share the same repertoires of coda types united by a common structural theme [14]. Two vocal clans were common around the Galápagos Islands in 1980-1990's: the *Regular* clan, consisting of social units that mostly make codas with regularly-spaced clicks; and *Plus-One* clan, most of whose codas have an extended interval before the last click. Two other clans were identified across the wider Tropical Pacific: the *Short* clan which mostly produced brief codas with fewer than 5 clicks; and the *Four-Plus* clan which mostly produced codas with a base of 4-regular clicks [14]. These distinct coda dialects are stable over at least a decade [15]. Among clans, there is extensive sharing of mitochondrial DNA haplotypes, thus, taken with the degree of sympatry, it is almost certain that these dialect variations are cultural in nature [16]. Clans also differ in habitat use, foraging success, diet, social behaviour, and possibly calving rates [17-19], suggesting that clan membership has much wider implications than just vocal dialect. Thus, clans appear to be a significant structuring factor in sperm whale society.

Although highly socially structured, sperm whales in the Tropical Pacific display little geographic structure: clans overlap over very large areas [10,14]. While social units have ranges spanning about 2,000km, the clans to which they belong have wider distributions, spanning across the Tropical Pacific [14,20]. This nomadic behaviour likely reflects adaptive space use, probably driven by the effects of oceanographic conditions on variation in the distribution of their prey, deep ocean squid [20,21]. We surveyed sperm whale populations and coda repertoires over the last three decades, and use these data here to show a complete turnover in cultural dialects concurrent with a turnover in the pool of individuals around the Galápagos Islands.

5.3 METHODS

5.3.1 Field Methods, Photo-Identification, and Acoustic Recordings

Sperm whales were tracked visually and acoustically in deep waters (>1,000m) across the Tropical Pacific, day and night during 2- to 4-week surveys between 1985 and 2014 (Figure 5.1, Appendix D Tables S5.1- S5.3). Given the logistical challenges of offshore surveys, sampling was unevenly distributed; the Galápagos archipelago was the main study area (Appendix D, Tables S5.1-S5.3). Annual encounter rates off the Galápagos were calculated as number of groups of female and immature whales encountered divided by total hours of acoustic and visual search (i.e. total effort minus time following whales) [22].

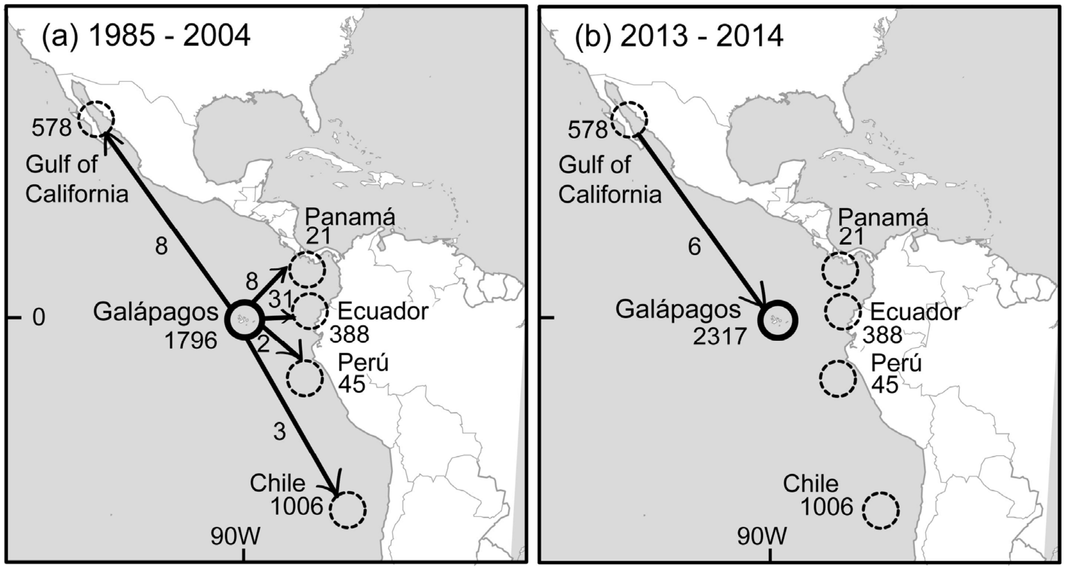

Figure 5.1. Re-sightings of individual female and immature sperm whales in the eastern Tropical Pacific, between (a) 1985-2004 and (b) 2013-2014. Dashed circles loosely indicate study areas, with numbers indicating total of photo-identified individuals. Numbers by arrows indicate match of individuals between areas.

Individuals were identified from photographs based on patterns of natural marks on the trailing edge of their tails, assisted by a semi-automated photo-identification protocol [23]. We rated each photograph from poor to very high quality (Q=1 to 5) based on focus, exposure, orientation, percent cover and tilt of the fluke [24]. Distinctively small animals (of about <2 years) were considered calves; distinctively large animals as mature males; the others were considered females and immatures [24]. We analyzed only $Q \geq 3$ photographs of females and immatures. From a total of 14,286 photographs, we identified 4,468 individuals (Appendix D5.1, Table S5.2).

Sperm whale codas were recorded using various hydrophone arrays and recording devices over the duration of the study (Appendix D5.11, Supplementary Methods 5.1)

[14]. All recordings were analyzed using Rainbow Click software [25] in which individual clicks were manually marked and designated as part of codas. From acoustic recordings from across the Pacific, we sampled 17,045 codas (Appendix D5.2, Table S5.3).

5.3.2 Assigning Coda Repertoires to Photo-Identified Groups

We assigned coda recordings to groups of individual whales photo-identified together. We considered all recordings made on the same day when continuously following a group of sperm whales to be of the same group [14]. Codas recorded on two different days were considered to be from the same group if least 25% of the photo-identified individuals were re-sighted [26]: $m_{ab}>0.25*min\{n_a, n_b\}$, where m_{ab} is the number of individuals photo-identified on both days, n_a is the number of individuals identified on the first day, and n_b on the second day. We discarded groups whose recorded repertoires contained less then 25 codas [14].

To account for any potential autocorrelation in coda production during the same day, all coda recordings on a given day from a given group represented a single repertoire. Under the assumption that coda production of a given group on a given day is independent of its production on a subsequent day, repertoires from different days were treated as replicates of a group's repertoire and were considered independent samples of a group's coda production [27]. We used permutations to test differences between group repertoires (Appendix D5.12, Supplementary Methods 5.2) [27].

5.3.3 Continuous and Categorical Similarity Between Coda Repertoires

We compared group repertoires using the absolute inter-click intervals (ICI, i.e. the time between the onset of one click to another in a coda sequence) to represent the temporal structure (rhythm and tempo) of their codas [27,28]. To quantify similarity between coda repertoires, we applied continuous and categorical metrics to this multivariate data set. The former was used to define the vocal clan partitions; the latter was used to define coda types that illustrate the differences in the patterning theme of the codas between clans (analyses pathway in Appendix D5.4, Figure S5.1).

For the continuous approach, we calculated the multivariate similarity of two codas of the same click length (i.e. same number of clicks) using the Euclidean distance between their inter-click interval vectors (Appendix D5.13, Supplementary Methods 5.3) [14]. With the categorical approach, we classified codas into discrete types based on their rhythm and tempo, illustrating how repertoires differed among clans. We assigned codas to categories using OPTICSxi hierarchical clustering [29] (in this context: [27]). We ran OPTICSxi on the absolute inter-click intervals independently for each set of codas of the same click length, using a sensitivity analysis to define the algorithm initial parameters (Appendix D5.14, Supplementary Methods 5.4). We labeled the coda types according to number of clicks and rhythm, based on previous nomenclature [14,26].

5.3.4 Assigning Photo-Identified Groups to Vocal Clans

The original partition of vocal repertoires into clans ([14], Supplementary Methods 5) used hierarchical clustering analyses based on the continuous multivariate similarities of standardized ICIs of codas, and the *k*-means algorithm to categorize codas into types [14]. Here we used the updated methods for comparing repertoires described above to re-analyze this data set together with the repertoires recorded off Galápagos in 2013 and 2014 (Appendices D5.3, D5.15: Table S5.3, Supplementary Methods 5.5). To assign the 2013 and 2014 groups to clans, we first built an average-linkage clustering dendrogram using the continuous multivariate similarity matrix for the combined dataset; then we identified whether these groups clustered together into a distinctive branch (indicating a new clan) or whether they clustered with previous clans. We measured the accuracy of the dendrogram representation using the cophenetic correlation coefficient (CCC), and considered CCC>0.8 to indicate a reliable representation. The dendrogram robustness was measured by bootstrap resampling [14]: all groups' coda repertoires were randomly sampled with replacement (100 replicates), their similarities were recalculated and the proportion of times a given branch was replicated used to indicate the robustness of that branch.

5.4 RESULTS

5.4.1 Photographic Matching and Movements

We identified 4,468 individuals across the Pacific study areas (Appendix D5.2, Table S5.2) with re-sightings illustrating the scale of movements individuals could undertake (Figure 5.1). Most individuals were identified off the Galápagos Islands; however, overall encounter rates there declined over the period 1985-2000 (Figure 5.2). Between 1985-1995, female and immature sperm whales were repeatedly found (1,085 identified individuals); encounters with whale groups became rarer in the late 1990's and by the 2000's they seemed to have left the area (Figure 5.2). Surveys from 1985-2004 suggested an eastward movement away from Galápagos (Figure 5.1A). Our 2013-2014 surveys indicated a modest, recent return of sperm whales to this area (Figures 5.1B, 5.2); however, this was by new individuals. The photographic recapture rate was very low: only 1% of the females and immatures (5/463) were sighted in both 2013 and 2014. From these recently photo-identified whales, none matched with the previous whales seen off Galápagos and only 6 females had been seen in in the Gulf of California in 2003 (Figure 5.1B).

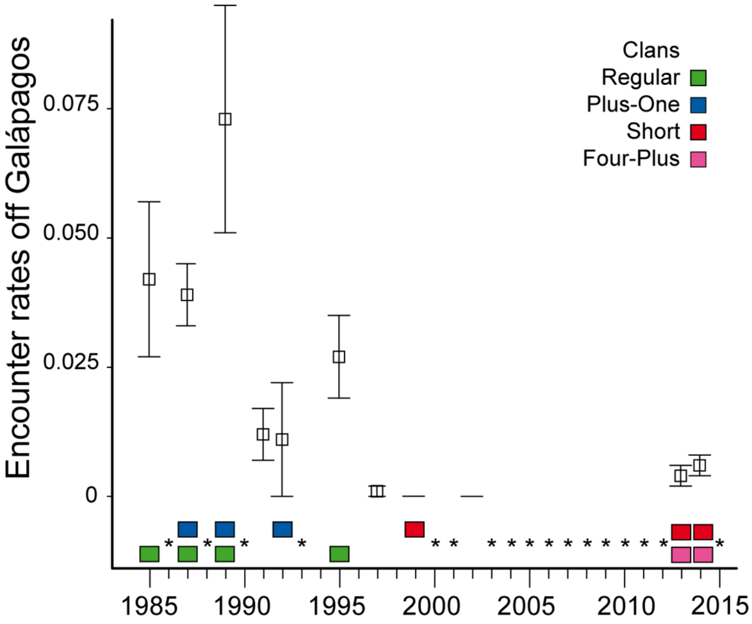

Figure 5.2. Encounter rates of sperm whale off the Galápagos Islands over 30 years across clans. Rates were higher in early 1980's, started declining during the 1990's and, after a hiatus in 2000's, started rising again. Color code indicates clan membership (Figure 5.3) of whales for which both photo-identification and acoustic data were available in that year. Whiskers represent standard errors (SE). Asterisks indicate years with no dedicated surveys off Galápagos (the larger gap in 2000's was mainly motivated by a lack of opportunistic sightings in the area), but in some of these years there were surveys in surrounding areas (Tables S5.1-S5.3).

5.4.2 Acoustic Repertoires

From 1985 to 1999, coda repertoires of 64 groups of female and immature were recorded across the Tropical Pacific [14]; in 2013-2014 we recorded 15 new groups off the Galápagos (Appendix D5.3, Table S5.3). Mantel tests confirmed that repertoire similarity between acoustic recordings from the same group was greater than between different groups indicating that groups had significantly different repertoires (Galápagos 2013-2014: $r=0.413$, $p<0.001$; Pacific 1985-1999: $r=0.170$, $p<0.001$; Combined: $r=0.176$, $p<0.001$).

The categorical analysis of the full data set identified 27 distinct coda types containing from 3 to 12 clicks varying in rhythm and tempo (Figure S5.2). Although the OPTICSxi algorithm classified only the most stereotyped codas (4,091/17,045 codas; 24%), discovery curves of classified coda types were nearly asymptotic (Figure S5.3), suggesting that most coda types made by the sampled groups were represented. Coda types were robust to variation across the OPTICSxi input parameter space (Figure S5.4). Coda type classification was used to describe the thematic differences in coda patterning driving clan partitioning defined by the continuous analysis that includes all codas (Figure 5.3).

5.4.3 Clan Structure

The original partitioning of clans in the Tropical Pacific [14] was preserved in our analysis, with *Regular*, *Four-Plus,* and *Short* clans depicted in our dendrogram as largely similar to the original analysis (Figure 5.3A). There were some minor changes: the groups recorded off Tonga and in the western Caribbean (branches with lower bootstrap support in the original analysis) clustered with groups belonging to the *Plus-One* clan; and four groups (two designated as *Short*, and two as *Regular*) clustered with different clan branches (Figure 5.3A). We expected some changes because our new analysis was different from the original [14] in two ways. First, we included the newer groups recorded off Galápagos (Figure S5.5). Second, we used absolute instead of the relative inter-click intervals used in the original clan partition, since recent studies [27,28] suggest that tempo, in addition to rhythm, is an important element of coda diversity. Nevertheless, the dendrogram in Figure 5.3A is an appropriate depiction of the coda repertoire similarity among groups of whales (CCC=0.896), with good support from the bootstrap analysis.

The new categorical coda classification reproduced the main thematic patterning expected for codas types in each clan (Figure 5.3B). For instance, groups belonging to the *Regular* clan mainly produced regularly-spaced codas from 6 to 12 clicks (*e.g.* 6R1, 6R2, 7R1, 7R2, 8R2, 9R2, 9R3, 10R2, 11R, 12R); groups from the *Short* clan mainly produced codas with 3 to 5 clicks (*e.g.* 3R, 2+1, 1+2, 4R, 1+2+1, 1+3+1); *Plus-One* groups produced mainly codas with an extended pause before the last click (*e.g.* 3+1, 1+3+1, 5+1, 4+1+1); *Four-Plus* groups produced codas with four regular clicks (*e.g.* 4R, 4+1+1). The groups recorded off Tonga and in the western Caribbean contained dominant codas with longer pauses at the end (e.g. Tonga: 4+1+1; Caribbean: 1+3+1, 5+1, 6I, 10I). These coda types may explain the tendency for Tonga and Caribbean groups to cluster with the *Plus-One* clan in our analysis. The patterns seen in the clustering analysis agreed with the distribution of coda types per clan in the multivariate space: some types were made by many clans, whereas other types were characteristic of some clans as described above (Figures S5.6, S5.7).

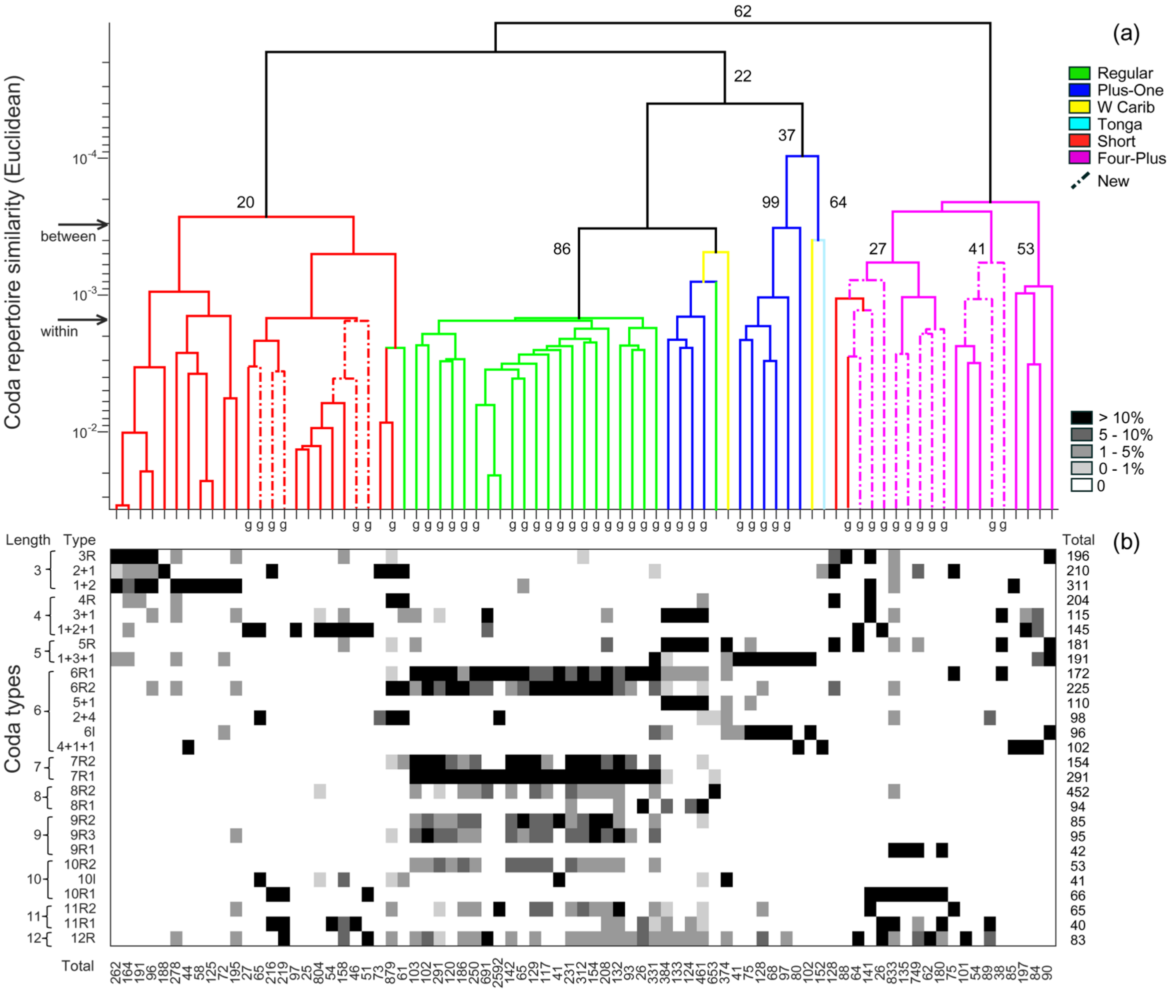

Figure 5.3. Coda repertoire similarity and clan structure of sperm whale groups from the Pacific between 1985 and 2014. (a) Hierarchical clustering dendrogram (CCC=0.896) depicts the multivariate similarity (Euclidean distances on absolute inter-click intervals) among coda repertoires of photo-identified groups of sperm whales (branches). Colour code and clan names follow original results [14]; 'g' indicate groups observed off

Galápagos; dashed branches indicate new groups observed in 2013-2014; arrows indicate mean similarity between and within clans; numbers besides nodes indicate the number of replications (out of 100) in bootstrap analysis. (b) Frequency of coda types containing up to 12 clicks (rows) classified into discrete types for each photo-identified group (columns). Shades of grey indicate the frequency of occurrence of coda types in a given group repertoire; coda type labels represent rhythm (see Figure S5.2); numbers under columns indicate total number of recorded codas from each group of whale used in the continuous analysis; numbers on the right indicate the total codas per type used in the categorical analysis.

The repertoires of groups recorded in 2013 and 2014 off Galápagos did not cluster by year of recording (Figure S5.5), indicating that different clans were present in both years. When these new groups were added into the Tropical Pacific clan analysis, they clustered with existing branches representing the *Four-Plus* and *Short* clans and not with the *Regular* and *Plus-One* clans previously heard off Galápagos (Figures 5.2, 5.3A). *Four-Plus* and *Short* were heard previously off Chile, Kiribati, and the Marshall Islands, and were very rare or absent off Galápagos in the past: in fact, only a single social unit of the *Short* clan was recorded in 1999 (Figure 5.2) [14]. Our acoustic results concurred with the photo-identification results: the lack of matches between the Galápagos whales from 1985-1999 and 2013-2014 (Appendix D5.2, Table S5.2); and the 6 whales seen in 2003 in the Gulf of California (Figure 5.1B) were found to be members of the *Four-Plus* clan in 2013 off Galápagos.

5.5 DISCUSSION

Our study demonstrates cultural turnover in the sperm whale dialects off the Galápagos Islands over the last 30 years. We attribute these changes to a turnover in the clans utilizing these waters: the shift in the acoustic repertoires matches the complete replacement of sperm whales identified off the Galápagos. These findings confirm previous suggestions that clans are stable over time (at least in repertoire, and almost certainly in membership) but dynamic over space [15]. Our long-term analysis indicates the coda repertoires remain little changed across three decades in the Pacific, highlighting that Pacific sperm whales roam over very wide geographical areas as members of large, long-lasting cultural clans [14,30].

None of the individual sperm whales using the waters off Galápagos in 2013 and 2014 were seen in the area during the previous three decades. Our photo-identification findings increased the number of individual sperm whales catalogued across the Tropical Pacific, but the rate of photographic recaptures off the Galápagos between 2013-2014 was low despite our long-term and large-scale sampling. Offshore surveys, however, impose several logistical challenges, making our sampling effort patchy in time and space (Table S5.1). We acknowledge the consequent uncertainty regarding presence of whales in waters near the Galápagos, as well as in unsampled years. Yet, our photo-identification data provide strong evidence for large-scale movements between discrete study areas and across years. We propose, therefore, that the drastic demographic change we report was driven by emigration of groups of whales from different clans.

There are four lines of evidence that support emigration out of Galápagos, rather than changes in the composition of the clans themselves, as the most likely mechanism for the local decline in sperm whale sightings. First, there were several re-identifications of Galápagos groups and clans off northern Chile and Gulf of California (Figure 5.1A, see also [20, 31]) evidencing that sperm whales do move long distances. Second, sperm whales seem not change their clan membership, or if so, only very rarely [24]. Third, sperm whales are slow-reproducing, long-living animals [24] and the last three decades is a relatively short window in their life span during which no high mortality was evident [22]; all of these make death and birth very unlikely the drivers of the replacement of individuals off Galápagos. Finally, errors in individual identification cannot be a major factor because marks used to photo-identify animals rarely change [32]; indeed, Atlantic sperm whale individuals have been re-identified across 30 years within a single study area much smaller than ours [12]. Combining these facts with our findings on coda repertoires, we suggest the same clans from three decades ago still populate the Tropical Pacific, but what seems to have occurred is a large shift in the habitat used by each of the clans.

Sperm whales are nomadic. In the Pacific, social units have wide ranges, performing long distance movements (mostly span about 2000 km, some over 4000 km) within relatively short temporal scales [20], emphasizing the magnitude of the spatial scale relevant for sperm whales. The long-distance movements are made by individuals travelling together, since sperm whales live in nearly-permanent social units [11]. These units belong to large clans with dynamic ranges [10,15], which are stable emergent social structures [30] within which coda usage is conserved over time [15]. Therefore, the radical cultural turnover in sperm whale dialects off Galápagos reflected a clan replacement, i.e. a local turnover in whales using the area in consequence of their natural movements in search for resources over large spatiotemporal scales. This contrasts with the cultural revolutions among humpback whales where songs changed dramatically but with little turnover of individuals [4-6].

The sperm whales recently identified off Galápagos are not members from the *Regular* and *Plus-One* clans once common in the area. Instead, they are members of two existing clans (*Four-Plus* and *Short*) previously heard across the Pacific but very rare or absent in Galápagos waters. The *Four-Plus* clan was consistently heard off northern Chile, while the *Short* clan spread over the Tropical Pacific and only few of its members (a single social unit) had been previously identified off Galápagos [14]. The new whales immigrated from neighboring waters in the wider Pacific. Our photo-identification data may give some indication of origin: there were some matches with *Four-Plus* clan members seen previously in Gulf of California, where both *Short* and *Four-Plus* clans may be present [33].

5.5.1 Why Were the Clans Replaced?

The Galápagos Islands, and more broadly the eastern Pacific, were historically important grounds for sperm whales [34]. Although there were numerous whales when our Galápagos studies started in 1985, emigration drastically reduced their numbers between 1990-2000. Following this exodus, members of different clans have been slowly repopulating the Galápagos. The fall and rise of cultural clans of sperm whale off Galápagos lead to two questions. Why did members of the original clans leave? Why are the new whales from other clans rather than return of the original clans? While our data show a clear shift in Galápagos sperm whale dialects, the underlying mechanisms for the large-scale displacement of clans are necessarily speculative. In what follows we describe two non-exclusive hypotheses.

The first scenario involves large-scale environmental shifts. Drastic environmental changes force cultural groups to adapt their strategies or move [e.g. 8]. Like many other predators as well as some herbivores, food availability is a major driver of movement for sperm whales. They tend to go where the prey is, moving from areas of low to high feeding success [35]. The abundance of preferred prey, for instance jumbo squid (*Dosidicus gigas* [21]), may fluctuate naturally across the Pacific and in response to environmental changes such as the El Niño Southern Oscillation (ENSO). ENSO events impose massive changes in the Pacific [36], including anomalous sea surface warming, large influx of deep warm waters, and fluctuations in primary productivity and nutrient cycling [36,37]. In particular, the extreme ENSO events in early 1980's and late 1990's represented remarkable warming in the equatorial Pacific, devastating marine fauna [36,38], including marine communities in the Galápagos region [39]. The reduced productivity of tropical and equatorial Pacific waters considerably decreased the feeding success of sperm whales off Galápagos [40]. ENSO events are becoming more frequent and intense [36,41]; due to cetaceans' high and adaptive mobility, leaving affected areas is their immediate response [42]. We know sperm whales from different clans tend to move and forage differently [17]. In years of normal temperatures, the foraging strategy of the *Regular* clan outperforms the *Plus-One*; whereas in the warmer, less productive ENSO years the foraging successes of both clans is reduced considerably but the *Plus-One*'s strategy becomes more efficient than the *Regular*'s [17]. Clans may conserve their foraging strategies even during remarkable environmental changes [17], thus living in this large-scale dynamic habitat, groups of whales from particular clans may relocate, moving to areas where their foraging strategies are likely to maximize their food intake. This assumed cultural inertia of foraging strategy—not uncommon in marine mammals [43,44]—implies that large-scale movement is favoured over remaining in a changing habitat and adapting to the new conditions. This may explain both why the original clans left and why the new immigrants are from different clans, but implies that changes to the ecosystem around Galápagos [37-39] are perceived differently by sperm whales from different clans.

The second scenario involves lagged responses to the population decline caused by modern whaling [22]. Sperm whales in the general vicinity of the Galápagos were heavily hit by nearly-unregulated, as well as pirate, whaling between 1957-1981 [45,46]. The extreme depletion of sperm whales of the eastern Pacific in those years focused on the relatively-inshore waters of the Humboldt Current off Perú and Chile as the legal whaling used catcher-boats operating from mainland ports [34,46]. The whaling may have left a surplus of sperm whale prey, re-opening a niche in the rich Humboldt Current waters. In case of density-dependent habitat selection [47], whales would redistribute themselves according to habitat quality—low whale density in productive coastal waters may have stimulated the eastward migration out of the Galápagos in the 1990's [22]. If the population slowly recovers, it would redistribute to first occupy high-quality coastal waters then adjacent areas [47], which may explain the modest and recent return to Galápagos waters documented here. In this scenario, the turnover of clans off the Galápagos would result from a general eastward movement: first of the *Regular* and *Plus-One* clans from the Galápagos to more coastal waters, and then of the *Four-Plus* and

Short clans from oceanic and northern waters to the Galápagos. The underlying assumption is that different cultural foraging strategies characteristic of each clan [17] performs similarly in different areas.

In both scenarios, the turnover of clans using Galápagos indicates that there may be social dynamics driving movement decisions. Group displacement implies a compromise between individual decision and group conformity [*e.g.* 48]. Thus, once some members of one clan have decided to leave a particular habitat, other members may choose to move with clan-mates rather than remain within that habitat—a within-clan gregariousness that could be mediated by specific codas identifying clan membership [27]. As associations with familiar conspecifics can facilitate acclimation to novel habitat [49], the benefits of foraging and associating with behaviourally similar clan members may outweigh the cost of displacement to a new habitat. This assumes that clan membership is important for the success of the individuals and social units that comprise them, which fits well with recent evidence that sperm whale movement decisions are shared [50] and that individuals conform to the predominant behaviour of clan members [30]. Overall, these findings show that tracking cultural traits can reveal large-scale population shifts, which further illustrates the key role culture can play in the structure and dynamics of animal populations and their communication systems.

5.5.2 Conclusions

Learned communication repertoires can be either stable across or change within generations in response to cultural selection and drift [51-53]; yet a population's repertoire is rarely completely replaced. We found an influx of immigrants from different cultural clans replacing those that used to be in the area decades ago. This local cultural turnover was an epiphenomenon of large-scale displacement of sperm whales organized by vocal clan, suggesting that clan structure is temporally stable but spatially flexible. The changes in sperm whale acoustic repertoires off Galápagos are clear, but the ultimate causes of this cultural turnover remain hypothetical. Unraveling the drivers of large-scale relocation of cultural groups will allow us to better understand animals' response to the changing ocean, the dynamics of depressed populations, and the importance of culture in animal societies.

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CHAPTER 6

CONCLUSIONS

"The most beautiful thing we can experience is the mysterious. It is the true source of all art and science. He to whom the emotion is a stranger, who can no longer pause to wonder and stand wrapped in awe, is as good as dead—his eyes are closed."

~ A. Einstein, 1930

In my thesis I posed the question on the interplay between animal society and culture, taking eastern Tropical Pacific sperm whales as a model. I investigated the causes, consequences and temporal stability of the highest level of their multilevel society—the vocal clans. I showed cultural processes giving rise to clans of sperm whales, which in turn affect the social behaviour of their members, in a two-way relationship that can be stable over temporal, but dynamic over spatial scales. This research fits within a formal conceptual framework of the study of the dynamic interactions between social structure and social learning in non-humans. My results on sperm whales strengthens the evidence for culture as a key aspect of their lives, as individuals, as members of family groups, and members of a larger population structured into sympatric cultural communities. These results further illustrate that important processes driving behavioural flexibility in humans—information transmission through biased social learning and cultural drift—can also operate in wild animal populations and structure their social relationships.

6.1. RESEARCH FINDINGS

6.1.1 Interplay: Society and Culture of Sperm Whales

Chapter 2 was set out to explore the reciprocal relationship between social structure and social learning, highlighting it as a wide-spread phenomenon, non-exclusive of human societies. I argued that social relationships define the content and the way information flows among individuals during social relationships, at the same time that social learning adjusts who socially interacts with whom. Using the formalism of adaptive networks (*e.g.* Gross & Blasius 2008), I delineated frameworks that organize the current findings in the topic, and also generate hypotheses to be later on confronted by data (Figures 2.1 and 2.4 in Chapter 2). While learning cultural behaviours during social relationships may be inherently tied to our lives, in my research I show the same two-way relationship playing a major role in the lives of cetaceans—especially sperm whales—shaping the large-scale structure of their societies.

6.1.2 Cause: Biased Social Learning

Sperm whales off the eastern Tropical Pacific are organized into sympatric clans of individuals with high similarity in their vocal communication repertoire (Rendell & Whitehead 2003). This is not only an emblematic example of culture structuring an animal society in the wild, but may be, potentially, the largest cooperative entity outside humans

(Whitehead & Rendell 2014). However, while the empirical pattern was clear, the literature was inconclusive about its causes. Chapter 3 sought to identify the underlying mechanisms giving rise to the vocal clans, and formally test the hypothesis of social learning being involved in the clan partition. It is logistically impossible to perform experiments over the large temporal and spatial scales relevant for the whales, so I developed a series of computer models in which virtual whale populations behave and live accordingly to the empirical rules observed for wild populations. Thus by trying to replicate the empirical pattern in the presence and absence of different transmission mechanisms of coda vocalization—individual learning, genetic inheritance, pure and biased social learning—I could backtrack the formation of clans to infer on its major drivers. I show that clans of whales with different dialects emerge when whales learn from each other, but in a specific way: conforming to the most similar individuals around them. So, on this side of the interplay, culture is a key ingredient in the partition of sperm whales into sympatric clans with different acoustic repertoires.

6.1.3 Consequence: Social Behaviour Diversity

Chapter 4 looked into the other side of the interplay—the consequences of clan membership for social behaviour. Using a long-term dataset, I found that the clan partition propels differences in a range of social metrics: individuals of one clan dived more synchronously and had more homogeneous and briefer relationships than the members of the other clan. I proposed cultural drift as a potential explanation for the such divergence—with individuals replicating the social norms experienced within their clans. Given that the social units are the fundamental social level in sperm whale societies, for which alloparental care giving is thought to be the primary driver (*e.g.* Gero *et al.* 2013), I speculated that differences in social relationship quality and duration, as well as surface time, can potentially cause differences in calf survival between clans. Much of what we know about mammal social learning and culture comes from foraging behaviour (*e.g.* Box & Gibson 1999). My findings expand the cultural divergence of sperm whales, by adding distinct social norms between clans. Combined with previous findings on movement and diet preferences (Whitehead & Rendell 2004, Marcoux *et al.* 2007), my results suggest that sperm whale culture is more diverse than previously recognized, encompassing a wider portion of their behavioural repertoire. This places sperm whales among few other animal species with rich, divergent cultural repertoires, such as primates (*e.g.* Whiten *et al.* 1999, van Schaik *et al.* 2003) and other cetaceans (*e.g.* Ford *et al.* 2000, Garland *et al.* 2011, Allen *et al.* 2013, Whitehead & Rendell 2014).

6.1.4 Stability: Temporal But Not Spatial

To this point, much of my research had been theoretical and/or based on previously collected data. By revisiting the sperm whales off the Galápagos Islands nearly thirty years after the start of behavioural studies (Chapter 5), I updated the current picture of the sperm whale societies using the waters off the archipelago with new empirical data. I documented the decline in occurrence of sperm whales off Galápagos through the 1990's, followed later by a slow return to these waters. This is a rare case of all individuals of a population being replaced by new ones; what is more, I found that the new individuals were members of different cultural clans. While the local population composition changed dramatically, the coda repertoires in the pool of sampled individuals in the Tropical

Pacific remained quite stable. Thus, I found that clan structure can be temporally stable, but spatially flexible. That is, sperm whales roam over very large areas but as members of long-lasting cultural clans. I hypothesize that such large-scale displacement of cultural clans could be a response to recent environment shifts, or to the collapse of the population following whaling in the area; but these remain hypotheses for future studies.

6.2. RESEARCH CONTRIBUTIONS

The outcomes of my thesis may be of interest of a wide portion of the academic community—from theoreticians interested in emergence of patterns in nature, to empiricists interested in the underlying mechanisms of social behaviour in the wild. I believe these findings are also relevant to a general audience beyond, interested in the lives of the enigmatic sperm whales. In what follows, I frame the specific contributions of my research into three different levels.

At the population level, my research adds important pieces to the unusual picture of sperm population structure that has emerged from studies of the eastern Tropical Pacific. After modern whaling decimated the population in the 1950's, 1960's and 1970's and uncertainty over the next few decades (Whitehead *et al.* 1997), my research brings good news. Sperm whales are persisting in the eastern Tropical Pacific, and show signs of return to areas where they were once abundant. As a cultural society, composed of matrilineally-based social units and clans, sperm whales have been roaming around the Tropical Pacific, eventually returning to the Galápagos archipelago.

At the species level, my research adds to our growing picture of sperm whale society: how much behaviour is culturally-driven, what factors contribute to the culturally-driven social patterns, how these patterns change over time and the implications they have for the social behaviour of the individuals. My findings provide new lines of evidence for social learning as a major driver of the large-scale structure of their populations, and added social behavioural variability to the diversity of their cultural repertoires. Taken together, these findings reinforce that membership of cultural groupings plays an important role in the structure and dynamics of sperm whale populations.

More broadly, my research contributes to the literature on animal culture, a much debated topic in academia. My findings illustrate and reinforce transmission of information as a source of phenotype diversity and behavioural flexibility, implying that proximate mechanisms occurring in shorter (few generations) time scales have profound implications for population and social structures of animals. By strengthening the hypotheses that culture is a source of intrapopulational variation in behaviour, and a driver of phenotypes, this research helps to bridge the unnecessarily large gap we have created between our conceptions of humans and other animals (*e.g.* Corbey & Lanjouw 2013).

6.3. LIMITATIONS AND THE WAY FORWARD

We may "never know a man to become as good at [distinguishing between individuals] as the animals themselves" (Timbergen 1953, pp. 108), let alone how they perceive each other, how they feel (Safina 2015) and what it means to be inside of an animal's mind (Gould 1998). The scientific advances in the fields of animal cognition, learning and sociality are remarkable; we think we already have a good—yet blurry and incomplete—picture of the cultural processes that operate in animal societies. But, truly, studying animal culture remains a challenge.

I learned throughout my research some of the numerous difficulties involved in studying societies and culture—starting with the basics, i.e. finding elusive animals in remote places. The amount of effort put by the research group over years in field work offshore is immense. The time invested in collecting data on sperm whales—months at the sea patiently waiting to hear the faintest clicks, spot a blow in the horizon; then making sure we keep tracking, recording, photographing the whales for as long as possible—and painstakingly processing these data in the lab is huge. The magnitude of the spatial and temporal scales relevant for sperm whales make it hard to eavesdrop informatively on their private lives. There are clear limitations in addressing culture and society of whales based on simulations and direct observations. At best, our approach provides sometimes sparse data—collected during short periods at the surface—other times cluttered data—during long periods of exchange of communication sounds among many whales underwater.

To afford a more comprehensive view of the mutual relationship of animal culture and societies, there is room for improvement in at least three basic aspects: collect more refined data, employ novel analytical methods, and consider other taxa. First, the more refined data one can get at the individual level, the better. The challenges of data collection are taxa-specific. The most used measure of social relationships in of vertebrates (and particularly in cetaceans) assumes the gambit-of-the-group, meaning individuals observed in close spatio-temporal proximity have had conditions to socially interact (Whitehead & Dufault 1999). This is a very useful proxy (*e.g.* Farine 2015) but it provides limited, coarse information on the content and quality of the social interactions (*e.g.* Castles *et al.* 2014) that ultimately make up the social structure of the population (Hinde 1976). Improving the recorded details of social interactions may not be much of a problem for species which behaviours are visible and easy to distinguish, such as terrestrial mammals. For cetaceans, new technologies for automated data collection (such as D-Tags, crittercams; *e.g.* Johnson & Tyack 2003, Calombokidis *et al.* 2007), are becoming increasingly available and promise to provide an incredibly detailed picture of how individuals behave and communicate above and underwater. However, these are still expensive and time-consuming techniques, so the number of sampled individuals is likely to be limited. More likely, observational studies may continue to provide the best quality of data at the individual level for many cetacean species in the near future (*e.g.* Mann *et al.* 2012, Gero *et al.* 2016). Continuing efforts to amass data in long-term field studies is imperative.

As individual identification data accumulate over the years, in addition to genetic, hormonal, behavioural information, we can begin to tease apart other drivers of social relationships of animals that may come along with learning and cultural processes (*e.g.* Whitehead 2009). These richer data can feed more sophisticated analytical tools to better describe social relationships (*e.g.* Whitehead & James 2015), social structure (*e.g.* Farine & Whitehead 2015) and account for other biological and ecological factors (*e.g.* Pinter-Wollman *et al.* 2013) that could mask whether aspects of the large-scale social structure are products of culture (*e.g.* Whitehead 2009, Mann *et al.* 2012). With long-term and detailed empirical data, network-based diffusion models on time-ordered data (*e.g.*

Hoppitt & Laland 2013) have been proven very powerful ways of tracking the spread of behaviours among individuals in the wild (*e.g.* Allen *et al.* 2013). Finally, experiments with natural populations can be great tools to test the function of a particular behaviour (*e.g.* through playback experiments; Sayigh *et al.* 1998) and if this behaviour is learned among conspecifics. For cetaceans, however, experiments in the wild are usually logistically challenging and some may be impractical—for instance seeding in a behavioural innovation to monitor how it spreads among social contacts (as done for primates and birds; *e.g.* Aplin *et al.* 2015, Whiten *et al.* 2016). Likewise, experiments removing the effect of a particular behaviour in a wild cetacean population is not only very difficult but ethically questionable. When a behavioural variation is naturally removed, one may be fortunate to test its effect on the social structure of a wild population without direct interference; although fortuitous, this approach is very revealing (*e.g.* Ansmann *et al.* 2012). Thus, theoretical work based on models and computer simulations—such set evolutionary theory (Tartina *et al.* 2011) and the agent-based modeling (Railsback & Grimm 2012) exercised in this thesis, to name a few—may continue to illuminate the dynamics of the interplay between social structure, learning, and their coevolution (see Nowak 2006).

Finally, the field will benefit from a broader investigation by increasing the number of taxa for which the interplay between society and culture is considered. Here I focused on oceanic examples, but I recommend the incorporation of culture in the context of social structure of any species for which social learning can drive behaviour; good candidates include birds, fish, terrestrial herbivore and carnivore mammals (*e.g.* Box & Gibson 1999, Laland & Hoppitt 2003). For some of these species, we are more likely to be able to directly test the interplay, for instance with diffusion and playback experiments (*e.g.* Whiten *et al.* 2016) both in captivity (*e.g.* Whiten *et al.* 2005) and in the wild (*e.g.* Aplin *et al.* 2015). Tying together observational, experimental, and theoretical work would be the ideal next leap for future studies; but meeting this agenda will not come without massive challenges.

6.4. CLOSING REMARKS

We have always "feared and worshipped, loved and hunted whales"—they are part of human cultures (*e.g.* Estes 2006, Sakakibara 2009). But there is still much debate as to whether culture is exclusive to humans (*e.g.* Laland & Galef 2009). My research strengthens the evidence for whales having their own kinds of culture (Rendell & Whitehead 2001), which is an important piece in the puzzle of the evolution of sociality. More personally, it fascinated me to see a society of completely different animals, living on a completely different environment, displaying key similarities with our own society. The outcomes of this work made me remember the similarities we have with other animals. Throughout the thesis I argued that similar individuals tend to interact—similarity breeds good relationships (*e.g.* McPherson *et al.* 2001). So I hope we improve our relationship with Nature before sperm whale societies, and other fascinating biological systems, are severely depleted.

The most obvious clash between human and whale cultures—the whaling industry—has already collapsed largely as a consequence of our societies' greedy decisions. But the destructive potential of our culture is far from finished. Culture, undoubtedly, equipped humans with unparalleled means to live abundantly in every corner of the planet (*e.g.* Boyd *et al.* 2011, Marean 2015)—this is arguably what distinguishes us from other life forms (*e.g.* Boyd & Richerson 1996, Tomasello 1999). I posit that just possessing culture may not be what makes us humans different; it may be the leftovers of our cultural decisions. Surely our culture is more complex, diverse and cumulative than other animals' (*e.g.* Tomasello 1999, Tennie *et al.* 2009). And so are its negative consequences.

Our culture promotes, directly and indirectly, many threats to the entire biosphere. This is not news to anyone: humans have caused rapid, drastic changes in all ecosystems (*e.g.* Estes *et al.* 2011), perhaps even triggering a sixth mass extinction (*e.g.* Koch & Barnosky 2006, Wake & Vredenburg 2008, Yeakel *et al.* 2014) and changing the pace of evolution (Palumbi 2002). Global warming (*e.g.* Whitehead *et al.* 2008, Cai *et al.* 2014), resource overexploitation (*e.g.* Myers & Worm 2003, Worm *et al.* 2006), noise and chemical pollution (*e.g.* Weilgart 2007, Jambeck *et al.* 2015)—to cite few perils—are increasingly threatening life on land and in the ocean, including the pelagic ecosystems whose remoteness may make them be erroneously perceived as pristine or of least concern.

Throughout the thesis, I also emphasized the importance of the individual, and individual behaviour. Individual actions may seem minor in comparison to the magnitude of the problems our society causes to nature; but yet these actions can, collectively, help to alleviate some of these major problems (*e.g.* Springmann *et al.* 2016). Let us learn from predecessors: our technological culture may not keep us insulated from environmental problems for as long as we hope (Diamond 2005, 2012). If culture makes humans change and adapt (Boyd *et al.* 2011), then it is time for us to change again. Minimizing, at least retarding, the malign by-products of our cultural behaviour is urgent. So may our minds be open to refrain from unsustainable life styles; may our eyes be open to look into Nature and wonder in awe with that Thoreauvian sympathy.

BIBLIOGRAPHY

CHAPTER 1

Allen, J., Weinrich, M., Hoppitt, W. and Rendell, L. 2013. Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. Science 340:485-488.

Amaral, L.A. and Ottino, J.M. 2004. Complex networks. The European Physical Journal B-Condensed Matter and Complex Systems 38:47-162.

Ansmann, I.C., Parra, G.J., Chilvers, B.L. and Lanyon, J.M. 2012. Dolphins restructure social system after reduction of commercial fisheries. Animal Behaviour 84:575-581.

Araújo, M.S., Bolnick, D.L. and Layman, C.A. 2011. The ecological causes of individual specialisation. Ecology Letters 14:948-958.

Arnbom, T., Papastavrou, V., Weilgart, L.S. and Whitehead, H. 1987. Sperm whales react to an attack by killer whales. Journal of Mammalogy 68: 450-453

Avital, E. and Jablonka, E. 2000. Animal traditions: Behavioural inheritance in evolution. Cambridge University Press.

Axelrod, R. 1997. The dissemination of culture: a model with local convergence and global polarization. Journal of Conflict Resolution 41:203-226.

Bentley, R.A., Lipo, C.P., Herzog, H.A. and Hahn, M.W. 2007. *Regular* rates of popular culture change reflect random copying. Evolution and Human Behavior 28:151-158.

Bentley, R.A., Hahn, M.W. and Shennan, S.J. 2004. Random drift and culture change. Proceedings of the Royal Society of London B 271:1443-1450.

Bergman, T.J. and Beehner, J.C. 2015. Measuring social complexity. Animal Behaviour 103:203-209.

Biro, D., Sousa, C. and Matsuzawa, T. 2006. Ontogeny and cultural propagation of tool use by wild chimpanzees at Bossou, Guinea: case studies in nut cracking and leaf folding. In: Cognitive development in chimpanzees (Matsuzawa, T., Tomonaga, M. and Tanaka, M., eds). Springer. 476-508pp.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H., Schreiber, S.J., Urban, M.C. and Vasseur, D.A. 2011 Why intraspecific trait variation matters in community ecology. Trends in Ecology Evolution 26:183-192.

Boran, J.R., and Heimlich, S.L. 1999. Social learning in cetaceans: hunting, hearing, hierarchies. In: Mammalian social learning: comparative and ecological perspectives (Box, H.O. and Gibson, K.R., eds). Cambridge University Press. 282-307pp.

Boyd, R. and Richerson, P.J. 2004. The origin and evolution of cultures. Oxford University Press.

Boyd, R. and Richerson, P.J. 1987. The evolution of ethnic markers. Cultural Anthropology 2:65-79.

Boyd, R. and Richerson, P. 1985. Culture and the evolutionary process. Chicago University Press.

Boyd, R., Richerson, P. and Henrich, J. 2011. The cultural niche: Why social learning is essential for human adaptation. Proceedings of the National Academic of Sciences USA 108:10918–10925

Braidwood, R.J. 1975. Prehistoric Men. Scott, Foresman and Company.

Bruck, J.N. 2013. Decades-long social memory in bottlenose dolphins. Proceedings of the Royal Society of London B 280:20131726

Byers, B.E., Belinsky, K.L. and Bentley, R.A. 2010. Independent cultural evolution of two song traditions in the chestnut-sided warbler. American Naturalist 176:476-489.

Camazine, S., Deneubourg, J.L., Franks, N.R., Sneyd, J., Theraula, G. and Bonabeau, E. 2001. Self-organization in biological systems. Princeton University Press.

Cantor, M. and Whitehead, H. 2013. The interplay between social networks and culture: theoretically and among whales and dolphins. Philosophical Transactions of the Royal Society of London B 368:20120340.

Cantor, M., Wedekin, L.L., Guimarães, P.R., Daura-Jorge, F.G., Rossi-Santos, M.R. and Simões-Lopes, P.C. 2012. Disentangling social networks from spatiotemporal dynamics: the temporal structure of a dolphin society. Animal Behaviour 84:641-651.

Castellano, C., Fortunato, S. and Loretto, V. 2009. Statistical physics of social dynamics. Reviews of Modern Physics 81:591-646.

Cassirer, E. 1944. An essay on man. Yale University Press.

Cavalli-Sforza, L.L. and Feldman, M.W. 1981. Cultural transmission and evolution: a quantitative approach. Princeton University Press.

Centola, D., Gonzalez-Avella, J.C., Eguiluz, V.M. and San Miguel, M. 2007. Homophily, cultural drift and the co-evolution of cultural groups. Journal of Conflict Resolution 51:905-929.

Christal, J. and Whitehead, H. 2001. Social affiliations within sperm whale (*Physeter macrocephalus*) groups. Ethology 107:323-340.

Christal, J., Whitehead, H. and Lettevall, E. 1998. Sperm whale social units: variation and change. Canadian Journal of Zoology 76:1431-1440

Clutton-Brock, T.H. 1989. Review lecture: mammalian mating systems. Proceedings of the Royal Society of London B 236:339-372.

Connor, R.C. 2000. Group living in whales and dolphins. In: Cetacean societies (Mann, J., Connor, R.C., Tyack, P.L. and Whitehead, H., eds). University of Chicago Press, Chicago. 199-218pp.

Connor, R.C., Mann, J., Tyack, P.L., Whitehead, H. 1998. Social evolution in toothed whales. Trends in Ecology and Evolution 13:228-232.

Coussi-Korbel, S. and Fragaszy, D.M. 1995. On the relation between social dynamics and social learning. Animal Behaviour 50:1441-1453.

Crossin, G.T., Phillips, R.A., Lattin, C.R., Romero, L.M. and Williams, T.D. 2013. Corticosterone mediated costs of reproduction link current to future breeding. General & Comparative Endocrinology 193:112-120.

Curio, E., Ernst, U. and Vieth, W.,1978. Cultural transmission of enemy recognition: one function of mobbing. Science 202:899-901.

Daura-Jorge, F.G., Cantor, M., Ingram, S.N., Lusseau, D. & Simões-Lopes, P.C. 2012. The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. Biology Letters 8:702-705.

Deecke, V.B., Ford, J.K.B., and Spong, P. 2000. Dialect change in resident killer whales: implications for vocal learning and cultural transmission. Animal Behavious 60:629–638.

Dunbar, R.I. and Shultz, S. 2007. Evolution in the social brain. Science 317:1344-1347.

Duboscq, J., Romano, V., MacIntosh, A. and Sueur, C. 2016. Social Information Transmission in Animals: Lessons from Studies of Diffusion. Frontiers in Psychology 7:1147.

Fayet, A.L., Tobias, J.A., Hintzen, R.E. and Seddon, N. 2014. Immigration and dispersal are key determinants of cultural diversity in a songbird population. Behavioral Ecology 25:744-753.

Filatova, O.A. and Miller, P.J. 2015. An agent-based model of dialect evolution in killer whales. Journal of Theoretical Biology 373:82-91.

Filatova, O.A., Miller, P.J., Yurk, H., Samarra, F.I., Hoyt, E., Ford, J.K., Matkin, C.O. and Barrett-Lennard, L.G. 2015. Killer whale call frequency is similar across the oceans, but varies across sympatric ecotypes. Journal of the Acoustic Society of America 138:251-257.

Ford, J.K.B. 1991. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Canadian Journal of Zoology 69:1454-1483.

Ford, J.K.B., Ellis, G.M., Barrett-Lennard, L.G., Morton, A.B., Palm, R.S. and Balcomb III, K.C. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Canadian Journal of Zoology 76:14-56-1471.

Frank, S.A. 1998. Foundations of social evolution. Princeton University Press.

Frantzis, A. and Alexiadou, P. 2008. Male sperm whale (*Physeter macrocephalus*) coda production and coda-type usage depend on the presence of conspecifics and the behavioural context. Canadian Journal of Zoology 86:62–75.

Franz, M. and Nunn, C.L. 2009. Rapid evolution of social learning. Journal Evolutionary Biology 22:1914-1922.

Freeberg, T.M., Dunbar, R.I. and Ord, T.J. 2012. Social complexity as a proximate and ultimate factor in communicative complexity. Philosophical Transactions of the Royal Society of London B 367:1785-1801.

Garland, E.C., Goldizen, A.W., Rekdahl, M.L., Constantine, R., Garrigue, C., Hauser, N.D., Poole, M.M., Robbins, J. and Noad, M.J. 2011. Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. Current Biology 21:687-691.

Gero, S. and Rendell, L. 2015. Oceanic societies: studying cetaceans with a social network approach. In: Animal social networks (Krause, J., James, R., Franks, D.W. and Croft, D.P., eds). Oxford University Press. 139-149pp.

Gero, S., Whitehead, H. and Rendell, L. 2016a. Individual, unit, and vocal clan level identity cues in sperm whale codas. Royal Society Open Science 3:150372.

Gero, S., Bøttcher, A., Whitehead, H., and Madsen, P.T. 2016b. Socially segregated, sympatric sperm whale clans in the Atlantic Ocean. Royal Society Open Science 3:160061.

Gero, S., Milligan, M., Rinaldi, C., Francis, P., Gordon, J., Carlson, C., Steffen, A., Tyack, P., Evans, P. and Whitehead, H. 2014. Behavior and social structure of the sperm whales of Dominica, West Indies. Marine Mammal Science 30:905-922.

Gero, S., Gordon, J. and Whitehead, H. 2013. Calves as social hubs: dynamics of the social network within sperm whale units. Proceedings of the Royal Society B 280:20131113.

Gero, S., Engelhaupt, D., Rendell L. and Whitehead, H. 2009. Who Cares? Between-group variation in alloparental care-giving in sperm whales. Behavioral Ecology 20: 838-843.

Gowans, S., Würsig, B. and Karczmarski, L. 2007. The social structure and strategies of delphinids: Predictions based on an ecological framework. Advances in Marine Biology 53:195-294.

Hahn, M.W. and Bentley, R.A. 2003. Drift as a mechanism for cultural change: an example from baby names. Proceedings of the Royal Society of London B 270:S120-S123.

Hamilton, W.D. 1964. The genetical evolution of social behaviour II. Journal of Theoretical Biology 7:17-52.

Hemelrijk, C. 2005. Self-organisation and evolution of biological and social systems. Cambridge University Press.

Heyes, C.M. 1994. Social learning in animals: categories and mechanisms. Biological Review 69:207-231.

Hinde, R.A. 1976. Interactions, relationships and social structure. Man 11:1-17.

Hoppitt, W. and Laland, K.N. 2008. Social processes influencing learning in animals: a review of the evidence. Advances in the Study of Behavior 38:105-165.

Horn, A.G. and Leonard, M.L. 2005. Nestling begging as a communication network. In: Animal communication networks (McGregor, P., ed). Cambridge University Press. 170-190pp.

Jablonka, E. and Lamb, M.J. 2014. Evolution in four dimensions, revised edition: genetic, epigenetic, behavioral, and symbolic variation in the history of life. MIT press.

Janik, V.M. 2005. Underwater acoustic communication networks in marine mammals. In: Animal Communication Networks (McGregor, P., ed). Cambridge University Press. 390-415pp.

Janik, V.M.,2014. Cetacean vocal learning and communication. Current Opinion in Neurobiology 28:60-65.

Janik, V.M. and Slater, P.J. 2000. The different roles of social learning in vocal communication. Animal Behaviour 60:1-11.

Jaquet, N. 1996. How spatial and temporal scales influence understanding of sperm whale distribution: a review. Mammal Review 26:51-65.

Ji, L.J. and Yap, S. 2016. Culture and cognition. Current Opinion in Psychology 8:105-111.

Kappeler, P.M., Barret, L. Blumstein, D.T. and Clutton-Brock, T.H. 2013. Constraints and flexibility in mammalian social behaviour: introduction. Philosophical Transactions of the Royal Society B 368:20120337.

King, S.L. and Janik, V.M. 2015. Come dine with me: food-associated social signalling in wild bottlenose dolphins (*Tursiops truncatus*). Animal cognition 18:969-974.

King, S.L., Harley, H.E. and Janik, V.M. 2014. The role of signature whistle matching in bottlenose dolphins, *Tursiops truncatus*. Animal Behaviour 96:79-86.

King, S.L. and Janik, V.M. 2013. Bottlenose dolphins can use learned vocal labels to address each other. Proceedings of the National Academy of Sciences 110:13216-13221.

King, S.L., Sayigh, L.S., Wells, R.S., Fellner, W. and Janik, V.M. 2013. Vocal copying of individually distinctive signature whistles in bottlenose dolphins. Proceedings of the Royal Society of London B 280:20130053.

Kirby, S., Tamariz, M., Cornish, H. and Smith, K. 2015. Compression and communication in the cultural evolution of linguistic structure. Cognition 141:87-102.

Koerper, H.C. & Stickel, *E.G.* 1980. Cultural drift: a primary process of culture change. Journal of Anthropological Ressearch 36:463-469.

Krause, J. and Ruxton, G.D. 2002. Living in groups. Oxford University Press.

Krause, J., James, R. and Croft, D.P. 2010. Personality in the context of social networks. Philosophical Transactions of the Royal Society of London B 365:4099-4106.

Krebs JR, Kroodsma DE. 1980 Repertoires and geographical variation in bird song. Advances in the Study of Behaviour 11:143-177.

Laland, K.N. 2004. Social learning strategies. Animal Learning & Behavior 32:4-14.

Laland, K.N. and O’Brien, M.J. 2012. Cultural niche construction: an introduction. Biological Theory 6:191-202.

Laland, K.N. and Galef, B.G. 2009. The question of animal culture. Harvard University Press.

Laland, K.N. and Janik, V.M. 2006. The animal cultures debate. Trends in Ecology & Evolution 21:542-547.

Laland, K.N. and Hoppitt, W. 2003. Do animals have culture? Evolutionary Anthropology 12:150-159.

Laland, K.N., Odling-Smee, J. and Myles, S., 2010. How culture shaped the human genome: bringing genetics and the human sciences together. Nature Reviews Genetics 11:137-148.

Laland, K.N., Odling-Smee, J. and Feldman, M.W. 2001. Cultural niche construction and human evolution. Journal of Evolutionary Biology 14:22-33.

Laland, K., Uller, T., Feldman, M., Sterelny, K., Müller, G.B., Moczek, A., Jablonka, E., Odling-Smee, J., Wray, G.A., Hoekstra, H.E. and Futuyma, D.J. 2014. Does evolutionary theory need a rethink? Nature 514:161-164.

Lefebvre, L., Reader, S.M. and Sol, D. 2004. Brains, innovations and evolution in birds and primates. Brain, Behavior and Evolution 63:233-246.

Lehner, P.N. 1998. Handbook of ethological methods. Cambridge University Press.

Lopez, J.C. and Lopez, D. 1985. Killer whales (*Orcinus orca*) of Patagonia, and their behavior of intentional stranding while hunting near shore. Journal of Mammalogy 66:181-183.

Lott, D. L. 1984. Intraspecific variation in the social systems of wild vertebrates. Behaviour 88:266-325.

Lusseau, D., Wilson, B., Hammond, P.S., Grellier, K., Durban, J.W., Parsons, K.M., Barton, T.R. and Thompson, P.M. 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. Journal of Animal Ecology 75:14–24.

Lyrholm, T., Leimar, O., Johanneson, B. and Gyllensten, U. 1999. Sex–biased dispersal in sperm whales: contrasting mitochondrial and nuclear genetic structure of global populations. Proceedings of the Royal Society of London B 266:347-354.

Mann, J,, Stanton, M.A., Patterson, E.M., Bienenstock, E.J. and Singh, L.O. 2012. Social networks reveal cultural behaviour in tool-using using dolphins. Nature Communications 3: 980.

Mann, J., Connor, R.C., Tyack, P.L. and Whitehead, H. 2000. Cetacean societies. Chicago University Press.

Marino, L., Connor, R.C., Fordyce, R.E., Herman, L.M., Hof, P.R., Lefebvre, L., Lusseau, D., McCowan, B., Nimchinsky, E.A., Pack, A.A., Rendell, L., Reidenberg, J.S., Reiss, D., Uhen, M.D., Van der Gucht, E. and Whitehead, H. 2007. Cetaceans have complex brains for complex cognition. PLoS Biology 5:e139.

Marshall-Pescini, S. and Whiten, A. 2008. Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: an experimental approach. Animal Cognition 11:449-456.

Matsuzawa, T., Tomonaga, M. and Tanaka, M. 2006. Cognitive development in Chimpanzees. Springer.

May-Collado, L.J., Agnarsson, I. and Wartzok, D. 2007. Phylogenetic review of tonal sound production in whales in relation to sociality. BMC Evolutionary Biology 7:136.

McGregor, P.K. 2005. Animal communication networks. Cambridge University Press.

McGregor, P.K. and Horn, A. 2015. Communication and social networks. In: Animal social networks (Krause, J., James, R., Franks, D.W. and Croft, D.P., eds). Oxford University Press. 84-94pp.

McPherson, M., Smith-Lovin, L. and Cook, J.M. 2001. Birds of a feather: homophily in social networks. Annual Review of Sociology 27:415-44.

Mesoudi, A., Magid, K. and Hussain, D. 2016. How Do People Become WEIRD? Migration reveals the cultural transmission mechanisms underlying variation in psychological processes. PloS One 11: e0147162.

Mesoudi, A. 2011. Cultural evolution: how Darwinian theory can explain human culture and synthesize the social sciences. University of Chicago Press.

Morgan, T.J.H. and Laland, K.N. 2012. The biological bases of conformity. Frontiers in Neuroscience 6:87.

Nelson, D.A., Hallberg, K.I. and Soha, J.A. 2004. Cultural evolution of Puget sound white-crowned sparrow song dialects. Ethology 110:879-908.

Noad, M.J., Cato, D.H., Bryden, M.M., Jenner, M.N. and Jenner, K.C.S. 2000. Cultural revolution in whale songs. Nature 408:537-537.

Norenzayan, A. 2011. Explaining human behavioral diversity. Science 332:1041-1042.

Nunn, C.L., Thrall, P.H., Bartz, K., Dasgupta, T. and Boesch, C. 2009. Do transmission mechanisms or social systems drive cultural dynamics in socially structured populations? Animal Behaviour 77:1515-1524.

Oliveira, R. 2005. Hormones, social context and animal communication. In: Animal Communication Networks (McGregor, P., ed). Cambridge University Press. 481-519pp.

Patterson, E.M., Krzyszczyk, E. and Mann, J. 2015. Age-specific foraging performance and reproduction in tool-using wild bottlenose dolphins. Behavioral Ecology 164. doi: 10.1093/beheco/arv164

Perreault, C. 2012. The pace of cultural evolution. Plos One 7: e45150.

Perreault, C., Moya, C. and Boyd, R. 2012. A bayesian approach to the evolution of social learning. Evolution and Human Behaviour 33:449-459.

Perry, S. 2009. Are nonhuman primates likely to exhibit cultural capacities like those of humans. In: The question of animal culture (Laland, K.N. and Galef, B.G., eds) Harvard University Press. 247-268pp.

Pitman, R.L. and Durban, J.W. 2012. Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. Marine Mammal Science 28:16-36.

Podos, J. and Warren, P.S. 2007. The evolution of geographic variation in birdsong. Advances in the Study of Behavior 37:403-458.

Rendell, L. and Whitehead, H. 2003. Vocal clans in sperm whales (*Physeter macrocephalus*). Proceedings of the Royal Society B 270:225-231.

Rendell, L. and Whitehead, H. 2001. Culture in whales and dolphins. Behavioral Brain Sciences 24:309-324.

Rendell, L., Mesnick, S.L., Dalebout, M.L., Burtenshaw, J. and Whitehead, H. 2012. Can genetic differences explain vocal dialect variation in sperm whales, *Physeter macrocephalus*? Behavior Genetics 42:332-343.

Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M.W., Fogarty, L., Ghirlanda, S., Lillicrap, T. and Laland, K.N. 2010. Why copy others? Insights from the social learning strategies tournament. Science 328:208-213.

Rendell, L., Fogarty, L., Hoppitt, W.J., Morgan, T.J., Webster, M.M., Laland, K.N. 2011. Cognitive culture: theoretical and empirical insights into social learning strategies. Trends in cognitive sciences 15:68-76.

Rice, D.W. 1989. Sperm whale *Physeter macrocephalus* Linnaeus, 1758. In: Handbook of Marine Mammals. 177-233 pp.

Richard, K. R., Dillon, M.C., Whitehead, H. and Wright, J.M. 1996. Patterns of kinship in groups of free-living sperm whales (*Physeter macrocephalus*) revealed by multiple molecular genetic analyses. Proceedings of the National Academy of Science USA 93:8792-8795.

Richerson, P.J. and Boyd, R. 2005. Not by genes alone: How culture transformed human evolution. Chicago University Press.

Schradin, C. 2013. Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. Philosophical Transactions of the Royal Society B 368:20120346.

Schulz, T., Whitehead, H., Gero, S. and Rendell, L. 2008. Overlapping and matching of codas in vocal interactions between sperm whales: insights into communication function. Animal Behaviour 76:1977-1988.

Sih, A., Cote, J., Evans, M., Fogarty, S. and Pruitt, J. 2012. Ecological implications of behavioural syndromes. Ecology Letters 15:278–289.

Simões-Lopes, P.C., Fabián, M.E. & Menegheti, J.O. 1998. Dolphin interactions with the mullet artisanal fishing on southern Brazil: a qualitative and quantitative approach. Revista Brasileira de Zoologia 15:709-726.

Slabbekoorn, H. and Boer-Visser, A. 2006. Cities change the songs of birds. Current Biology 16:2326-2331.

Slater, P.J.B. and Ince, S.A. 1979. Cultural evolution in chaffinch song. Behaviour 71:146-166.

Smith J.N., Goldizen, A.W., Dunlop, R.A., and Noad, M.J. 2008. Songs of male humpback whales, *Megaptera novaeangliae*, are involved in intersexual interactions Animal Behaviour 76:467–477

Smuts, B.B., Cheney, D.L., Seyfarth, R.M. and Wrangham, R.W. 2008. Primate societies. University of Chicago Press.

Tamariz, M. and Kirby, S. 2016. The cultural evolution of language. Current Opinion in Psychology 8:37-43.

Tanaka, T., Sugiura, H. and Masataka, N. 2006. Cross-sectional and longitudinal studies of the development of group differences in acoustic features of coo calls in two groups of japanese macaques. Ethology 112:7-21.

Tennie, C., Call, J. and Tomasello, M. 2009. Ratcheting up the ratchet: on the evolution of cumulative culture. Philosophical Transactions of the Royal Society of London B 364:2405-2415.

Tinbergen, J. 1953. Social behaviour in animals: with special reference to vertebrates. Methuen & Co.

Tobias, J.A., Aben, J., Brumfield, R.T., Derryberry, E.P., Halfwerk, W., Slabbekoorn, H. and Seddon, N, 2010. Song divergence by sensory drive in Amazonian birds. Evolution 64: 2820-2839.

Tyack, P.L. 1998. Acoustic communication under the sea. In: Animal acoustic communication: Sound analysis and research methods (Hopp, S.L., Owren, M.J. and Evans, C.S., eds.). Springer Berlin Heidelberg. 163-220pp.

van Schaik, C.P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C.D., Singleton, I., Suzuki, A., Utami, S.S. and Merrill, M. 2003. Orangutan cultures and the evolution of material culture. Science 299:102-105.

Voelkl, B. and Noë, R. 2010. Simulation of information propagation in real-life primate networks: Longevity, fecundity, fidelity. Behavioral Ecology and Sociobiology 64:1449-1459.

Voelkl, B. and Noë, R. 2008 The influence of social structure on the propagation of social information in artificial primate groups: A graph-based simulation approach. Journal of Theoretical Biology 252:77-86.

Watkins, W.A. and Schevill, W.E. 1977. Sperm whale codas. The Journal of the Acoustical Society of America 62:1485-1490.

Weaver, W. 1948. Science and complexity. American Scientist 36: 536-544.

Williams, H., Levin, I.I., Norris, D.R., Newman, A.E. and Wheelwright, N.T. 2013. Three decades of cultural evolution in Savannah sparrow songs. Animal Behaviour 8:213-223.

Wilson, E.O. 1975. Sociobiology: The New Synthesis. Cambridge.

White, D.J., Gersick, A.S. and Snyder-Mackler, N. 2012. Social networks and the development of social skills in cowbirds. Philosophical Transactions of the Royal Society B 367:1892-1900.

Whitehead, H. 2008a. Social and cultural evolution in the ocean: Convergences and contrasts with terrestrial systems. In: The Deep Structure of Biology (Conway-Morris, S. ed.). Templeton Foundation Press. 143-160pp.

Whitehead, H. 2008b. Analyzing animal societies: Quantitative methods for vertebrate social analysis. Chicago University Press.

Whitehead, H. 200. Sperm whales: Social evolution in the ocean. Chicago University Press.

Whitehead, H. 1989. Foraging formations of Galápagos sperm whales. Canadian Journal of Zoology 67:2131-2139.

Whitehead, H. and Rendell, L. 2014. The cultural lives of whales and dolphins. University of Chicago Press.

Whitehead, H. and Lusseau, D. 2012. Animal social networks as substrate for cultural behavioural diversity. Journal of Theoretical Biology 294:19–28.

Whitehead, H. and Richerson, P. 2009. The evolution of conformist social learning can cause population collapse in realistically variable environments. Evolution and Human Behaviour 30:261–273.

Whitehead, H. and Weilgart, L.S. 1991. Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. Behaviour 118:275-296.

Whitehead, H. and Arnbom, T. 1987. Social organization of sperm whales off the Galápagos Islands, February-April 1985. Canadian Journal of Zoology 65:913-919.

Whitehead. H, Antunes, R., Gero, S., Wong, S.N.P., Engelhaupt, D. and Rendell, L. 2012. Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: Why are they so different? International Journal of Primatology 33:1142-1164.

Whitehead, H., Waters, S. and Lyrholm, T. 1991. Social organization in female sperm whales and their offspring: constant companions and casual acquaintances. Behavioral Ecology and Sociobiology 29:385-389.

Whiten, A. and Whiten, A. 2011. The scope of culture in chimpanzees, humans and ancestral apes. Philosophical Transactions of the Royal Society B 366:997-1007.

Whiten, A., Caldwell, C.A. and Mesoudi, A. 2016. Cultural diffusion in humans and other animals. Current Opinion in Psychology 8:15-21.

Whiten, A., Horner, V. and de Waal, F.B.M. 2005. Conformity to cultural norms of tool use in chimpanzees. Nature 437:737-740.

Whiten, A, Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.*E.G.* Wrangham, R.W. and Boesch, C. 1999. Cultures in Chimpanzees Nature 399:682–685.

Wolf, M. and Weissing, F.J. 2012. Animal personalities: consequences for ecology and evolution. Trends in Ecology and Evolution 27:452-461.

CHAPTER 2

1. Kappeler, P. M., Barret, L. Blumstein, D. T. & Clutton-Brock, T. H. 2013 Introduction: Constraints and flexibility in mammalian social behaviour: introduction and synthesis *Phil. Trans. R. Soc. B,* **368**. 20120337. doi: 10.1098/rstb.2012.0337.

2. Ghalambor, C. K., McKay, J. K., Carroll, S. P. & Reznick, D. N. 2007 Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Func. Ecol.* **21**, 394-407. (doi: 10.1111/j.1365-2435.2007.01283.x)
3. Laland, K. N. & O'Brien, M. J. 2012 Cultural niche construction: an introduction. *Biol. Theory.* (doi: 10.1007/s13752-012-0026-6)
4. Via, S., Gomulkiewicz, R., DeJong, G., Scheiner, S. M., Schlichting, C. D. & Van Tiendern, P. H. 1995 Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol. Evol.* **10**, 212-217. (doi: 10.1016/S0169-5347(00)89061-8)
5. Boyd, R. & Richerson, P. J. 1985 *Culture and the Evolutionary Process*. Chicago University Press.
6. Agrawal, A. A. 2001 Phenotypic plasticity in the interactions and evolution of species. *Science*. **294**, 321-326. (doi: 10.1126/science.1060701)
7. Henrich, J. & McElreath, R. 2003 The evolution of cultural evolution. *Evol. Anthropol.* **12**, 123-135. (doi: 10.1002/evan.10110)
8. Laland, K. N. 2004 Social learning strategies. *Learn. Behav.* **32**, 4-14. (doi: 10.3758/BF03196002)
9. Perreault, C., Moya, C. & Boyd, R. 2012 A Bayesian approach to the evolution of social learning. *Evol. Hum. Behav.* **33**, 449-459. (doi: 10.1016/j.evolhumbehav.2011.12.007)
10. Heyes, C. M. 1994 Social learning in animals: categories and mechanisms. *Biol. Rev.* **96**, 207-231. (doi: 10.1111/j.1469-185X.1994.tb01506.x)

11. Franz, M. & Nunn, C. L. 2009 Rapid evolution of social learning. *J. Evol. Biol.* **22**, 1914-1922. (doi: 10.1111/j.1420-9101.2009.01804.x)
12. Laland, K. N. & Hoppitt, W. 2003 Do animals have culture? *Evol. Anthropol.* **12**, 150-159. (doi: 10.1002/evan.10111)
13. Norenzan, A. 2011 Explaining human behavioral diversity. *Science* **332**, 1041-1042. (doi: 10.1126/science.1207050)
14. Croft, D. P., James, R. & Krause, J. 2008 *Exploring animal social networks*. Princeton, New Jersey: Princeton University Press.
15. Voelkl, B. & Nöe, R. 2010 Simulation of information propagation in real-life primate networks: longevity, fecundity, fidelity. *Behav. Ecol. Sociobiol.* **64**, 1449-1459. (doi: 10.1007/s00265-010-0960-x)
16. Voelkl, B. & Nöe, R. 2008 The influence of social structure on the propagation of social information in artificial primate groups: a graph-based simulation approach. *J. Theor. Biol.* **252**, 77-86. (doi: 10.1016/j.jtbi.2008.02.002)
17. Whitehead, H. & Lusseau, D. 2012 Animal social networks as substrate for cultural behavioural diversity. *J. Theor. Biol.* **294**, 19-28. (doi: 10.1016/j.jtbi.2011.10.025)
18. Hinde, R. A. 1976 Interactions, relationships and social structure. *Man* **11**, 1-17.
19. Boccaletti, S., Latora, V., Moreno, Y., Chavez, M. & Hwang, D. U. 2006 Complex networks: structure and dynamics. *Phys. Rep.* **424**, 175-308. (doi: 10.1016/j.physrep.2005.10.009)
20. Axelrod, R. 1997 The dissemination of culture: a model with local convergence and global polarization. *J. Confl. Resol.* **41**, 203-226. (doi: 10.1177/0022002797041002001)

21. McPherson, M., Smith-Lovin, L. & Cook, J. M. 2001 Birds of a feather: homophily in social networks. *Annu. Rev. Sociol*. **27**, 415-44.

22. Centola, D., González-Avella, J. C., Eguíluz, V. M. & San Miguel, M. 2007 Homophily, cultural drift, and the co-evolution of cultural groups. *J. Conflict Resol*. **51**, 905-929. (doi: 10.1177/0022002707307632)

23. Morgan, T. J .H. & Laland, K. N. 2012 The biological bases of conformity. *Front. Neurosci*. (doi: 10.3389/fnins.2012.00087)

24. Boyd, R. & Richerson, P. J. 1987 The evolution of ethnic markers. *Cult. Anthrop*. **2**, 65-79. (doi: 10.1525/can.1987.2.1.02a00070)

25. Gross, T. & Blasius, B. 2008 Adaptive coevolutionary networks: a review. *J. R. Soc. Interface* **5**, 259-271. (doi: 10.1098/rsif.2007.1229)

26. Castellano, C., Fortunato, S. & Loretto, V. 2009 Statistical physics of social dynamics. *Rev. Mod. Phys.* **81**, 591-646. (doi: 10.1103/RevModPhys.81.591)

27. Zimmermamm, M. G., Eguíluz, V. M. & San Miguel, M. 2004 Coevolution of dynamical states and interactions in dynamic networks. *Phys. Rev. E* **69**, 065102. (doi: 10.1103/PhysRevE.69.065102)

28. Holme, P. & Newman, M. E .J. 2006 Nonequilibrium phase transition in the coevolution of networks and opinions. *Phys. Rev. E* **74**, 056108. (doi: 10.1103/PhysRevE.74.056108)

29. Grabowski, A. & Kosiński, R. A. 2006 Evolution of a social network: the role of cultural diversity. *Phys. Rev. E* **73**, 016135. (doi: 10.1103/PhysRevE.73.016135)

30. Bryden, J., Funk, S., Geard, N., Bullock, S. & Jansen, V. A. A. 2011 Stability in flux: community structure in dynamic networks. *J. Roy. Soc. Interface* **8**, 1031-1040. (doi: 10.1098/rsif.2010.0524)

31. Skyrms, B. & Pemantle, R. 2000 A dynamic model of social network formation. *Proc.Natl. Acad. Sci. USA*. **97**, 9340-9346. (doi: 10.1073/pnas.97.16.9340)

32. Rosvall, M. & Sneppen, K. 2006 Modeling self-organization of communication and topology in social networks. *Phys. Rev. E* **74**, 016108. (doi: 10.1103/PhysRevE.74.016108)

33. Rosvall, M. & Sneppen, K. 2009 Reinforced communication and social navigation generate groups in model networks. *Phys. Rev. E* **79**, 026111. (doi: 10.1103/PhysRevE.79.026111)

34. Deffuant, G., Neau, D., Amblard, F. & Weisbuch, G. 2000 Mixing beliefs among interacting agents. *Adv. Comp. System* **3**, 87-98.

35. Lusseau, D., Whitehead, H. & Gero, S. 2008 Incorporating uncertainty into the study of animal social networks. *Anim. Behav*. **75**, 1809-1815. (doi: 10.1016/j.anbehav.2007.10.029)

36. Connor, R. C., Mann, J., Tyack, P. L. & Whitehead, H. 1998 Social evolution in toothed whales. *Trends Ecol. Evol*. **13**, 228-232. (doi: 10.1016/S0169-5347(98)01326-3)

37. Rendell, L. & Whitehead, H. 2001 Culture in whales and dolphins. *Behav. Brain Sci*. **24**, 309-324.

38. Whitehead, H. 2009 How might we study culture? A perspective from the ocean. In *The question of animal culture* (eds. R.N. Laland & B. Galef), pp. 125-152. Cambridge: Harvard University Press.
39. Pastor-Satorras, R. & Vespignani, A. 2001 Epidemic dynamics and endemic states in complex networks. *Phys. Rev. E* **63**, 066117. (doi: 10.1103/PhysRevE.63.066117)
40. Amblard, F. & Deffuant, G. 2004 The role of network topology on extremism propagation with the relative agreement opinion dynamics. *Physica A* **343**, 725-738. (doi: 10.1016/j.physa.2004.06.102)
41. Meyers, L., Pourbohloul, B., Newman, M., Skowronski, D., Brunham, R. 2005 Network theory and SARS: predicting outbreak diversity. *J. Theor. Biol.* **232**, 71-81. (doi: 10.1016/j.jtbi.2004.07.026)
42. Guimarães, P. R., Argollo de Menezes, M., Baird, R. W., Lusseau, D., Guimarães, P & Reis, S.F. 2007 Vulnerability of a killer whale social network to disease outbreaks. *Phys. Rev. E* **76**, 042901. (doi: 10.1103/PhysRevE.76.042901)
43. Salathé, M. & Jones, J. H. 2010 Dynamics and control of diseases in networks with community structure. *PLoS Comput. Biol.* **6**, e1000736. (doi:10.1371/journal.pcbi.1000736)
44. Christensen, C., Albert, I., Grenfell, B., & Albert, R. 2010 Disease dynamics in a dynamic social network. *Phys. A* **389**, 2663-2674. (doi: 10.1016/j.physa.2010.02.034)
45. Griffin R. H. & Nunn, C. L. 2012 Community structure and the spread of infectious disease in primate social networks *Evol. Ecol.* **26**,779–800. (doi: 10.1007/s10682-011-9526-2)

46. Nunn, C. L., Thrall, P. H., Bartz, K., Dasgupta, T. & Boesch, C. 2009 Do transmission mechanisms or social systems drive cultural dynamics in socially structured populations? *Anim. Behav.* **77**, 1515-1524. (doi: 10.1016/j.anbehav.2009.02.023)

47. Coussi-Korbel, S. & Fragaszy, D. M. 1995 On the relation between social dynamics and social learning. *Anim. Behav.* **50**, 1441-1453. (doi: 10.1016/0003-3472(95)80001-8)

48. Kendal, R. L., Custance, D. M., Kendal, J. R., Vale, G., Stoinski, T. S., Rakotomalala, N. L. & Rasamimanana, H. 2010 Evidence for social learning in wild lemurs (*Lemur catta*). *Learn. Behav.* **38**, 220-234. (doi: 10.3758/LB.38.3.220)

49. Vital, C. & Martins, E. P. 2009 Using graph thery metrics to infer information flow through animal social groups: a computer simulation analysis. *Ethology* **115**, 347-355. (doi: 10.1111/j.1439-0310.2009.01613.x)

50. Wittemyer, G., Douglas-Hamilton, I. & Getz, W. M. 2005 The socio-ecology of elephants: analysis of the processes creating multitiered social structures. *Anim. Behav.* **69**, 1357-1371. (doi: 10.1016/j.anbehav.2004.08.018)

51. Krause, J., James, R. & Croft, D. P. 2010 Personality in the context of social networks. *Phil. Trans. R. Soc. B* **365**, 4099-4106. (doi: 10.1098/rstb.2010.0216)

52. Boogart, N. J., Reader, S. M., Hoppit, W. & Laland, K. N. 2008 The origin and spread of innovations in starlings. *Anim. Behav.* **75**, 1509-1518. (doi:10.1016/j.anbehav.2007.09.033)

53. Hoppitt, W. J. E., Boogert, N. J. & Laland, K. N. 2010 Detecting social transmission in networks. *J. Theor. Biol*. **263**, 544-555. (doi: 10.1016/j.jtbi.2010.01.004)

54. Kendal, R. L., Galef, B. G. Jr. & van Schaik, C. P. 2010 Social learning research outside the laboratory: How and why? *Learn. Behav*. **38**, 187-194. (doi: 10.3758/LB.38.3.187)

55. Donaldson R., Finn, H., Bejder, L., Lusseau, D. & Calver, M. 2012 The social side of human-wildlife interaction: wildlife can learn harmful behaviours from each other. *Anim. Conserv*. **15**,427-435. (doi: 10.1111/j.1469-1795.2012.00548.x)

56. Payne, K. 1999 The progressively changing songs of humpback whales: a window on the creative process in a wild animal. In *The origins of music* (eds. N.L. Wallin, B. Merker & S. Brown), pp. 135-150. Cambridge: MIT Press.

57. Wilson, E. O. 1975 *Sociobiology: the new synthesis*. Cambridge, MA: Belknap Press.

58. Laland, K. N. & Janik, V. M. 2006. The animal culture debate. *Trends Ecol. Evol.* **21**, 542-547. (doi: 10.1016/j.tree.2006.06.005)

59. Acevedo, A. & Smultea, M. A. 1995 First records of humpback whales including calves at Golfo Dulce and Isla del Coco, Costa Rica, suggesting geographical overlap of northern and southern hemishere populations. *Mar. Mamm. Sci*. **11**, 554-560. (doi: 10.1111/j.1748-7692.1995.tb00677.x)

60. Payne, R. & Guinee, L. N. 1983 Humpback whale, *Megaptera novaeangliae*, songs as an indicator of "stocks". In *Communication and behavior of whales* (ed. R. Payne), pp. 333-358. Colorado: Westview Press.

61. Cerchio, S., Jacobsen, J. K. & Norris, T. F. 2001 Temporal and geographical variation in songs of humpback whales, *Megaptera novaeangliae*: synchronous change in Hawaiian and Mexican breeding assemblages. *Anim. Behav*. **62**, 313-329. (doi: 10.1006/anbe.2001.1747)

62. Garland, E. C., Goldizen, A. W., Rekdahl, M. L., Constantine, R., Garrigue, C., Hauser, N. D, Poole, M. M, Robbins, J. & Noad, M. J. 2011 Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Curr. Biol.* **21**, 687-691. (doi: 10.1016/j.cub.2011.03.019)
63. Noad, M. J., Cato, D. H., Bryden, M. M., Jenner, M. N. & Jenner, K. C. S. 2000 Cultural revolution in whale songs. *Nature* **408**, 537. (doi: 10.1038/35046199)
64. Payne, R.S. & McVay, S. 1971 Songs of humpback whales. *Science* **173**, 585-597. (doi 10.1126/science.173.3997.585)
65. Gracia-Lázaro, C., Quijandría, L., Hernández, L., Floría, L. M. & Moreno, Y. 2011 Coevolutionary network approach to cultural dynamics controlled by intolerance. *Phys. Rev. E* **84**, 067101. (doi: 10.1103/PhysRevE.84.067101)
66. Wolf, M. & Weissing, F. J. 2012 Animal personalities: consequences for ecology and evolution. *Trends Ecol. Evol.* **27**, 452-461. (doi: 10.1016/j.tree.2012.05.001)
67. Sih, A., Hanser, S. F. & McHugh, K. A. 2009 Social network theory: new insights and issues for behavioral ecologists. *Behav. Ecol. Sociobiol.* **63**, 975-988. (doi: 10.1007/s00265-009-0725-6)
68. Sargeant, B. L. & Mann, J. M. 2009 Developmental evidence for foraging traditions in wild bottlenose dolphins. *Anim. Behav.* **78**, 715-721. (doi: 10.1016/j.anbehav.2009.05.037)
69. Pike, T. W., Samanta, M., Lindström, J. & Royle, N. J. 2008 Behavioural phenotype affects social interactions in an animal network. *Proc. R. Soc. B* **275**, 2515-2520. (doi: 10.1098/rspb.2008.0744)

70. Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. & Forister, M. L. 2003 The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* **161**, 1-28. (doi: 10.1086/343878)

71. Estes, J. A., Riedman, M. L., Staedler, M. M., Tinker, M. T. & Lyon, B. E. 2003 Individual variation in prey selection by sea otters: patterns, causes and implications. *J. Anim. Ecol*. **72**, 144-155. (doi: 10.1046/j.1365-2656.2003.00690.x)

72. Mann, J., Stanton, M. A., Patterson, E. M., Bienenstock, E. B. & Singh, L. O. 2012 Social networks reveal cultural behaviour in tool-using using dolphins. *Nature* (doi: 10.1038/ncomms1983)

73. Ansmann, I. C., Parra, G. J., Chilvers, B. L. & Lanyon, J. M. 2012 Dolphins restructure social system after reduction of commercial fisheries. *Anim. Behav*. **84**, 575-581. (doi: 10.1016/j.anbehav.2012.06.009)

74. Bacher, K., Allen, S., Lindholm, A. K., Bejder, L. & Krützen, M. 2010 Genes or culture: are mitochondrial genes associated with tool use in bottlenose dolphins (*Tursiops* sp.)? *Behav. Genet.* **40**, 706-714 (doi: 10.1007/s10519-010-9375-8)

75. Kopps, A. M. & Sherwin W. B. 2012 Modelling the emergence and stability of a vertically transmitted cultural trait in bottlenose dolphins. *Anim. Behav.* (doi: 10.1016/j.anbehav.2012.08.029)

76. Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L. & Sherwin, W. B. 2005 Cultural transmission of tool use in bottlenose dolphins. *Proc. Natl. Acad. Sci. USA*. **102**, 8939-8943. (doi: 10.1073/pnas.0500232102)

77. Chilvers, B. L. & Corkeron, P. J. 2001 Trawling and bottlenose dolphins' social structure. *Proc. R. Soc. Lond. B* **268**, 709-726. (doi: 10.1098/rspb.2001.1732)

78. Henrich, J. & Gil-White, F. 2001 The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evol. Hum. Behav*. **22**, 165-196. (doi: 10.1016/S1090-5138(00)00071-4)
79. Henrich, J. & Boyd, R. 1998 The evolution of conformist transmission and the emergence of between group differences. *Evol. Hum. Behav*. **19**, 215-242. (doi: 10.1016/S1090-5138(98)00018-X)
80. Mesnick, S. L. 2001 Genetic relatedness in sperm whales: evidence and cultural implications. *Behav. Brain Sci*. **24**, 346-347 (doi: 10.1017/S0140525X01463965)
81. Ford, J. K. B., Ellis, G. M. & Balcomb, K. C. 2000 *Killer whales*. Vancouver, British Columbia: UBC Press.
82. Whitehead, H., Antunes, R., Gero, S., Wong, S. N. P., Engelhaupt, D. & Rendell, L. 2012 Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: why are they so different? *Int. J. Primat.* (doi: 10.1007/s10764-012-9598-z)
83. Deecke, V. B., Ford, J. K. B. & Spong, P. 2000 Dialect change in resident killer whales: implications for vocal learning and cultural transmission. *Anim. Behav*. **40**, 629-638.
84. Whitehead, H., Rendell, L., Osborne, R. W. & Würsig, B. 2004 Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. *Biol. Conserv*. **120**, 431-441. (doi: 10.1016/j.biocon.2004.03.017)
85. Perry, S. 2009 Are non-human primates likely to exhibit cultural capacities like those of humans? In *The question of animal culture* (eds. K.N. Laland & B.G. Galef Jr), pp. 247-268. Cambridge, MA: Harvard University Press.

86. Ford, J. K. B. 1989 Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Can. J. Zool*. **67**, 727-745.

87. Ford, J. K. B. 1991 Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Can. J. Zool*. **69**, 1454-1483.

88. Yurk, H., Barrett-Lennard, L., Ford, J. K. B. & Matkin, C. O. 2002 Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. *Anim. Behav*. **63**, 1103-1119. (doi: 10.1006/anbe.2002.3012)

89. Rendell, L. & Whitehead, H. 2003 Vocal clans in sperm whales (*Physeter macrocephalus*). *Proc. R. Soc. B*. **270**, 225-231. (doi: 10.1098/rspb.2002.2239)

90. Whitehead, H. & Rendell, L. 2004 Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. *J. Anim. Ecol*. **73**, 190-196. (doi: 10.1111/j.1365-2656.2004.00798.x)

91. Antunes, R. N. C. 2009 Variation in sperm whale (*Physeter macrocephalus*) coda vocalizations and social structure in the North Atlantic Ocean. PhD thesis. University of St. Andrews. (http://hdl.handle.net/10023/827).

92. Whitehead, H. 2008 *Analyzing animal societies: quantitative methods for vertebrate social analysis*. Chicago: University of Chicago Press.

93. Costa, L. da F., Rodrigues, F. A., Travieso, G. & Villas Boas, P. R. 2007 Characterization of complex networks: a survey of measurements. *Adv. Phys.* **56**, 167-242. (doi: 10.1080/00018730601170527)

94. Newman, M. E. J. 2010 *Networks: an introduction*. Oxford University Press.

95. Croft, D. P., Madden, J. R., Franks, D. W. & James, R. 2011 Hypothesis testing in animal social networks. *Trends. Ecol. Evol.* **26**, 502-507. (doi: 10.1016/j.tree.2011.05.012)

96. Kendal, R. L., Kendal, J. R., Hoppitt, W. & Laland, K. N. 2009 Identifying social learning in animal populations: A new "option-bias" method. *PLoS ONE* **4**, e6541. (doi: 10.1371/journal.pone.0006541)

97. Franz, M. & Nunn, C. L. 2009 Network-based diffusion analysis: a new method for detecting social learning. *Proc. R. Soc. B* **276**, 1829-1836. (doi: 10.1098/rspb.2008.1824)

98. Franz, M. & Nunn, C. L. 2010 Investigating the impact of observation errors on the statistical performance of network-based diffusion analysis. *Learn. Behav.* **38**, 235-242. (doi: 10.3758/LB.38.3.235)

99. Dekker, D., Krackhardt, D. & Snijders, T. A. B. 2007 Sensitivity of MRQAP tests to collinearity and autocorrelation conditions. *Psychometrika* **72**, 563-581. (doi: 10.1007/s11336-007-9016-1)

100. Matthews, L. J. 2009 Intragroup behavioral variation in white-fronted capuchin monkeys (*Cebus albifrons*): mixed evidence for social learning inferred from new and established analytical methods. *Behaviour* **146**, 295-324. (doi: 10.1163/156853909X410937)

101. Vazquez, A. 2006 Spreading dynamics on heterogeneous populations: multitype network approach. *Phys. Rev. E* **74**, 066114. (doi: 10.1103/PhysRevE.74.066114)

102. Wang, B., Cao, L., Suzuki, H. & Aihara, K. 2011 Epidemic spread in adaptive networks with multitype agents. J. Phys. A: Math. Theor. **44**, 035101. (doi:10.1088/1751-8113/44/3/035101)

103. Daura-Jorge, F. G., Cantor, M., Ingram, S. N., Lusseau, D. & Simões-Lopes, P. C. 2012 The structure of a bottlenose dolphin society in coupled to a unique foraging cooperation with artisanal fishermen. *Biol. Lett*. (doi: 10.1098/rsbl.2012.0174)

104. Simões-Lopes, P. C., Fabián, M. E. & Menegheti, J. O. 1998 Dolphin interactions with the mullet artisanal fishing on southern Brazil: a qualitative and quantitative approach. *Rev. Bras. Zool.* **15**, 709-726. (doi: 10.1590/S0101-81751998000300016)

105. Pike, T. W. & Laland, K. N. 2010 Conformist learning in nine-spined sticklebacks' foraging decisions. *Biol. Lett.* **23**, 466-468. (doi: 10.1098/rsbl.2009.1014)

CHAPTER 3

1. Hinde, R. A. Interactions, relationships and social structure. *Man* **11**, 1-17 (1976).

2. Clutton-Brock, T. H. Review lecture: mammalian mating systems. *Proc. R. Soc. B.* **236**, 339-372 (1989).

3. Kappeler, P. M., Barrett, L., Blumstein, D. T. & Clutton-Brock, T. H. Constraints and flexibility in mammalian social behaviour: introduction and synthesis. *Phil. Trans. R. Soc. B* **368,** 20120337 (2013).

4. Zhou, W., Sornette, D., Hill, R. & Dunbar, R. Discrete hierarchical organization of social group sizes. *Proc. R. Soc. B* **272,** 439-444 (2005).

5. Hamilton, M. J., Milne, B. T., Walker, R. S., Burger, O. & Brown, J. H. The complex structure of hunter–gatherer social networks. *Proc. R. Soc. B.* **274,** 2195–2202 (2007).

6. Grueter, C. C., Chapais, B. & Zinner, D. Evolution of multilevel social systems in nonhuman primates and humans. *Intl. J. Primatol.* **33,** 1002-1037 (2012).

7. Hill, R. A., Bentley, R. A. & Dunbar, R. I. M. Network scaling reveals consistent fractal pattern in hierarchical mammalian societies. *Biol. Lett.* **4,** 748-751 (2008).

8. Wittemeyer, G., Douglas-Hamilton, I. & Getz, W. M. The socioecology of elephants: analysis of the processes creating multitiered social structures. *An. Behav.* **69,** 1357–1371 (2005).

9. Ford, J. K. B., Ellis, G. M. & Balcomb, K. C. *Killer Whales* (University of British Columbia Press, 2000).

10. Krause, J. & Ruxton, G. D. *Living in Groups* (Oxford University Press, 2002).

11. Swedell, L. & Plummer, T. A papionin multilevel society as a model for hominin social evolution. *Intl. J. Primatol*. **33**, 1165-1193 (2012).

12. Dunbar, R. I. M. Neocortex size as a constraint on group size in primates. *J. Hum. Evol.* **22,** 469-493 (1992).

13. Sutcliffe, A., Dunbar, R., Binder, J. & Arrow, H. Relationships and the social brain: integrating psychological and evolutionary perspectives. *Brit. J. Psychol.* **103,** 149–168 (2012).

14. Laland K. N. & Hoppitt, W. Do animals have culture? *Evol. Anthropol.* **12,** 150-159 (2003).

15. Laland, K. N. & Janik, V. M. The animal cultures debate. *Trends Ecol Evol*. **21**, 542–547 (2006).

16. Cantor, M. & Whitehead, H. The interplay between social networks and culture: theoretically and among whales and dolphins. *Phil. Trans. R. Soc. B* **368,** 20120340 (2013).

17. McPherson, M., Smith-Lovin, L. & Cook, J. M. Birds of a feather: homophily in social networks. *Ann. Rev. Sociol.* **27,** 415-44 (2001).

18. Axelrod, R. The dissemination of culture: a model with local convergence and global polarization. *J. Conf. Resol.* **41,** 203-226 (1997).

19. Morgan, T. J .H. & Laland, K. N. The biological bases of conformity. *Front. Neurosci.* **6,** 1-7 (2012).

20. Boyd, R. & Richerson, P. J. The evolution of ethnic markers. *Cult. Anthropol*. **2,** 65-79 (1987).

21. Moffett, M. W. Human identity and the evolution of societies. *Hum. Nat.* **24,** 219-267 (2013).

22. Nunn, C. L., Thrall, P. H., Bartz, K., Dasgupta, T. & Boesch, C. Do transmission mechanisms or social systems drive cultural dynamics in socially structured populations? *An. Behav.* **77,** 1515-1524 (2009).

23. Perreault, C., Moya, C. & Boyd, R. A Bayesian approach to the evolution of social learning. *Evol. Hum. Behav.* **33,** 449-459 (2012).

24. McElreath, R., Boyd, R. & Richerson, P. J. Shared norms and the evolution of ethnic markers. *Curr. Anthropol*. **44**, 122-130 (2003).

25. Efferson, C., Lalive, R. & Fehr, E. The coevolution of cultural groups and ingroup favoritism. *Science* **321**, 1844-1849 (2008).

26. Centola, D., González-Avella, J. C., Eguíluz, V. M. & San Miguel, M. Homophily, cultural drift, and the co-evolution of cultural groups. *J. Confl. Resol.* **51,** 905-929 (2007).

27. Whiten, A. *et al.* Cultures in chimpanzees. *Nature* **399**, 682-685 (1999).

28. Mann, J., Stanton, M. A., Patterson, E. M., Bienenstock, E. B. & Singh, L. O. Social networks reveal cultural behaviour in tool-using using dolphins. *Nat. Commun.* **3,** 1-7 (2012).

29. Jenkins, P. Cultural transmission of song patterns and dialect development in a free-living bird population. *Anim. Behav*. **26**, 50-78 (1978).

30. Rendell, L. & Whitehead, H. Vocal clans in sperm whales (*Physeter macrocephalus*). *Proc. R. Soc. B* **270,** 225-231 (2003).

31. Krützen, M., Willems, E. P. & van Schaik, C. P. Culture and geographic variation in orangutan behavior. *Curr. Biol.* **21**, 1808–1812 (2011).

32. Podos, J. & Warren, P. The evolution of geographic variation in birdsong. *Adv. Stud. Behav*. **37**, 403-458 (2007).

33. Cavalli-Sforza, L. L. & Feldman, M. W. *Cultural transmission and evolution.* (Princeton University Press, 1981).

34. Ellers, J. & Slabbekoorn, H. Song divergence and male dispersal among bird populations: a spatially explicit model testing the role of vocal learning. *Anim. Behav.* **65**, 671-681 (2003).

35. Fayet, A. L., Tobias, J. A., Hintzen, R. E. & Seddon, N. Immigration and dispersal are key determinants of cultural diversity in a songbird population. *Behav. Ecol.* **25**, 744-753 (2014).

36. Boyd, R. & Richerson, P. J. Culture and the Evolutionary Process. (Chicago University Press, 1985).

37. Mann, J., Connor, R. C., Tyack, P. L. & Whitehead, H. *Cetacean societies: field studies of dolphins and whales*. (University of Chicago Press, 2000).

38. Whitehead, H. & Rendell, L. *Oceans of Culture: Cultures of Whales and Dolphins*. (Chicago University Press, 2014).

39. Whitehead, H., Antunes, R., Gero, S., Wong, S. N. P., Engelhaupt, D. & Rendell, L. Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: Why are they so different? *Intl. J. Primatol.* **33,** 1142-1164 (2012).

40. Weilgart, L. & Whitehead, H. Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behav. Ecol. Sociobiol.* **40,** 277-285 (1997).

41. Janik, V. M. Cetacean vocal learning and communication. *Curr. Opin. Neurobiol.* **28**, 60-65 (2014).

42. Whitehead, H., Dillon, M., Dufault, S., Weilgart, L. & Wright, J. Nongeographically based population structure of South Pacific sperm whales: Dialects, fluke-markings and genetics. *J. Anim. Ecol*. **67**, 253-262 (1998).

43. Rendell, L., Mesnick, S. L., Dalebout, M. L., Burtenshaw, J. & Whitehead, H. Can genetic differences explain vocal dialect variation in sperm whales, *Physeter macrocephalus*? *Behav. Gen.* **42**, 332-343 (2012).

44. Antunes, R. N. C. *Variation in Sperm Whale (*Physeter macrocephalus*) Coda Vocalizations and Social Structure in the North Atlantic Ocean*. PhD thesis. (University of St. Andrews, 2009).

45. Christal, J., Whitehead, H. & Lettevall, E. Sperm whale social units: variation and change. *Can. J. Zool.* **76,** 1431-1440 (1998).

46. Burnside, W. R., Brown, J. H., Burger, O., Hamilton, M. J., Moses, M. & Bettencourt, L. Human macroecology: linking pattern and process in big-picture human ecology. *Biol. Rev.* **87,** 194-208 (2012).

47. Carr, G. M. & Macdonald, D. W. The sociality of solitary foragers: a model based on resource dispersion. *An. Behav.* **34,** 1540-1549 (1986).

48. Gowans, S., Würsig, B. & Karczmarski, L. The social structure and strategies of delphinids: predictions based on an ecological framework. *Adv. Mar. Biol.* **53,** 195-294 (2007).

49. Daura-Jorge, F. G., Cantor, M., Ingram, S. N., Lusseau, D. & Simões-Lopes, P. C. The structure of a bottlenose dolphin society in coupled to a unique foraging cooperation with artisanal fishermen. *Biol. Lett.* **8,** 702-705 (2012).

50. Whitehead, H. & Rendell, L. Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. *J. An. Ecol.* **73,** 190-196 (2004).

51. Schulz, T. M., Whitehead, H., Gero, S. & Rendell, L. Overlapping and matching of codas in vocal interactions between sperm whales: insights into communication function. *An. Behav.* **76,** 1977-1988 (2008).

52. Filatova, O. A., Guzeev, M. A., Fedutin, I. D., Burdin, A. M. & Hoyt, E. Dependence of killer whale (*Orcinus orca*) acoustic signals on the type of activity and social context. *Biol. Bull*. **40,** 790-796 (2013).

53. Quick, N. J. & Janik, V. M. Whistle rates of wild bottlenose dolphins (*Tursiops truncatus*): influences of group size and behavior. *J. Comp. Psychol.* **122**, 305-311 (2008).

54. Kopps, A. M. & Sherwin, W. B. Modelling the emergence and stability of a vertically transmitted cultural trait in bottlenose dolphins. *An. Behav.* **84,** 1347-1362 (2012).

55. Henrich, J. & Boyd, R. The evolution of conformist transmission and the emergence of between group differences. *Evol. Hum. Behav.* **19,** 215-242 (1998).

56. Boyd, R. & Richerson, P. J. *Culture and the Evolutionary Process.* (Chicago University Press, 1985).

57. Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* **518**, 538–541 (2014).

58. Riesch, R., Barrett-Lennard, L. G., Ellis, G. M., Ford, J. K. & Deecke, V. B. Cultural traditions and the evolution of reproductive isolation: ecological speciation in killer whales? *Biol. J. Linn. Soc.* **106,** 1-17 (2012).

59. Deecke, V. B., Ford, J. K. B. & Spong, P. Dialect change in resident killer whales: implications for vocal learning and cultural transmission. *An. Behav.* **40,** 629-638 (2000).

60. Slater, P.J. The cultural transmission of bird song. *Trends Ecol. Evol.* **1**, 94-97 (1986).

61. Filatova, O. A., Burdin, A. M., & Hoyt, E. Is killer whale dialect evolution random? *Behav. Proc.* **99**, 34-41 (2013).

62. Laland, K. N. & Galef, B. G. *The Question of Animal Culture* (Harvard University Press, 2009).

63. Whitehead H. *Sperm Whales: Social Evolution in the Ocean*. (Chicago University Press, 2003).

64. R Core Team. *R: A Language and Environment for Statistical Computing*. (R Foundation for Statistical Computing, 2013).

65. Grimm, V. *et al.* A standard protocol for describing individual-based and agent-based models. *Ecol. Model.* **198,** 115-126 (2006).

66. Marcoux, M., Whitehead, H. & Rendell, L. Coda vocalizations recorded in breeding areas are almost entirely produced by mature female sperm whales (*Physeter macrocephalus). Can. J. Zool*. **84**, 609-614 (2006).

67. Chiquet, R. A., Ma, B., Ackleh, A. S., Pal, N. & Sidorovskaia, N. Demographic analysis of sperm whales using matrix population models. *Ecol. Model.* **248**, 71-79 (2013).

68. Pons, P. & Latapy, M. Computing communities in large networks using random walks. *Comp. Inf. Sci.* 284-293 (2005).

69. Newman, M. E. Modularity and community structure in networks. *Proc. Natl. Acad. Sci. U.S.A*. **103,** 8577-8582 (2006).

70. Opsahl, T. Colizza, V., Panzarasa, P. & Ramasco, J. J. Prominence and control: the weighted rich-club effect. *Phys. Rev. Lett.* **101,** 169702 (2008).

CHAPTER 4

Allen, J., M. Weinrich, W. Hoppitt and L. Rendell. 2013. Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. Science 340:485-488.

Ansmann, I. C., G. J. Parra, B. L. Chilvers and J. M. Lanyon. 2012. Dolphins restructure social system after reduction of commercial fisheries. Animal Behaviour 84: 575-581.

Aplin, L. M., D. R. Farine, J. Morand-Ferron and B. C. Sheldon. 2012. Social networks predict patch discovery in a wild population of songbirds. Proceedings of the Royal Society: Biological Sciences 279: 4199-4205.

Atton N., B. J. Galef, W. Hoppitt, M. M. Webster and K. N. Laland. 2014 Familiarity affects social network structure and discovery of prey patch locations in foraging stickleback shoals. Proceedings of the Royal Society B 281: 20140579. doi:10.1098/rspb.2014.0579.

Baird, R. W. 2000. The killer whale—foraging specializations and group hunting. Pages 127–53 *in* Mann, J., R. C. Connor, P. Tyack and H. Whitehead, eds. Cetacean societies. University of Chicago Press, Chicago.

Boyd, R. and P. J. Richerson. 1985. Culture and the evolutionary process. University of Chicago Press, Chicago.

Burnham, K.P. and D. R. Anderson. 2002. Model Selection and multimodel inference: A practical information-theoretic approach. Springer–Verlag, New York.

Cantor, M. and H. Whitehead. 2013. The interplay between social networks and culture: theoretically and among whales and dolphins. Philosophical Transactions of the Royal Society: Biological Sciences 368:20120340. doi:10.1098/rstb.2012.0340

Cavalli-Sforza, L.L. and M. W. Feldman. 1981. Cultural transmission and evolution. Princeton University Press, Princeton.

Centola, D., J. C. González-Avella, V. M. Eguíluz and M. San Miguel. 2007. Homophily, cultural drift, and the co-evolution of cultural groups. Journal of Conflict Resolution 51:905-929.

Christal, J and H. Whitehead. 2001. Social affiliations within sperm whale (*Physeter macrocephalus*) groups. Ethology.107:323-340.

Christal, J., H. Whitehead, and H. Lettevall. 1998. Sperm whale social units: variation and change. Canadian Journal of Zoology 76:1431-1440.

Croft D. P., J. Krause, S. K. Darden, I.W. Ramnarine, J. J. Faria and R. James. 2009. Behavioural trait assortment in a social network: patterns and implications. Behavioral Ecology and Sociobiology 63:1495–1503.

Cronin, K. A., E. J. Van Leeuwen, V. Vreeman and D. Haun. 2014. Population-level variability in the social climates of four chimpanzee societies. Evolution and Human Behavior. doi: 10.1016/j.evolhumbehav.2014.05.004

Daura-Jorge, F.G., M. Cantor, S. N. Ingram, D. Lusseau and P. C. Simões-Lopes. 2012. The structure of a bottlenose dolphin society in coupled to a unique foraging cooperation with artisanal fishermen. Biology Letters 8: 702-705.

Farine, D. R. 2014. Measuring phenotypic assortment in animal social networks: Weighted associations are more robust than binary edges. Animal Behaviour 89: 141-153.

Gero, S., J. Gordon and H. Whitehead. 2013. Calves as social hubs: Dynamics of the social network within sperm whale units. Proceedings of the Royal Society: Biological Sciences 280: 20131113. doi:10.1098/rspb.2013.1113

Hahn, M, W. and R. A. Bentley. 2003. Drift as a mechanism for cultural change: An example from baby names. Proceedings of the Royal Society: Biological Sciences 270:S120-S123.

Kappeler, P.M., L. Barret, D. T. Blumstein and T. H. Clutton-Brock. 2013. Constraints and flexibility in mammalian social behaviour: introduction. Philosophical Transactions of the Royal Society: Biological Sciences 368:20120337. doi:10.1098/rstb.2012.0337

Koerper, H. C. and E. G. Stickel. 1980. Cultural drift: a primary process of culture change. Journal of Anthropological Research 36:463-469.

Krause, J. and G. D. Ruxton. 2002. Living in groups. Oxford University Press, Oxford.

Laland, K. N. and B N. Galef. 2009. The question of animal culture. Harvard University Press, Cambridge.

Laland, K. N. and W. Hoppitt. 2003. Do animals have culture? Evolutionary Anthropology 12:150-159.

Lott, D. L. 1984. Intraspecific variation in the social systems of wild vertebrates. Behaviour. 88:266-325.

Mace, R. 2014. Human behavioral ecology and its evil twin. Behavioral Ecology 25: 443–449.

Mann, J., M. A. Stanton, E. M. Patterson, E. B. Bienenstock, and L. O. Singh. 2012. Social networks reveal cultural behaviour in tool-using using dolphins. Nature Communications 3: 980. doi: 10.1038/ncomms1983.

Marcoux, M., H. Whitehead and L. Rendell. 2007*a*. Sperm whale feeding variation by location, year, social group and clan: evidence from stable isotopes. Marine Ecology Progress Series 333:309-314.

Marcoux, M., L. Rendell and H. Whitehead. 2007*b*. Indications of fitness differences among vocal clans of sperm whales. Behavioral Ecology and Sociobiology 61:1093-1098.

Morin, P. A., F. I. Archer, A. D. Foote *et al.* 2010. Complete mitochondrial genome phylogeographic analysis of killer whales (*Orcinus orca*) indicates multiple species. Genome Research 20:908-16.

Otis, D. L., K. P. Burnham, G. C. White and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife monographs 62:3-135.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.Rendell, L. and H. Whitehead. 2003. Vocal clans in sperm whales (*Physeter macrocephalus*). Proceedings of the Royal Society: Biological Sciences 270:225-231.

Rendell, L., S. L. Mesnick, M. L. Dalebout, J. Burtenshaw and H. Whitehead. 2012. Can genetic differences explain vocal dialect variation in sperm whales, *Physeter macrocephalus*? Behavior Genetics 42: 332-343.

Riesch, R., L. G. Barrett-Lennard, G. M. Ellis, J. K. B. Ford, and V. B. Deecke. 2012. Cultural traditions and the evolution of reproductive isolation: ecological speciation in killer whales? Biological Journal of the Linnean Society 106:1–17.

Sachser, N., S. Kaiser and M. B. Hennessy. 2013. Behavioural profiles are shaped by social experience: When, how and why. Philosophical Transactions of the Royal Society: Biological Sciences 368:20120344. doi:10.1098/rstb.2012.0344

Schradin, C. 2013. Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. Philosophical Transactions of the Royal Society: Biological Sciences 368:20120346. doi:10.1098/rstb.2012.0346

Schulz, T. M., H. Whitehead, S. Gero and L. Rendell. 2008. Overlapping and matching of codas in vocal interactions between sperm whales: Insights into communication function. Animal Behaviour 76:1977-1988.

Voelkl, B. and Nöe, R. 2010. Simulation of information propagation in real-life primate networks: longevity, fecundity, fidelity. Behavioral Ecology and Sociobiology 64: 1449-1459.

Whitehead, H. 2009*a*. SOCPROG programs: Analysing animal social structures. Behavioral Ecology and Sociobiology 63: 765-778.

Whitehead, H. 2009*b*. How might we study culture? A perspective from the ocean. Pages 125-152 *in* Laland R. N. and B. Galef, eds. The question of animal culture. Harvard University Press, Cambridge, MA.

Whitehead, H. 2008*a*. Analyzing animal societies: Quantitative methods for vertebrate social analysis. University of Chicago Press, Chicago.

Whitehead, H. 2008*b*. Precision and power in the analysis of social structure using associations. Animal Behaviour 75: 1093-1099.

Whitehead, H. 2003. Sperm whales: Social evolution in the ocean. University of Chicago Press, Chicago.

Whitehead, H. 1999. Variation in the visually observable behavior of groups of Galápagos sperm whales. Marine Mammal Science 15:1181-1197.

Whitehead, H. 1996. Babysitting, dive synchrony, and indications of alloparental care in sperm whales. Behavioral Ecology and Sociobiology 38: 237-244.

Whitehead, H. 1995. Investigating structure and temporal scale in social organizations using identified individuals. Behavioral Ecology 6:199-208.

Whitehead, H. and D. Lusseau. 2012. Animal social networks as substrate for cultural behavioural diversity. Journal of Theoretical Biology 294:19-28.

Whitehead, H. and L. Rendell. 2014. The cultural lives of whales and dolphins. University of Chicago Press, Chicago.

Whitehead, H. and L. Rendell. 2004. Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. Journal of Animal Ecology 73:190-196.

Whitehead, H., Antunes, R., Gero, S., Wong, S.N.P., Engelhaupt, D. and Rendell, L. 2012. Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: Why are they so different? International Journal of Primatology 33:1142-1164.

Whitehead, H., M. Dillon, S. Dufault, L. Weilgart and J. Wright. 1998. Nongeographically based population structure of South Pacific sperm whales: Dialects, fluke-markings and genetics. Journal Animal Ecology 67:253–262.

Whiten, A., J. Goodal, W. C. McGrew *et al.* 1999. Cultures in chimpanzees. Nature. 399:682-685.doi:10.1038/21415

Wolf, M. and J. Krause. 2014. Why personality differences matter for social functioning and social structure. Trends in Ecology & Evolution 29:306-308.

CHAPTER 5

1. Avital E, Jablonka E. 2000 *Animal traditions: behavioural inheritance in evolution*. New York, NY: Cambridge University Press.

2. Richerson PJ, Boyd R. 2005 *Not by genes alone: How culture transformed human evolution*. Chicago, IL: University of Chicago Press.
3. Cavalli-Sforza LL, Feldman MW. 1981 *Cultural transmission and evolution: a quantitative approach.* Princeton, NJ: Princeton University Press.
4. Garland EC, Goldizen AW, Lilley MS, Rekdahl ML, Garrigue C, Constantine R, Hauser ND, Poole MM, Robbins J, Noad MJ. 2015 Population structure of humpback whales in the western and central South Pacific Ocean as determined by vocal exchange among populations. *Conserv. Biol.* **29**, 1198-1207. (doi: 10.1111/cobi.12492)
5. Noad MJ, Cato DH, Bryden MM, Jenner MN, Jenner KC. 2000 Cultural revolution in whale songs. *Nature* **408**, 537-537. (doi:10.1038/35046199)
6. Garland EC, Goldizen AW, Rekdahl ML, Constantine R, Garrigue C, Hauser ND, Poole MM, Robbins J, Noad MJ. 2011 Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Curr. Biol.* **21**, 687-691. (doi:10.1016/j.cub.2011.03.019)
7. Allen J, Weinrich M, Hoppitt W, Rendell L. 2013 Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science* **340**, 485-488. (doi: 10.1126/science.1231976)
8. Swift J. 1977 Sahelian pastoralists: underdevelopment, desertification, and famine. *Ann. Rev. Anthropol.* **6**, 457-478.
9. Sinclair ARE, Fryxell JM. 1985 The Sahel of Africa: Ecology of a disaster. *Can. J. Zool.* **63**, 987-994.

10. Whitehead H, Antunes R, Gero S, Wong SN, Engelhaupt D, Rendell L. 2012 Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: why are they so different? *Intl. J. Primatol.* **33**, 1142-1164. (doi: 10.1007/s10764-012-9598-z)
11. Christal J, Whitehead H, Lettevall E. 1998 Sperm whale social units: variation and change. *Can. J. Zool.* **76**, 1431–1440.
12. Gero S, Milligan M, Rinaldi C, Francis P, Gordon J, Carlson C, Steffen A, Tyack P, Evans P, Whitehead H. 2014 Behavior and social structure of the sperm whales of Dominica, West Indies. *Mar. Mam. Sci.* **30**, 905-922. (doi: 10.1111/mms.12086)
13. Watkins WA, Schevill WE. 1977 Sperm whale codas. *J. Acoust. Soc. Am.* **62**, 1485-1490.
14. Rendell L, Whitehead H. 2003 Vocal clans in sperm whales (*Physeter macrocephalus*). *Proc. R. Soc. B* **270**, 225-231. (doi: 10.1098/rspb.2002.2239)
15. Rendell L, Whitehead H. 2005 Spatial and temporal variation in sperm whale coda vocalisations: Stable usage and local dialects. *An. Behav.* **70**, 191-198. (doi:10.1016/j.anbehav.2005.03.001)
16. Rendell L, Mesnick SL, Dalebout ML, Burtenshaw J, Whitehead H. 2012 Can genetic differences explain vocal dialect variation in sperm whales, *Physeter macrocephalus*? *Behav. Gen.* **42**, 332-43. (doi: 10.1007/s10519-011-9513-y)
17. Whitehead H, Rendell L. 2004 Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. *J. An. Ecol.* **73**, 190-196. (doi: 10.1111/j.1365-2656.2004.00798.x)

18. Marcoux M, Whitehead H, Rendell L. 2007 Sperm whale diet variation by sex, location, year, social group and clan: evidence from stable isotopes. *Mar. Ecol. Prog. Ser*. **333**, 309-314. (doi: http://dx.doi.org/10.3354/meps333309)
19. Cantor M, Whitehead H. 2015 How does social behavior differ among sperm whale clans? *Mar. Mam. Sci.* **31**, 1275-90. (doi: 10.1111/mms.12218)
20. Whitehead H, Coakes A, Jaquet N, Lusseau S. 2008 Movements of sperm whales in the tropical Pacific. *Mar. Ecol. Prog. Ser.* **361**, 291-300.
21. Clarke R, Paliza O, Aguayo A. 1988 Sperm whales of the southeast Pacific. Part IV: fatness, food and feeding. *Invest. Cetacea* **21**, 53-195.
22. Whitehead H, Christal J, Dufault S. 1997 Past and distant whaling and the rapid decline of sperm whales off the Galápagos Islands. *Conserv. Biol.* **11**, 1387-1396. (doi: 10.1046/j.1523-1739.1997.96246.x)
23. Whitehead H. 1990 Computer assisted individual identification of sperm whale flukes. *Rep. Intl. Whal. Comm.* **12**, 71–77.
24. Whitehead H. 2003 *Sperm whale societies: Social evolution in the ocean*. Chicago, IL: University of Chicago Press.
25. Gillespie D. 1997 An acoustic survey for sperm whales in the Southern Ocean Sanctuary conducted from the R/V *Aurora Australis*. *Rep. Intl. Whal. Comm*. **47**, 897-908.
26. Weilgart L, Whitehead H. 1997 Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behav. Ecol. Sociobiol.* **40**, 277-285.

27. Gero S, Whitehead H, Rendell L. 2016 Individual, unit, and vocal clan level identity cues in sperm whale codas. *R. Soc. Open Sci.* **3**, 150372. (doi: http://dx.doi.org/10.1098/rsos.150372)

28. Antunes R, Schulz T, Gero S, Whitehead H, Gordon J, Rendell L. 2011 Individually distinctive acoustic features in sperm whale codas. *An. Behav.* **81**, 723-730. (doi:10.1016/j.anbehav.2010.12.019)

29. Ankerst M, Breunig MM, Kriegel H-P, Sander J. 1999 OPTICS: ordering points to identify the clustering structure. *Proc. SIGMOD'99. Intl. Conf. Manag. Data* **28**, 49–60. (doi:10.1145/304181.304187)

30. Cantor M, Shoemaker LG, Cabral RB, Flores CO, Varga M, Whitehead H. 2015 Multilevel animal societies can emerge from cultural transmission. *Nat. Comm.* **6**, 8091. (doi:10.1038/ncomms9091)

31. Jaquet N, Gendron D, Coakes A. 2003 Sperm whales in the Gulf of California: residency, movements, behavior, and the possible influence of variation in food supply. *Mar. Mamm. Sci*. **19**, 545-62. (doi: 10.1111/j.1748-7692.2003.tb01320.x)

32. Dufault S, Whitehead, H. 1995 An assessment of changes with time in the marking patterns used for photo-identification of individual sperm whales, *Physeter macrocephalus*. *Mar. Mamm. Sci.* **11**, 335-343. (doi: 10.1111/j.1748-7692.1995.tb00289.x)

33. Álvarez-Torres AM, Rendell L, Jaquet N, Gendron D. 2006. Rango de distribución de clanes de cachalote: el Golfo de California y el Pacífico Sur. In *Reunión Internacional sobre el Estudio de los Mamíferos Acuáticos* (eds Gendron D, Siciliano S), pp. 4. Mérida, Mexico: SOLAMAC.

34. Smith TD, Reeves RR, Josephson EA, Lund JN. 2012 Spatial and seasonal distribution of American whaling and whales in the age of sail. *PloS One* **7**, 4905. (doi: http://dx.doi.org/10.1371/journal.pone.0034905)

35. Whitehead H. 1996 Variation in the feeding success of sperm whales: temporal scale, spatial scale and relationship to migrations. *J. An. Ecol.* **65**, 429-438.

36. Cai W *et al.* 2014 Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Clim. Change* **4**, 111-116. (doi:10.1038/nclimate2100)

37. Strutton PG, Chavez FP. 2000 Primary productivity in the equatorial Pacific during the 1997–1998 El Niño. *J. Geophys. Res.* **105**, 26089-26101. (doi: 10.1029/1999JC000056)

38. Barber RT, Chavez FP. 1983 Biological consequences of El Niño. *Science* **222**, 1203-1210. (doi: 10.1126/science.222.4629.1203)

39. Merlen G. 1984 The 1982–1983 El Niño: Some of its consequences for Galápagos wildlife. *Oryx* **18**, 210-214.

40. Smith SC, Whitehead H. 1993 Variations in the feeding success and behaviour of Galápagos sperm whales (*Physeter macrocephalus*) as they relate to oceanographic conditions. *Can. J. Zool.* **71**, 1991-1996.

41. Lee T, McPhaden MJ. 2010 Increasing intensity of El Niño in the central-equatorial Pacific. *Geophys. Res. Lett.* **37**, L14603 (doi:10.1029/2010GL044007)

42. Ramirez P, Urquizo W. 1985 Los cetáceos mayores y el fenómeno El Niño 1982-1983. In *El Niño, su impacto en la fauna marina* (eds Arntz WE, Landa A, Tarazona J), pp 201-206. Callao, Perú: Boletin Instituto del Mar de Perú.

43. Ford JK, Ellis GM, Barrett-Lennard LG, Morton AB, Palm RS, Balcomb III KC. 1998 Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Can. J. Zool*. **76**, 1456-71.
44. Estes JA, Riedman ML, Staedler MM, Tinker MT, Lyon BE. 2003 Individual variation in prey selection by sea otters: patterns, causes and implications. *J. An. Ecol*. **72**, 144–155. (doi: 10.1046/j.1365-2656.2003.00690.x)
45. Ramirez P. 1989 Captura de cachalote en Paita, 1976-1981. *Bol. Lima* **63**, 81-88.
46. Whitehead H. 2002 Estimates of the current global population size and historical trajectory for sperm whales. *Mar. Ecol. Prog. Ser.* **242**, 295-304.
47. Whitehead H. 2000 Density-dependent habitat selection and the modeling of sperm whale (*Physeter macrocephalus*) exploitation. *Can. J. Fish. Aqu. Sci.* **57**, 223-230. (doi: 10.1139/f99-227)
48. Strandburg-Peshkin A, Farine DR, Couzin ID, Crofoot MC. 2015 Shared decision-making drives collective movement in wild baboons. *Science* **348**, 1358-1361. (doi: 10.1126/science.aaa5099)
49. Pinter-Wollman N, Isbell LA, Hart LA. 2009 The relationship between social behaviour and habitat familiarity in African elephants (*Loxodonta africana*). *Proc. R. Soc. B* **276**, 1009-1014. (doi:10.1098/rspb.2008.1538)
50. Whitehead H. *In press*. Consensus movements by groups of sperm whales. *Mar. Mam. Sci.*
51. Deecke VB, Ford JKB, Spong P. 2000 Dialect change in resident killer whales: Implications for vocal learning and cultural transmission. *An. Behav.* **60**, 629–638. (doi:10.1006/anbe.2000.1454)

52. Nelson DA, Hallberg KI, Soha JA. 2004 Cultural evolution of Puget sound white-crowned sparrow song dialects. *Ethology* **110**, 879-908. (doi: 10.1111/j.1439-0310.2004.01025.x)

53. Williams H, Levin II, Norris DR, Newman AE, Wheelwright NT. 2013 Three decades of cultural evolution in Savannah sparrow songs. *An. Behav.* **85**, 213-223. (doi:10.1016/j.anbehav.2012.10.028)

CHAPTER 6

Allen, J., Weinrich, M., Hoppitt, W. and Rendell, L. 2013. Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. Science 340:485-488.

Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cockburn, A., Thornton, A. and Sheldon, B.C. 2015. Experimentally induced innovations lead to persistent culture via conformity in wild birds. Nature 518:538-541.

Ansmann, I.C., Parra, G.J., Chilvers, B.L. and Lanyon, J.M. 2012. Dolphins restructure social system after reduction of commercial fisheries. Animal Behaviour 84:575-581.

Box, H.O. and Gibson, K.R. 1999. Mammalian social learning: comparative and ecological perspectives. Cambridge University Press.

Boyd, R. and Richerson, P.J. 1996. Why culture is common, but cultural evolution is rare. Proceedings of the British Academy 88:77–93.

Boyd, R., Richerson, P. and Henrich, J. 2011. The cultural niche: Why social learning is essential for human adaptation. Proceedings of the National Academic of Sciences USA 108:10918–10925.

Calambokidis, J., Schorr, G.S., Steiger, G.H., Francis, J., Bakhtiari, M., Marshall, G., Oleson, E.M., Gendron, D. and Robertson, K. 2007. Insights into the underwater diving, feeding, and calling behavior of blue whales from a suction-cup-attached video-imaging tag (CRITTERCAM). Marine Technology Society Journal 41:19-29.

Cai, W., Borlace, S., Lengaigne, M., Van Rensch, P., Collins, M., Vecchi, G., Timmermann, A., Santoso, A., McPhaden, M.J., Wu, L. and England, M.H. 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. Nature Climate Change 4:111-116.

Castles, M., Heinsohn, R., Marshall, H.H., Lee, A.E., Cowlishaw, G. and Carter, A.J. 2014. Social networks created with different techniques are not comparable. Animal Behaviour, 96:59-67.

Corbey, R. and Lanjouw, A. 2013. The politics of species: Reshaping our relationships with other animals. Cambridge University Press.

Diamond, J. 2012. The world until yesterday: What can we learn from traditional societies? Penguin.

Diamond, J. 2005. Collapse: How societies choose to fail or succeed. Penguin.

Estes, J.A. 2006. Whales, whaling, and ocean ecosystems. University of California Press.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B. and Marquis, R.J. 2011. Trophic downgrading of planet Earth. Science 333:301-306.

Farine, D.R. 2015. Proximity as a proxy for interactions: issues of scale in social network analysis. Animal Behaviour 104:1–5.

Farine, D.R. and H. Whitehead. 2015. Constructing, conducting and interpreting animal social network analysis. Journal of Animal Ecology 84:1144–1163.

Ford, J.K.B., Ellis, G.M. and Balcomb, K.C. 2000. Killer Whales. University of British Columbia Press.

Garland, E.C., Goldizen, A.W., Rekdahl, M.L., Constantine, R., Garrigue, C., Hauser, N.D., Poole, M.M., Robbins, J. and Noad, M.J. 2011. Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. Current Biology 21:687-691.

Gero, S., Whitehead, H. and Rendell L. 2016 Individual, unit, and vocal clan level identity cues in sperm whale codas. Royal Society Open Science 3:150372.

Gero, S., Gordon, J. and Whitehead, H. 2013. Calves as social hubs: Dynamics of the social network within sperm whale units. Proceedings of the Royal Society B 280:20131113.

Gould, S.J. 1998. Leonardo's mountain of clams and the diet of worms. Harmony Books.

Gross, T. and Blasius, B. 2008. Adaptive coevolutionary networks: a review. Journal of the Royal Society Interface 5:259-271.

Hinde, R.A. 1976. Interactions, relationships and social structure. Man 11:1-17.

Hoppitt, W. and Laland, K.N. 2013. Social learning: an introduction to mechanisms, methods, and models. Princeton University Press.

Jambeck, J.R., Geyer, R., Wilcox, C., Siegler, T.R., Perryman, M., Andrady, A., Narayan, R. and Law, K.L.,2015. Plastic waste inputs from land into the ocean. Science 347:768-771.

Johnson, M.P. and Tyack, P.L. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. IEEE Journal of Oceanic Engineering 28:3-12.

Koch, P.L. and Barnosky, A.D. 2006. Late Quaternary extinctions: state of the debate. Annual Review of Ecology, Evolution, and Systematics 37:215-250.

Laland, K.N. and Galef, B.G. 2009. The question of animal culture. Harvard University Press.

Laland, K.N. and Hoppitt, W. 2003. Do animals have culture? Evolutionary Anthropology 12:150-159.

Mann, J., Stanton, M.A., Patterson, E.M., Bienenstock, E.J. and Singh, L.O. 2012. Social networks reveal cultural behaviour in tool-using using dolphins. Nature Communications 3:980.

Marcoux, M., Whitehead, H. and Rendell, L. 2007. Sperm whale feeding variation by location, year, social group and clan: evidence from stable isotopes. Marine Ecology Progress Series 333:309-314.

Marean C.W. 2015. The most invasive species of all. Scientific American 313.

McPherson, M., Smith-Lovin, L. and Cook, J.M. 2001. Birds of a feather: homophily in social networks. Annual Review of Sociology 27:415-44.

Myers, R.A. and Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. Nature 423:280-283.

Nowak, M.A. 2006. Evolutionary dynamics: exploring the equations of life. Harvard University Press.

Palumbi, S.R. 2002. The evolution explosion: how humans cause rapid evolutionary change. WW Norton & Company.

Pinter-Wollman, N., Hobson, E.A., Smith, J.E., Edelman, A.J., Shizuka, D., De Silva, S., Waters, J.S., Prager, S.D., Sasaki, T., Wittemyer, G. and Fewell, J. 2013. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. Behavioral Ecology 25:242-255.

Railsback, S.F. and Grimm, V. 2013. Agent-based and individual-based modeling: a practical introduction. Princeton University Press.

Rendell, L.E. and Whitehead, H. 2003. Vocal clans in sperm whales (*Physeter macrocephalus*). Proceedings of the Royal Society of London B 270:225-231.

Rendell, L. and Whitehead, H. 2001. Culture in whales and dolphins. Behavioral Brain Sciences 24:309-324.

Safina, C. 2015. Beyond words: what animals think and feel. Macmillan.

Sakakibara, C., 2009. ‘No whale, no music’: Inupiaq drumming and global warming. Polar Record 45:289-303.

Sayigh, L.S., Tyack, P.L., Wells, R.S., Solow, A.R., Scott, M.D. and Irvine, A.B. 1998. Individual recognition in wild bottlenose dolphins: a field test using playback experiments. Animal Behaviour 57:41-50.

Springmann, M., Godfray, H.C.J., Rayner, M. and Scarborough, P. 2016. Analysis and valuation of the health and climate change cobenefits of dietary change. Proceedings of the National Academy of Sciences of the USA. doi: 10.1073/pnas.1523119113.

Tarnita, C.E., Antal, T., Ohtsuki, H. and Nowak, M.A. 2009. Evolutionary dynamics in set structured populations. Proceedings of the National Academy of Sciences of USA 106:8601-8604.

Tennie, C., Call, J. and Tomasello, M. 2009. Ratcheting up the ratchet: on the evolution of cumulative culture. Philosophical Transactions of the Royal Society of London B 364:2405-2415.

Tinbergen, J. 1953. Social behaviour in animals: with special reference to vertebrates. Methuen & Co. Press.

Tomasello, M. 1999. The Human Adaptation for Culture. Annual Review of Anthropology 28: 509-529.

van Schaik, C.P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C.D., Singleton, I., Suzuki, A., Utami, S.S. and Merrill, M. 2003. Orangutan cultures and the evolution of material culture. Science 299:102-105.

Wake, D.B. and Vredenburg, V.T. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proceedings of the National Academy of Sciences of the USA 105:11466-11473.

Weilgart, L.S. 2007. The impacts of anthropogenic ocean noise on cetaceans and implications for management. Canadian Journal of Zoology 85:1091-1116.

Whitehead, H. 2009. How might we study culture? A perspective from the ocean. In: The question of animal culture. (R.N. Laland and B. Galef, eds). Harvard University Press 125-152pp.

Whitehead, H. and James, R. 2015. Generalized affiliation indices extract affiliations from social network data. Methods in Ecology and Evolution 6:836-844.

Whitehead, H. and Rendell, L. 2014. The cultural lives of whales and dolphins. University of Chicago Press.

Whitehead, H. and Rendell, L. 2004. Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. Journal of Animal Ecology 73:190-196.

Whitehead, H. and Dufault, S. 1999. Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. Advances in the Study of Behavior 28:33-74.

Whitehead, H., McGill, B. and Worm, B. 2008. Diversity of deep-water cetaceans in relation to temperature: implications for ocean warming. Ecology Letters 11:1198-1207.

Whitehead, H., Christal, J. and Dufault, S. 1997, Past and distant whaling and the rapid decline of sperm whales off the Galápagos Islands. Conservation Biology 11:1387-1396.

Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E., Wrangham, R.W. and Boesch, C. 1999. Cultures in chimpanzees. Nature 399:682-685.

Whiten, A., Caldwell, C.A. and Mesoudi, A. 2016. Cultural diffusion in humans and other animals. Current Opinion in Psychology 8:15-21.

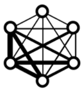
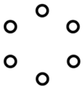
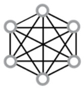
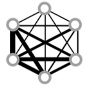
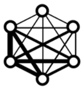
Whiten, A., Horner, V. and de Waal, F.B.M. 2005. Conformity to cultural norms of tool use in chimpanzees. Nature 437:737-740.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B., Lotze, H.K., Micheli, F., Palumbi, S.R. and Sala, E. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314:787-790.

Yeakel, J.D., Pires, M.M., Rudolf, L., Dominy, N.J., Koch, P.L., Guimarães, P.R. and Gross, T. 2014. Collapse of an ecological network in Ancient Egypt. Proceedings of the National Academy of Sciences of the USA 111:14472-14477.

APPENDIX A: SUPPLEMENTARY MATERIAL FOR CHAPTER 2[13]

A2.1 TABLE S2.1. Glossary of network terminology and its interpretation in the context of animal societies, based on refs. 1-7.

	Definition	**Meaning in the animal social context**
Network, graph 	Collection of points (see "nodes") joined in pairs by lines (see "edges") according to a defined relationship.	Population of individuals represented by nodes and connected by their social relationships represented by edges.
Nodes, vertices 	Points in the network diagram, representing the elements of the studied system. Nodes can have different states.	Usually represent identified individuals, but can represent higher levels of social structure. States of nodes include sex, age, behaviour types.
Edges, links, ties 	Connecting lines between two nodes in the network, representing a relationship between the elements of the system.	Represents the social relationship between two individuals.
Binary edges 	Edges can be present or absent and represent the presence of a qualitative relationship between two nodes in a network.	Presence or absence of a social relationship (or social interactions) between two identified individuals.
Weighted edges 	Quantitative relationships between two nodes in a network, whose weights are proportional to the relationship intensity.	Quantitative measure of social relationships. Commonly, weighted edges represent the proportion of time two individuals spend associated, estimated by association indices [7], or the rate at which they interact per unit time.
One-mode network 	Networks in which all nodes have the possibility of being connected.	Animal social networks themselves are examples of one-mode networks: all pairs of individuals may have a relationship.
Two-mode network	Networks whose nodes are divided into two distinct sets, with edges only occurring	Figure 2.4 is a two-mode network, illustrating individuals connected to the behaviour types that they perform.

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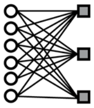
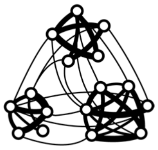
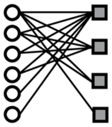
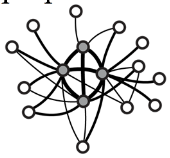
[13] *This appendix available online at http://rstb.royalsocietypublishing.org/content/royptb/suppl/2013/03/28/rstb.2012.0340.DC1/rstb20120340supp1.pdf as supplementary material for the manuscript: Cantor M. & Whitehead H. 2013. The interplay between social networks and culture: theoretically and among whales and dolphins. Philosophical Transactions of the Royal Society B. 368. 1618, 20120340. doi: 10.1098/rstb.2012.0340*

	between different sets of nodes.	
Coevolutionary (or adaptive) network	Network exhibiting a feedback loop between the local and topological dynamics, i.e. the state of the nodes and the evolution of the network structure.	We suggest that this feedback loop can represent the interplay between changes in individual behaviour and the social structure, mediated by social learning occurring during social relationships (see Figure 2.1b).
Topology of the network	The arrangement of the nodes and the pattern of relationships between them; the structure of a network.	The topology of a social network is an illustration of the social structure of a population.
Modular structure 	Network composed of weakly interlinked groups of nodes, which are strongly internally connected.	A modular social network depicts sets of individuals that interact or associate at high frequency with each other, and at lower frequency with individuals of other modules.
Nested structure 	In a nested two-mode network, some nodes have more interactions than others and there is a tendency for interactions of nodes with few interactions to be a proper subset of the interactions of nodes with more interactions	Figure 2.4 contains a nested individual-strategy network in which individuals that perform few strategies tend to perform a proper subset of the behavioural strategies performed by the individuals that perform several strategies.
Small-world properties 	Networks in which two nodes that are both linked to a third node tend to be themselves linked and in which there is a small average shortest path length between individuals.	In a small-world network, most individuals are not directly related to each other, but almost everyone can be reached from every other by a small number of relationship steps.
Shortest path length	The least number of steps between two connected individuals that separate two nodes in a network.	Measures the shortest distance between two individuals in a social network, in terms of number of intermediate relationships. It is a measure of the efficiency of information transmission.
Connectance	The proportion of realized edges in relation to possible edges.	Total number of dyadic relationships given the total number of possible dyadic relationships.
Strength	The sum of the weights of all edges connected to a node.	Sum of intensity of all social relationships of a given individual, sometimes called gregariousness.
Closeness centrality	Total distance of a given node to all other nodes in the network, defined by the inverse sum of its	A measure of how related an individual is to all others in the social network.

	shortest distances to all other nodes.	
Betweenness centrality	Measures the degree to which a node lies on the shortest path between two other nodes.	Measures the number of shortest paths that passes through an individual; thus individuals with high betweenness may funnel and control the flow of information through the social network.

A2.2 SUPPLEMENTARY REFERENCES

1. Boccaletti, S., Latora, V., Moreno, Y., Chavez, M. & Hwang, D. U. 2006 Complex networks: structure and dynamics. *Phys. Rep.* **424**, 175-308. (doi: 10.1016/j.physrep.2005.10.009)
2. Costa, L. da F., Rodrigues, F. A., Travieso, G. & Villas Boas, P. R. 2007 Characterization of complex networks: a survey of measurements. *Adv. Phys.* **56**, 167-242. (doi: 10.1080/00018730601170527)
3. Croft, D. P., James, R. & Krause, J. 2008 *Exploring animal social networks*. Princeton, New Jersey: Princeton University Press.
4. Gross, T. & Blasius, B. 2008 Adaptive coevolutionary networks: a review. *J. R. Soc. Interface* 5, 259-271. (doi: 10.1098/rsif.2007.1229)
5. Newman, M. E. J. 2010 *Networks: an introduction*. Oxford University Press.
6. Vital, C. & Martins, E. P. 2009 Using graph theory metrics to infer information flow through animal social groups: a computer simulation analysis. *Ethology* **115**, 347-355. (doi: 10.1111/j.1439-0310.2009.01613.x)
7. Whitehead, H. 2008 *Analyzing animal societies: quantitative methods for vertebrate social analysis*. Chicago: University of Chicago Press.

A2.3 COPYRIGHT RELEASE: PERMISSION TO REPRODUCE PUBLISHED ARTICLE

Published article:
Cantor M. & Whitehead H. 2013. The interplay between social networks and culture: theoretically and among whales and dolphins. Philosophical Transactions of the Royal Society B. 368. 1618, 20120340. doi: 10.1098/rstb.2012.0340

Ph.D. Thesis:
On the interplay between society and culture: causes, consequences and stability of sperm whale clans
1355 Oxford Street, Department of Biology, Dalhousie University, Halifax NS, B3H 4J1, Canada

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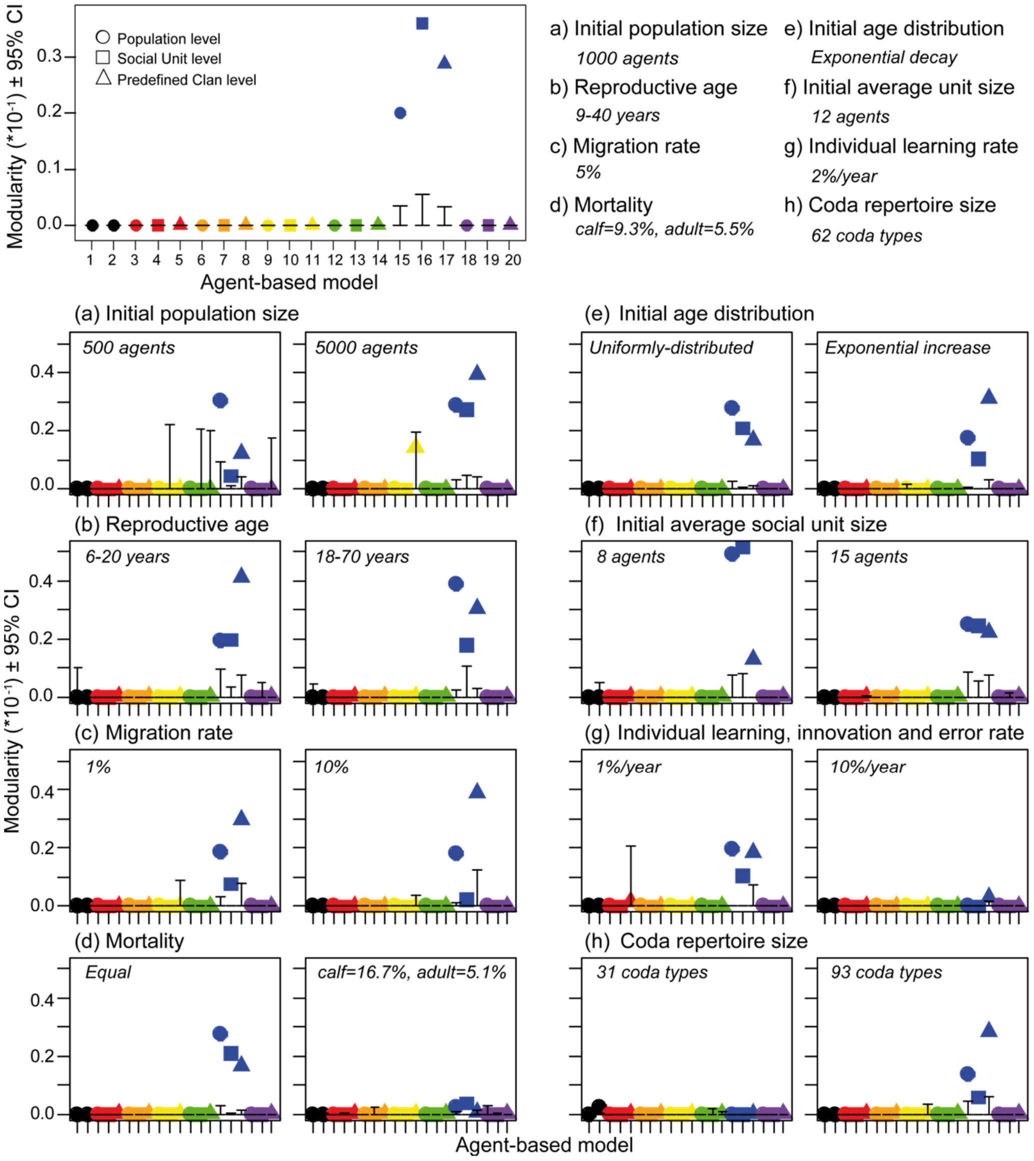
APPENDIX B: SUPPLEMENTARY MATERIAL FOR CHAPTER 3[14]

B3.1 SUPPLEMENTARY FIGURE S3.1



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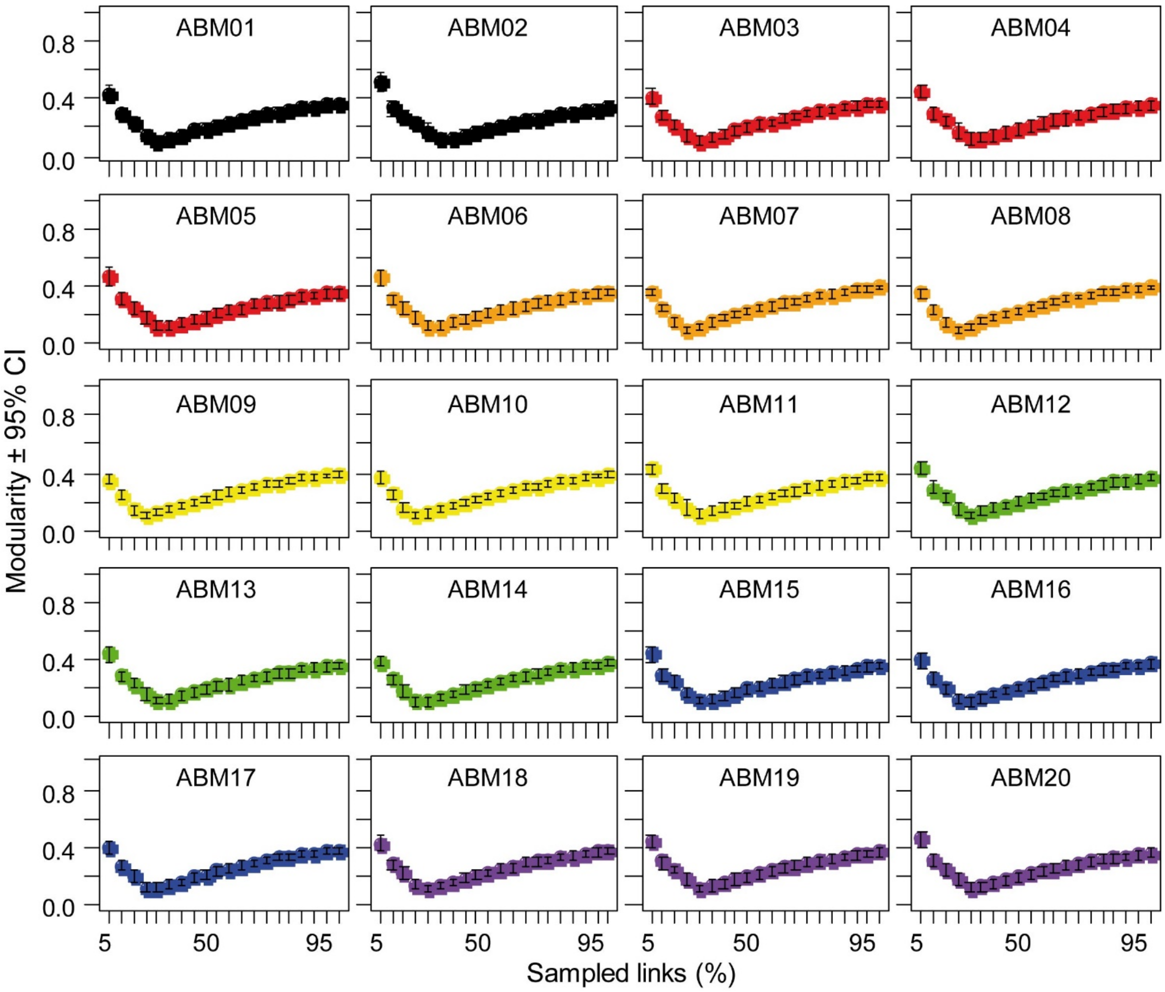
[14] *This appendix is available online at http://www.nature.com/ncomms/2015/150908/ncomms9091/extref/ncomms9091-s1.pdf as supplementary material for the manuscript: Cantor M, Shoemaker LG, Cabral RB, Flores CO, Varga M, Whitehead H. 2015. Multilevel animal societies can emerge from cultural transmission. Nature Communications 6: 8091. doi:10.1038/ncomms9091*

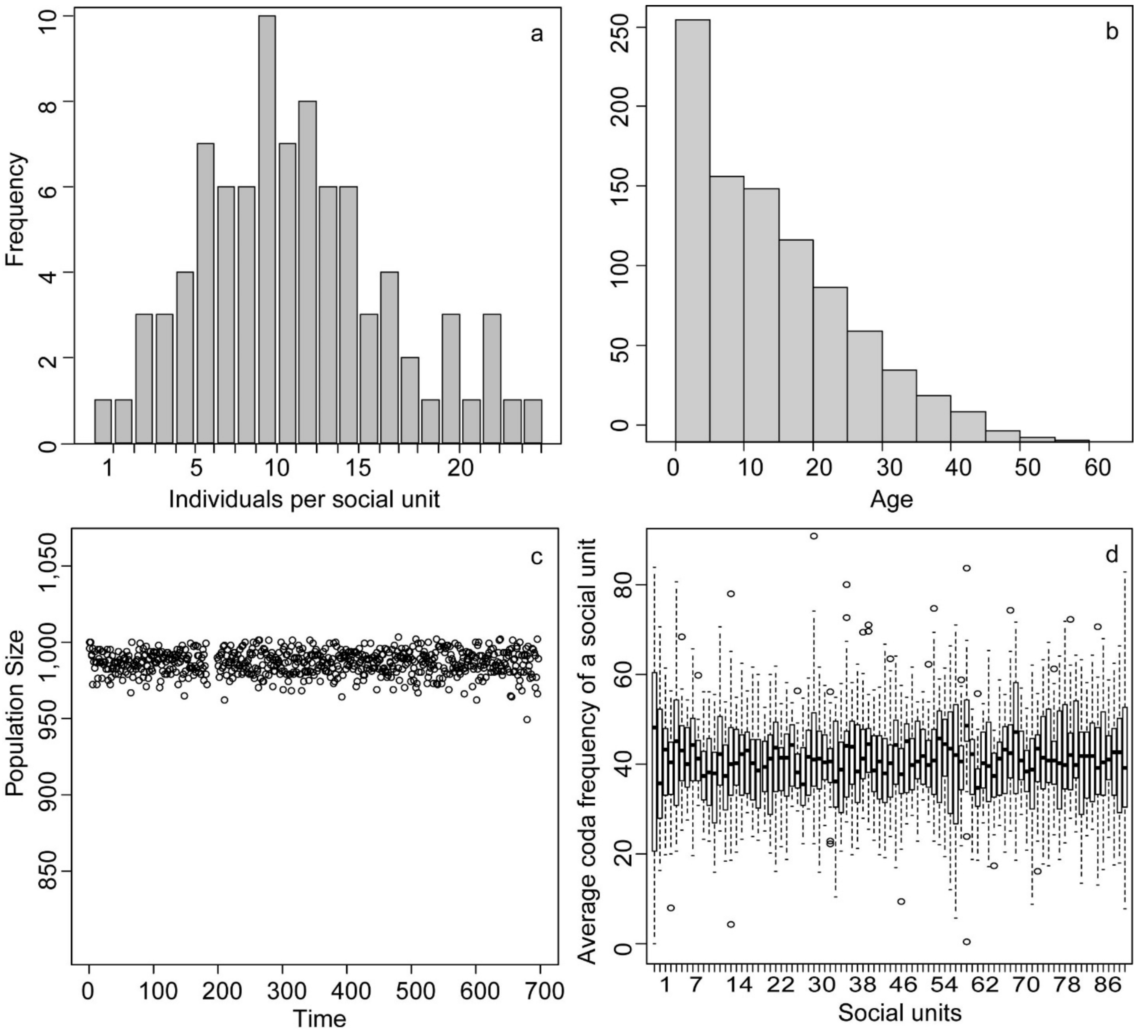
Supplementary Figure S3.1. Sensitivity analysis of parameterization and initial conditions in the emergence of clans in the 20 simulated scenarios. Clan emergence is evaluated by the weighted modularity *Q*-value (y-axis) in each of the acoustic networks simulated by the 20 agent-based models (x-axis). Color code denotes similar transmission mechanisms of coda types among agents operating at different social levels (see Figure 3.3A, main text); shapes represent the social level at which the transmission operated (circle: population, square: social unit, circle: predefined geographical clan); whiskers represent the 95% confidence intervals (CI) estimated by an appropriate theoretical model, based on 1000 iterations and 10 replicates for each model. Significant *Q*-values, those falling outside of the 95% CI of the benchmark distribution ($P < 0.001$), indicate a reliable partition in the acoustic networks, i.e. a modular topology with subsets of social units (nodes) more strongly connected with each other than with the rest of the network (see Figure 3.4, main text). The top plot illustrates our main results (Figure 3.3C, main text), followed by their initial parameters values. In each of the 16 new scenarios below (a-h), a single parameter was changed at a time for all 20 models with values representing the extremes of a biologically meaningful range (the parameter value is indicated in the top left of the plot). Note that each small plot resembles very much the main pattern shown in the top plot, indicating that the clan emergence presented in the main text is robust to variation in the parameters and initial conditions.

B3.2 SUPPLEMENTARY FIGURE S3.2



Supplementary Figure S3.2. Sensitivity analysis of the weighted modularity metric along a gradient of increasing sampling of the link weights in the acoustic networks. The modularity metric defines a reliable partition in the acoustic networks (i.e. emergent clans) simulated by each of the 20 agent-based models (ABMs). Whiskers represent the 95% confidence intervals (CI) given by 1000 replicates in the bootstrap procedure (link weight resampling with replacement). Color code denotes similar transmission mechanisms of coda types among agents operating at different social levels (following Figure 3.3A, main text). Note the strikingly similar pattern in all scenarios, conferring robustness to our chosen metric for clan partition across the range of possible weights for a link (coda repertoire similarity) between nodes (social units) in the simulated networks.

B3.3 SUPPLEMENTARY FIGURE S3.3



Supplementary Figure S3.3. Typical simulated dataset. Output of a representative simulated dataset, with social learning of coda types within social units (ABM04), after 700 simulated years: (A) Social unit size distribution (number of agents); (B) Age distribution (in simulated years, i.e. time steps in the simulation); (C) Population size over time (number of agents); (D) Coda frequency of all repertoires of all agents within each social unit. Each boxplot represents the frequency distribution of a social unit; boxes represent 1st and 3rd quantiles; black horizontal bars represent median; dashed whiskers represent minimum and maximum frequencies; circles indicate outliers.

B3.4 Supplementary Table S3.1. Modularity results and averaged acoustic similarity in all 20 agent-based models.

ABM	**Transmission process and level of operation**	**Modularity**		**Average acoustic similarity ± SD**				
				Emergent social units		**Emergent clans**		
		Q	**95% CI**	**within**	**between**	**#**	**within**	**between**
01	Individual learning (IL)	0	0 – $0.6*10^{-8}$	0.3301±0.0122	0.3297±0.0079	1	0.3301	-
02	Genetic inheritance (GI)	$0.1*10^{-8}$	0 – $0.8*10^{-8}$	0.4405±0.0533	0.3902±0.0312	1	0.3913	-
03	Social learning (SL) at population level	0	0 – $1.7*10^{-8}$	0.5026±0.0196	0.5017±0.0127	1	0.5026	-
04	Social learning (SL) at unit level	0	0 – $0.2*10^{-8}$	0.4958±0.0170	0.4956±0.0120	1	0.4958	-
05	Social learning (SL) at clan level	0	0 – $0.4*10^{-8}$	0.4874±0.0138	0.4875±0.0106	1	0.4872	-
06	SL+Homophily (H) at population level	0	0 – $0.9*10^{-8}$	0.9592±0.0139	0.9545±0.0106	1	0.9592	-
07	SL+Homophily (H) at unit level	0	0 – $0.2*10^{-8}$	0.9546±0.0196	0.9494±0.0142	1	0.9546	-
08	SL+Homophily (H) at clan level	0	0 – $0.5*10^{-8}$	0.9613±0.0103	0.9570±0.0077	1	0.9575	-
09	SL+Conformism (C) at population level	$0.2*10^{-8}$	0 – $0.9*10^{-8}$	0.7477±0.0122	0.7470±0.0101	1	0.7495	-
10	SL+Conformism (C) at unit level	0	0 – $0.9*10^{-8}$	0.7538±0.0171	0.7536±0.0123	1	0.7538	-
11	SL+Conformism (C) at clan level	$0.6*10^{-8}$	0 – $0.7*10^{-8}$	0.7094±0.0119	0.7086±0.0082	1	0.7086	-
12	SL+Symbolic Marking (SM) at population	0	0 – $0.3*10^{-8}$	0.4246±0.0100	0.4253±0.0068	1	0.4246	-
13	SL+Symbolic Marking (SM) at unit level	0	0 – $1.0*10^{-8}$	0.4821±0.0171	0.4813±0.0103	1	0.4821	-
14	SL+Symbolic Marking (SM) at clan level	$1.0*10^{-8}$	0 – $0.5*10^{-8}$	0.4794±0.0199	0.4801±0.0127	1	0.4808	-
15	SL+H+C at population level	0.020	0 – 0.003	0.7625±0.0540	0.7494±0.0491	3	0.7343±0.0684	0.7302±0.0054
16	SL+H+C at unit level	0.036	0 – 0.006	0.7582±0.0639	0.7437±0.0498	2	0.7183±0.0852	0.7115±0.0046
17	SL+H+C at clan level	0.029	0 – 0.003	0.8210±0.0730	0.8089±0.0581	2	0.8191±0.0112	0.8189±0.0056
18	SL+H+SM at population level	$0.9*10^{-8}$	0 – $1.7*10^{-8}$	0.9581±0.0152	0.9531±0.0110	1	0.9538	-
19	SL+H+SM at unit level	0	0 – $0.7*10^{-8}$	0.9546±0.0179	0.9479±0.0148	1	0.9546	-
20	SL+H+SM at clan level	$0.5*10^{-8}$	0 – $1.5*10^{-8}$	0.9567±0.0142	0.9509±0.0103	1	0.9524	-

For each agent-based models (ABM01-20), modularity *Q* ± 95% confidence intervals (CI) calculated with theoretical models, and averaged coda repertoire similarity ± standard deviation (s.d.) within and between social units and emergent clans are presented. ABMs are composed by a transmission process (individual learning, genetic inheritance, social learning (SL)), with/without a transmission bias (homophily (H), conformism (C), symbolic marking (SM)), occurring at three different social levels (population, social unit, predefined geographically-segregated clan).

B3.5 SUPPLEMENTARY TABLE S3.2. Parameters tested in sensitivity analysis of the agent-based model parameterization and initial conditions.

Parameter or starting condition	**Lower estimate**	**Chosen condition**	**Upper estimate**
a) Starting population size and carrying capacity (agents)	$N_0 = 500$	$N_0 = 1000$	$N_0 = 5000$
b) Reproductive age (years)	6 to 20	9 to 40	18 to 70
c) Migration rate among social units (agents year^{-1})	$c = 0.01$	$c = 0.05$	$c = 0.10$
d) Mortality probability (year^{-1})	Uniform (equal to all agents)	Age-dependent [1] ($M_{calves} = 0.093$, $M_{adults} = 0.055$)	Age-dependent [2] ($M_{calves} = 0.1679$, $M_{adults} = 0.0505$)
e) Initial age distribution (years)	Normal distribution (all ages are equally probable)	Exponential decay (more younger, less older agents)	Exponential increase (more older, less younger agents)
f) Initial average social unit size (agents)	$tvu = 8$	$tvu = 12$	$tvu = 15$
h) Individual learning rate (year^{-1})	$ilearn = 0$	$ilearn = 0.02$	$ilearn = 0.10$
g) Repertoire length (coda types)	$nCodas = 31$	$nCodas = 62$	$nCodas = 93$

Tested parameters were common to all of the 20 agent-based models. Three conditions for each parameter were tested: a lower extreme estimate, the chosen condition, and an upper extreme estimate.

B3.6 SUPPLEMENTARY NOTE 3.1

Collectively, the sensitivity analysis evaluated the robustness of the clan partition across various demographic, learning, and coda-specific parameterizations (see Sensitivity analysis of parameterization and initial conditions in the agent-based models, Supplementary Methods). The different effects considered were the proportion of potential tutors (adult agents) as source of cultural traits (coda types) [3], their dispersal rates [4,5] as seeding of copying errors and innovations [6,7] between social units on the transmission of coda types among learners (calves), the diversity of cultural traits in the population and hence the emergence distinct cultural groups [8], here the clans of sperm whales. The results were very robust to changes in the initial conditions and parameterization (Supplementary Figure S3.1). This is clear in two key ways. First, in all of the 16 cases with different initial conditions, there was no reliable clan partition in the models in which they originally have not emerged (ABMs 1-11, 13-14, 18-20). In these cases, modularity was zero or non-significant and 2 to 3 orders of magnitude smaller than in the cases where clans emerged (Supplementary Figure S3.1). Second, clans emerged only in the very same three models with biased social learning of coda types (ABMs 15-17) in which we originally observed partition of the acoustic networks into modules (Figure 3.4, main text).

Although the overall pattern is robust to the initial conditions, there were a few deviant situations (10%: 5 situations/(3 models*16 cases)) in which these three models that originally yielded clans did not produce them when the parameters were set to extreme estimates (Supplementary Figure 3.1). These were when: a) individual learning rate was excessively high in ABMs 15 and 16; and c) coda repertoire length was excessively small in ABMs 15, 16 and 17. We interpret these findings as follow. First, with very high rate of individual learning, the social learning efficiency decreases. Such rates (10% per year) would represent very low fidelity in copying coda types and/or very high rate of innovation by calves. Either way, the overall diversity increases, dismantling possible homogeneity in coda repertoires within potential clans. Second, with very small coda repertoires (c), there are few coda types and consequently little room for variation. When averaging the repertoires of all individuals of social units, the overall diversity decreases, leading to the convergence of all units' repertoires and consequently to no partition into clans.

B3.7 SUPPLEMENTARY NOTE 3.2

Our sensitivity analysis of our metric for the clan partition (see Sensitivity analysis of clan partition, Supplementary Methods) suggests that the clan emergence is robust to the variation in the averaged acoustic similarity among social units (acoustic network links) (Supplementary Figure 3.2). In all the 20 agent-based models, the pattern was strikingly similar: modularity values were high, stable (with small 95% confidence intervals) and consistent from 5 to 100% of the sampled links (despite an overall decrease around 30%). This confers robustness to our chosen metric for clan partition across the range of possible weights for a link (coda repertoire similarity) between nodes (social units) in the simulated networks.

B3.8 SUPPLEMENTARY METHODS 3.1. The *balabm* R package.

Agent-based models are available in the R package *balabm v.1.1,* which is deposited open-sourced at the Bitbucket repository https://bitbucket.org/maucantor/balabm. The package also makes available the empirical data used in this work.

1. Installation: The package can be installed from the repository:
   a. Launch *R*. Install and/or load the package '*devtools*' with the command:
   if(!require(devtools)){install.packages('devtools'); library(devtools)}
   b. Install and load '*balabm*' with the command:
   install_bitbucket("maucantor/balabm"); library(balabm)
2. Running the models.
   a. Browse your local machine for the folder where *R* was installed and find the folder */library/balabm.*
   b. The folder */abm/* contains the scripts for each of the ABM (Check README.txt). Copy the content of this folder to your working directory.
   c. Open the *R* scripts for the agent-based models in *R* (or *RStudio*) to run the models.

When using these models or data, please cite the R package along with the original paper:

citation("balabm")

B3.9 SUPPLEMENTARY METHODS 3.2. Empirical support for the agent-based models.

We built agent-based models based on the following empirical socioecological findings:

a. Social structure parameters

i. Female and immature sperm whales are found in nearly-permanent social units that include related, as well as unrelated, animals [9]. Mature males lead quasi-solitary lives and spend a great part of their lives near the poles, associate only briefly with female social units for mating [9], and rarely perform coda vocalizations [10]. Therefore, males would not play any important role in the behavioural learning mechanisms we addressed here, and thus the simulated social units contained only female agents.

ii. Calves experience high natal group philopatry, i.e. they remain in the natal social unit since they are highly dependent on their mothers [9,11]. Thus, agents with 0, 1 and 2 years old do not change social unit membership, i.e., the probability of remaining with the mothers in their natal social unit (i.e. retaining the social unit membership label) was $rem = 1$.

iii. Changes in social unit membership are very rare. Social units are long-term entities that are composed of females and immatures that live and move together for many years and likely their entire lives [9,12]. Thus, adult females have very low probability of migrating to other social units [13]. There is a rough estimate of 6.3% probability of individuals to be involved in social unit merging, splitting or transferring of individuals within a given year [13]. Thus, in our models there was a very low probability, $c = 0.05$, of adult agents migrating to another social unit (i.e., of randomly changing their social unit label) through their lives. In the abovementioned study [13], the individuals who changed social units were relatively young females. Thus, in our models the migration probability was age-dependent, inversely proportional to the agents' age, with youngster agents more prone to change their social unit.

iv. Therefore, with *i, ii*, and *iii*, the social units emerge in the simulations as nearly-permanent and nearly-matrilineal, as in the empirical data. Although four other short-term aggregative levels have been described for sperm whales, none of them are considered a social level *per se* [9] either because they are temporary (small temporal scale: clusters, groups) or because they do not involve social interaction among individuals (large spatial scale: aggregations, concentrations). Clusters are ephemeral sets of individuals swimming closely at the water surface for periods of minutes, and groups are sets of units moving together in a coordinate manner for periods of few hours to few days [9]. Concentrations are patches of whales spanning a few hundred kilometers, within which aggregations of individuals within 10-20 kilometers may occur [9]. Therefore, these short-term aggregative levels were not represented in the models.

b. Population parameters

v. Empirical social units were delineated using individuals re-sighted at least three times, with at least two other individuals during at least two 12h-identification periods spaced out by at least 30 days [13]. Off the Galápagos Islands, there were 174 photo-identified individual sperm whales that meet the above criteria and were assigned to 18 known social units [13]. To account for undersampling, the simulated initial population size was more than 5 times larger (N_0 = 1000 individuals) than the empirical number of photo-identified individuals, but still a reasonable number of sperm whales (excluding mature males) to be using the waters off the Galápagos Islands [14].

vi. The mean social unit size off the Galápagos Islands is about 12 members (including sometimes juvenile males) [14,15]. The maximum initial number of simulated social units was a function of the initial population size: $T_{VU} = N_0 / SU$ where T_{VU} is the total number of social units at time step t=1, N_0 is the initial population size, and SU is a random integer from the uniform distribution $\epsilon[8,14]$.

vii. Social units rarely split, merge, or experience abrupt membership changes [9,13]. With stochastic demographic processes in the simulations, social units may increase or decrease in size over the simulated time (see Appendix B3.3, Supplementary Figure 3.3A). To prevent the simulated social units from growing indefinitely, they split in half when their size doubled the maximum initial social unit size at time step t=1. All agents of a splitting social unit had the same probability of remaining in their original unit or being part of a new social unit. That is, half of the agents of that social unit were randomly selected with equal probabilities to keep their social unit membership labels, while the other half had their social unit membership replaced by the new label T_{vu_t} +1, where T_{vu_t} is the maximum number of social units existent at the time step t.

viii. Although precise ages are hard to estimate empirically, female sperm whales are thought to become sexually mature after at about the age of 9, stop reproducing after about 40 years old, and live 70 years on average [9]. In the simulations, agents followed these characteristics. The simulation were started with agents' age being randomly assigned from an exponential distribution ($f(age) = \lambda \cdot e^{(-\lambda \cdot age)}$, $age \geq 0$, $\lambda = 0.08$), so the initial population was mostly young, with ages typically varying from 0 to 70 years old. Agents reproduced from 9 to 40 years old (i.e. newborn calf agents are added to their simulated social units), and demographic rates were chosen such that most whales lived 70 years (although some could die earlier and a few live longer) (Appendix B3.3, Supplementary Figure S3.3B).

ix. The empirical female sperm whale reproduction rate is age-specific and estimated [16] to be $b_{emp\_i} = 0.257 - (0.0038 \times age_i)$, where b_{emp_i} is the empirical birth rate and age_i is the age in years of the individual *i*. Because we were interested only in female agents, we simulated female offspring only, so the simulated birth rate was half of the empirical one ($b_i = b_{emp\_i} / 2$), assuming a 1:1 sex ratio in birth events. At each time step *t,* a birth probability b_{i_t} was calculated for all agents of the population who reached sexual maturity, which have the same probability of giving birth. In the social unit of the selected reproductive agents there will be an addition of one agent with age 0 and an empty coda repertoire vector.

x. Population was modeled as density-dependent. We assumed that all social unit members compete for the same foraged resources, and thus the population fluctuated around the carrying capacity (i.e., the initial population size, N_0 = 1000 individuals) over time (see Appendix B3.3, Supplementary Figure 3.3C).

xi. Mortality rates (m_t) were defined as $m_t = [(B_t + N_t) - N_0] / (B_t + N_t),$ where B_t is the number of births in year *t*, N_t is the population size in year *t*, and N_0 is the initial population size. Calves usually have higher mortality than adults, and classic and recent empirical estimates corroborate this pattern [9,10]. In our models, to account for age-dependence in mortality we calculated the number of agents that would die in each time step, m_t, and removed agents from the simulation according to empirical estimates of mortality rates [9] (calf = 0.093 year^{-1}; adult and juveniles = 0.055 year^{-1}). Therefore, all agents in the population at the time step *t* had a probability of dying according to their age class. The death of selected agents was represented by the removal of their coda repertoires, social unit membership, and age labels from the model.

xii. The simulations lasted for *t* = 700 years, a period 10 times longer than the empirical life expectancy [9] and long enough to achieve a steady state in the simulations.

c. Learning parameters

xiii. While sperm whales mainly produce echolocation sounds (continuous series of clicks), they also produce codas, stereotypical patterns of 3-40 broadband clicks lasting less than 3 seconds in total [17]. Codas are performed in a social context [9,18,19] almost exclusively by females [10] and their major function seems to be labelling and reinforcing social bonds [20].

xiv. Sperm whale social units have vocal repertoires of about 31 coda types (usually 3-4 commonly used plus about 25 to 28 uncommonly used coda types) [19,21]. In our simulations, agent calves started with coda repertoires of 31 random codas (frequencies of which were drawn from the uniform distribution ϵ[0,100]). Along the simulation, they could change their repertoires and add frequencies of up to 62 coda types, which is twice as long as the empirical coda repertoires to correct for undersampling of empirical data.

xv. Individuals gradually develop their codas in early ages [22,23] and rarely change coda repertoire as adults. The precise age for learning the acoustic repertoire is genuinely difficult to estimate given the impossibilities of experimental intervention with sperm whales in the wild. While the empirical evidence is inherently scarce, it suggests that individuals mainly compose their vocal repertoires at early ages, rather than over the course of their lives. Based on the best available empirical data, we defined a calf as an agent up to 3 years old—since after this age sperm whales are usually larger and begin to wean and perform deeper dives [12]. Learning was modelled such that calf agents change their coda repertoires between the ages of 0 and 3 years old (see Figure 3.2, main text).

xvi. To account for copying errors and innovations [6,24], in all models calf agents were subjected to a low probability (0.02) of replacing the frequency of one randomly chosen coda type (62 codas * 0.02 ≈ 1) by a value drawn from the uniform distribution $\epsilon[0,100]$ each year (at ages 0, 1 and 2 year old). This effect represented individual learning, i.e. the chance of deliberately creating new coda types (innovation), or randomly creating a new type by copying an existent one with low fidelity (copying error). Therefore, with *xii* and *xiii,* changes in the coda repertoire occurred three times for each calf agent and after the age of 3, their repertoires were fixed.

xvii. Individuals within social units have very similar (but not identical) coda repertoires [21,23,25,26]; and social units of the same clans have similar (but not identical) coda repertoires [21,23]. Therefore, just as with the empirical data [21], we evaluated possible clan segregation based on the coda repertoire of the social units. In our simulations, we used the averaged coda repertoires of the social units to examine whether they cluster in the simulated acoustic networks (i.e., by testing for modularity).

xviii. Social units from different clans in the same area have very distinct coda repertoires [21], which justifies clustering of social units with high coda repertoire similarity as emergent clans in the simulations.

xix. Demographic effects and individual movements—such as migration, immigration and dispersal—can be important drivers of cultural diversity [27]. Our models were explicitly temporally-structured and implicitly spatially-structured. To account for the potential demographic and movement effects in coda transmission, while respecting the structure of the sperm whale societies with nearly-permanent social units, we simulated different levels of population mixing. We replicated all the models with social learning and transmission biases in the three social levels that are relevant for sperm whales: social unit, predefined geographical clans and population. In doing so, it is reasonable to assume that the mean distance between an individual and other members of its unit is less than that between the individual and other members of its clan, which in turn is less than the distance between two members of the whole population. We represented the case in which social units are fairly closed structures by allowing the calf agents to learn only within their own social units. We represented learning between social units that are spatially segregated by starting the simulations with predefined clans mimicking the geographically-segregated clans found in the Atlantic [28], and allowing calf agents to copy from agents of other units, but only from those within their clans. Finally, we represented the case of a completely mixed population by allowing the calf agents learn from any agent in the population.

B3.10 SUPPLEMENTARY METHODS 3.3. Sensitivity analysis of parameterization and initial conditions in the agent-based models.

Agent-based models usually rely on assumed parameters to modulate the agents' behaviour. In some cases, their empirical values are unknown. We have grounded the parameter estimates of our models using the best empirical evidence available (see Empirical support for the agent-based models, Appendix B3.9, Supplementary Methods 3.2). In our main analysis (Figures 3.3 and 3.4, main text), the parameters and initial conditions were fixed across scenarios, so we can directly compare differences in learning strategies—the overarching goal of this study—without having the confounding influence of changing parameter values or starting conditions.

Possibly, different starting points in the simulated scenarios could cascade into different model outputs. To evaluate the robustness of our findings on the partition of simulated social units of sperm whales into clans with distinct acoustic behaviour, we performed a sensitivity analysis of the parameters that were common to all of the 20 agent-based models. We assessed the impact of 6 initial demographic parameters in addition to 2 key parameters of coda transmission (Appendix B3.5, Supplementary Table S3.2). Some demographic parameters could affect the number of learners (calf agents) and tutors (adult agents) in the population: *population size* (carrying capacity) controls number of agents; *reproductive age* controls addition of agents; *mortality* controls removal of agents; *initial age distribution* controls number of calves in the starting populations. Others tested demographic parameters could affect the probabilities of interaction between agents: *migration rates among social units* affect population mixing; *average social unit size* affect number of associates of an agent. Finally, the coda transmission parameters could affect learning fidelity and cultural trait diversity: *individual learning* controls the rate of innovations and leaning errors in producing new coda types; while *coda repertoire length* controls number of coda types to be learned.

To evaluate the clan partition, we ran the models changing a single parameter value at a time and calculated the modularity *Q*-metric for weighted one-mode networks, our measure of clan partition. Significantly high *Q*-values indicated a reliable partition in the acoustic network into modules, i.e., the emergent clans. The significance of *Q*-values was checked using an appropriate theoretical model reshuffling the link weights among social units, using 1000 iterations. Modularity was considered high and significant when the observed *Q*-value was higher than the expected by chance, falling outside of the 95% confidence intervals (CI) of the benchmark distribution generated by the theoretical model (for more details, see details in the main methods section).

Our models are computationally demanding; therefore, for each of the 8 parameters and initial conditions we tested two values (the extremes of a biologically-meaningful range) and replicated it 10 times for each model, amassing 3200 *Q*-values from independent runs of the agent-based models. Supplementary Table 3.2 (Appendix B3.5) displays all parameters and their tested ranges. We compared our modularity findings (Figures 3.3C and 3.4, main text) with 16 other situations, changing a single parameter at a time. This allowed us to parse out the effect of each parameter on our modularity results, rather than having confounding influences of multiple parameter changes as a time. While, ideally, we would examine interactions of parameters as well, due to computational limitations with agent-based models, it is common to examine changing a single parameter at a time [32,33]. The results are available in the Supplementary Figure 3.1 (Appendix B3.1) and Supplementary Note 3.1 (Appendix B3.6).

B3.11 SUPPLEMENTARY METHODS 3.4. Sensitivity analysis of clan partition.

We defined a clan, both in the empirical and simulated datasets, using a weighted modularity metric to evaluate the partition of the acoustic networks (i.e., nodes representing social units connected by weighted links representing similarity among their coda repertoires). Although the agent-based models simulated coda repertoires for each agent, the empirical data is not resolved at the individual level since it is logistically very difficult to assign coda production to individual whales in the wild (this has been achieved in just one case [26]). To make the simulated data comparable to the empirical data, we averaged the coda repertoires of all agents of the social units to build the acoustic networks (see Figure 3.4, main text). However, the simulation of coda repertoires with agent-based models represents a “complete sampling”, in the sense that we are able to record all codas of all agents of all social units. Clearly, this is not the case for the empirical data, for the same logistical challenges.

We have used the weighted counterpart of the modularity metric to account for fine-scale variation in the similarities among simulated social units. To evaluate if the metric is robust to variation in the levels of sampling in the individual coda repertoires—and make simulated and real-world acoustic networks even more comparable—we performed a sensitivity analysis to the resultant weighted modularity *Q*-values in the simulations. We resampled (with replacement, 1000 iterations) the simulated network links of all 20 ABMs and evaluated the modularity values with increasing sampling gradient, from 5% to 100% with increment of 5% of the links at a time (bootstrap procedure). The results are available in the Supplementary Figure 3.2 (Appendix B3.2) and Supplementary Note 3.2 (Appendix B3.7).

B3.12 SUPPLEMENTARY METHODS 3.5. Differences between empirical and simulated coda types.

Codas are stereotypical patterns of 3-40 broadband clicks lasting less than 3 seconds in total [17]. The empirical codas types are classified according to inter-click intervals, i.e., the proportion of time between the clicks [19,21]. For instance, a coda type labelled as 5R contains 5 regularly-spaced clicks (so 4 equal inter-click intervals), while a 4+1 coda also contains 5 clicks but with an extended period between the 4th and 5th clicks (so 3 equal and one extended inter-click interval). Sperm whales can produce several coda types [19,21]. Here, we simulated the absolute frequency of the different coda types each whale can make, not inter-click intervals that define coda types. In our agent-based models, each agent has a coda repertoire represented by a vector with maximum of 62 elements denoting absolute continuous frequencies of different coda types from 0 (absent) to 100 (always performed coda type). For instance, consider a whale *A* that always performs 5 codas types 3R, 4R, 5R, 4+1, 5+1; and a whale *B* that mostly performs the codas 3R, 4R, 7R but sometimes also performs the codas 6R, 2+1, 3+4, 2+4. The repertoire of a simulated agent representing *A* is given by a vector of 62 elements, 5 of which have frequency 100% and the rest is zeroed. Likewise, the repertoire of the agent *B* is also a 62-element vector but with 3 elements with 100%, 4 elements with intermediate frequency (say 30, 40, 60, 50%) and the rest is zeroed. Therefore, the two vectors differ both in number of zeroed elements and in the frequencies of the non-zeroed ones. Note that we simulated and compared frequencies of use of labelled codas, not the codas themselves, because we are interested in evaluating the diversity of codas individuals end up producing under different coda transmission scenarios (to further quantify and compare the similarity of their coda repertoires).

B3.13 SUPPLEMENTARY METHODS 3.6. Differences between empirical and simulated coda transmission.

The principal mechanism for the acquisition of coda repertoire is hypothesized to be social learning, in which individuals reproduce the coda types they are exposed to [19,21,23,29,30]. The main goal of our agent-based models is to test which transmission mechanisms, if any, can reproduce the empirical patterns (distinct vocal clans of sperm whales with highly similar coda repertoires), presumably generated by social learning of coda types among whales. Therefore, we modeled changes in the agents' coda repertoires (i.e. changes in the frequency of codas used) occurring due to varieties of social learning and other alternative transmission processes, to observe under which combination of transmission processes vocal clans (clusters of social units with similar coda repertoire) emerged. Briefly, the transmission processes modelled were: genetic inheritance or vertical transmission (agents copy the exact mother's repertoire), individual learning (agents are assigned to random coda types and frequencies), and oblique social learning (see main text and Figure 3.2).

Oblique social learning was simulated as agents copying different proportions of other older agents' repertoires (i.e. coda types and their frequencies of usage). For an example of a typical social learning simulated event, consider the two abovementioned fictional whales *A* and *B*. When the agent *A* "learns" from *B,* it randomly selects a coda type *i* from *B'*s repertoire (62-element coda vector) and copies their frequency of use so the *i*th element in *A*'s repertoire will contain the same value as the *i*th element in *B*'s repertoire. The proportion of coda types copied is predefined, as well as from whom the codas were copied (only from individuals of the same social unit; or from individuals of different social units of the same vocal clan; or from any individuals of the population) (see main text and Figure 3.2A, iii). This "pure" social learning could also be biased by homophily, conformism, and/or symbolic marking. In the models with homophily, agents copied coda types from agents of social units with high coda repertoire similarity to the social unit they belong to, but not their own (Figure 3.2A, iv). In the models with conformism, agents disproportionately copied the most common coda types (within their social unit, within their clan, or within the entire population) (Figure 3.2A, v). Finally, in the models with symbolic marking, agent calves copied a specific subset (~10%) of the coda repertoire of their social unit to mark the social unit they belong to. This subset is represented by 6 coda types that individuals from a given social unit will always perform (i.e., all agents will have 6 specific elements with 100% frequencies in the coda vector) (Figure 3.2A, vi). In our 20 sub-models, these transmission processes could be combined and occur within the social unit (Figure 3.2B, vii), the pre-defined vocal clan (Figure 3.2B, viii), or entire population (Figure 3.2B, xi) (see also the main text and Figure 3.3A for full description).

B3.14 SUPPLEMENTARY METHODS 3.7. Differences between empirical and simulated coda repertoire comparison.

Empirical coda repertoires were assigned to the social units whose members were photo-identified within 2h of the recording at the field and had at least 25 codas recorded. The empirical repertoires of the social units were compared using two methods, one based on continuous and other on categorical measures [21,31]. The first method used an averaged multivariate similarity method to compare codas with the same number of clicks, based on the infinity-norm distance between the absolute and standardized intervals between adjacent clicks (inter-click intervals):

$$s_{AB} = \frac{\sum_{i=1}^{n_A} \sum_{j=1}^{n_B}{}_{l_{j=l_i}} \frac{0.001}{(0.001+d_{ij})}}{(n_A \cdot n_B)} \tag{1}$$

where s_{AB} is the coda similarity between the repertoires A and B, each with n_A and n_B codas respectively; l_i is the number of clicks in coda i of set A, l_j is the number of clicks in coda j of set B, and d_{ij} is the maximum distance (given by the infinity-norm) between the inter-click interval vectors of the codas i and j. The basal similarity was 0.001 to give a very fine scale comparison of codas on the order of 1 millisecond (although results are robust to variation) [31]. The multivariate similarity (s) was used to build the links among social units in the empirical acoustic networks, which we then used to analyze the clan partition. The second method categorized codas into nearly discrete types based on the number of clicks using a k-means clustering algorithm and a variance ratio criterion to choose the number of clusters [19,21]. Each coda type was given a representative label (*e.g.* 3R for codas with three regularly spaced clicks; 4+1 for 5-click codas with an extended interval before the last click). Two categorical coda types were considered similar if they were assigned to the same type (categorical similarity = 1) and dissimilar if assigned to different types (categorical similarity = 0) [19,21].

In our agent-based models, we simulated frequencies of usage of coda types (categories), and not the inter-click intervals of each coda, therefore the coda repertoire comparison resembles the second method. We chose the asymmetric weighted Bray-Curtis index as a feasible metric to compare the simulated data—the averaged frequency of usage of codas within members of a social unit—to calculate the similarity between the repertoires of the social units and further evaluate the emergence of clans. For each two coda repertoires, the similarity of the frequencies of use of coda types was given by:

$$BC_{AB} = 1 - \left(\frac{2C_{AB}}{S_A+S_B}\right) \tag{2}$$

where BC_{AB} is the sum of the lowest frequency of the coda types that are common to both repertoires of the social unit A and B; S_A is the total frequency of the codas in the repertoire of the social unit A, while S_B is the total frequency of codas in the repertoire of the social unit B. The original Bray-Curtis index measures dissimilarity, so here $1- BC_{AB}$ gives the similarity between repertoires: from 0 (completely different) to 1 (exactly equal repertoires). Note that this metric did not consider coda types that were simultaneously absent (double zeroes) in both repertoire vectors. Finally, the Bray-Curtis similarities between simulated social units were used to build the simulated acoustic networks from which we analyzed the potential partition into clans.

B3.15 SUPPLEMENTARY REFERENCES

1. Chiquet, R. A., Ma, B., Ackleh, A. S., Pal, N. & Sidorovskaia, N. Demographic analysis of sperm whales using matrix population models. *Ecol. Model.* **248**, 71-79 (2013).
2. Whitehead, H. & Gero, S. Positive observed rates of increase do not reflect a healthy population: conflicting rates of increase in the sperm whale population of the eastern Caribbean. *Endanger. Species Res.* **27**, 207-218 (2015).
3. Williams, J. & Slater, P. Modeling bird song dialects—the influence of repertoire size and numbers of neighbours. *J. Theor. Biol.* **145**, 487–496 (1990).
4. Ellers, J. & Slabbekoorn, H. Song divergence and male dispersal among bird populations: a spatially explicit model testing the role of vocal learning. *Anim. Behav.* **65**, 671–681 (2003).

5. Nunn, C., Thrall, P., Bartz, K., Dasgupta, T. & Boesch, C. Do transmission mechanisms or social systems drive cultural dynamics in socially structured populations? *Anim. Behav.* **77**, 1515–1524 (2009).

6. Slater, P. J. The cultural transmission of bird song. *Trends Ecol Evol*. **1**, 94–97 (1986).

7. Whiten, A., Goodall, J., McGrew, W., Nishida, T. & Reynolds V. Charting cultural variation in chimpanzees. *Behaviour* **138**, 1481–1516 (2001).

8. Cantor, M. & Whitehead, H. The interplay between social networks and culture: theoretically and among whales and dolphins. *Phil. Trans. R. Soc. B* **368**, 20120340 (2013).

9. Whitehead, H. *Sperm Whales: Social Evolution in the Ocean*. (Chicago University Press, 2003).

10. Marcoux, M., Whitehead, H. & Rendell, L. Coda vocalizations recorded in breeding areas are almost entirely produced by mature female sperm whales (*Physeter macrocephalus*). *Can. J. Zool.* **84**, 609-614 (2006).

11. Gero, S., Gordon, J. & Whitehead, H. Calves as social hubs: dynamics of the social network within sperm whale units. *Proc. R. Soc. B.* **280,** 20131113 (2013).

12. Gero, S. *et al.* Behavior and social structure of the sperm whales of Dominica, West Indies. *Mar. Mamm. Sci*. **30**, 905-922 (2014).

13. Christal, J., Whitehead, H. & Lettevall, E. Sperm whale social units: variation and change. *Can. J. Zool.* **76,** 1431-1440 (1998).

14. Whitehead, H., Christal, J. & Dufault S. Past and distant whaling and the rapid decline of sperm whales off the Galápagos Islands. *Conserv. Biol.* **11**, 1387-1396 (1997).

15. Whitehead, H., Antunes, R., Gero, S., Wong, S. N. P., Engelhaupt, D., & Rendell, L. Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: Why are they so different? *Intl. J. Primatol.* **33,** 1142-1164 (2012).

16. Whitehead, H. Estimates of the current global population size and historical trajectory for sperm whales. *Mar. Ecol. Prog. Ser.* **242,** 295-304 (2002).

17. Watkins, W. A. & Schevill, W. E. Sperm whale codas. *J. Acoust. Soc. Am*. **62**,1486-1490 (1977).

18. Whitehead, H. & Weilgart, L. Patterns of visually observable behavior and vocalizations in groups of female sperm whales. *Behaviour* **118,** 271-296 (1991).

19. Weilgart, L. & Whitehead, H. Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behav. Ecol. Sociobiol.* **40,** 277-285 (1997).

20. Schulz, T. M., Whitehead, H., Gero, S. & Rendell, L. Overlapping and matching of codas in vocal interactions between sperm whales: insights into communication function. *An. Behav.* **76,** 1977-1988 (2008).

21. Rendell, L. & Whitehead, H. Vocal clans in sperm whales (*Physeter macrocephalus*). *Proc. R. Soc. B* **270,** 225-231 (2003).

22. Watkins, W. A., Moore, K. E., Clark, C. W. & Dahlheim, M. E. in *Animal Sonar* (eds Nachtigall, P.E. & Moore, P.W.B.) 99-107 (Plenum, 1988).

23. Gero, S. *On the Dynamics of Social Relationships and Vocal Communication between Individuals and Social Units of Sperm Whales*. Ph.D. Thesis (Dalhousie University, 2012).

24. Filatova, O. A., Burdin, A. M. & Hoyt, E. Is killer whale dialect evolution random? *Behav. Proc.* **99**, 34–41 (2013).

25. Rendell, L. & Whitehead, H. Do sperm whales share coda vocalizations? Insights into coda usage from acoustic size measurement. *An. Behav.* **67,** 865-874 (2004).

26. Schulz, T. M., Whitehead, H., Gero, S. & Rendell, L. Individual vocal production in a sperm whale (*Physeter macrocephalus*) social unit. *Mar. Mam. Sci.* **27,** 149-166 (2010).

27. Fayet, A. L., Tobias, J. A., Hintzen, R. E., & Seddon, N. Immigration and dispersal are key determinants of cultural diversity in a songbird population. *Behav. Ecol*. **25**, 744-753 (2014).

28. Antunes, R. N. C. *Variation in Sperm Whale (*Physeter macrocephalus*) Coda Vocalizations and Social Structure in the North Atlantic Ocean*. PhD thesis. (University of St. Andrews, 2009).

29. Rendell, L., Mesnick, S. L., Dalebout, M. L., Burtenshaw, J. & Whitehead, H. Can genetic differences explain vocal dialect variation in sperm whales, *Physeter macrocephalus*? *Behav. Gen.* **42,** 332-343 (2012).

30. Whitehead, H. & Rendell, L. *Oceans of Culture: Cultures of Whales and Dolphins*. (Chicago University Press, 2014).

31. Rendell, L. & Whitehead, H. Comparing repertoires of sperm whale codas: a multiple methods approach. *Bioacoustics* **14**, 61-81 (2003).

32. Czaczkes, T. J. How to not get stuck—Negative feedback due to crowding maintains flexibility in ant foraging. *J. Theor. Biol.* **360**, 172-180 (2014).

33. Kanagaraj, R., Wiegand, T., Kramer-Schadt, S. & Goyal, S. P. Using individual-based movement models to assess inter-patch connectivity for large carnivores in fragmented landscapes. *Biol. Conserv.* **167**, 298-309 (2013).

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APPENDIX C: SUPPLEMENTARY MATERIAL FOR CHAPTER 4[15]

C4.1 Table S4.1. Summary of the social metrics among social units of two vocal clans of sperm whales off the Galápagos Islands (*Plus-One* and *Regular*). Unit size (number of photo-identified individuals), mean cluster size while foraging (number of individuals), dive synchrony (residuals of no-dive gap in minutes, from the dive synchrony regression model), social differentiation (*S*), association indices (HWI).

Clan	**Social Unit**	**Social unit size**	**Cluster size $\bar{x}$ ± SD**[a]	**Dive synchrony $\bar{x}$ ± SD**[a]	**S ± SE**[b]	**HWI $\bar{x}$ ± SD**
Plus-One	D	14	1.42 ± 0.06	-0.17 ± 3.36	0.00 ± 0.37	0.16± 0.21
Plus-One	F	12	2.01 ± 0.45	-1.08 ± 2.21	0.00 ± 0.25	0.17± 0.17
Plus-One	G	11	-	-	0.60 ± 0.20	0.22± 0.34
Plus-One	N	6	1.34	-	0.00 ± 0.09	0.41± 0.16
Plus-One	Q	6	1.85	3.21	0.00 ± 0.40	0.27± 0.27
Regular	A	24	1.68 ± 0.34	3.68 ± 5.06	0.67 ± 0.10	0.10± 0.14
Regular	B	22	1.45 ± 0.08	2.28 ± 1.45	0.33 ± 0.16	0.21± 0.17
Regular	E	18	1.30	6.46	0.79 ± 0.07	0.15± 0.20
Regular	J	9	1.79 ± 0.38	8.31	0.74 ± 0.34	0.15± 0.22
Regular	I	6	1.50 ± 0.18	13.05	0.00	0.11 ± 0.13
Regular	K	13	1.89 ± 0.49	8.30	0.22 ± 0.36	0.14± 0.22
Regular	L	11	1.63 ± 0.31	3.92 ± 2.78	0.00 ± 0.29	0.27± 0.17
Regular	O	8	1.20	-	0.33 ±0.30	0.07± 0.13
Regular	P	9	1.56 ± 0.34	-	0.52 ± 0.34	0.09± 0.16
Regular	S	6	1.49 ± 0.22	4.51 ± 7.65	0.00	0.07 ± 0.15

[a] SD: standard deviation; [b] SE: standard error; Dashes indicate unavailable data.

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[15] *This appendix is available at http://onlinelibrary.wiley.com/doi/10.1111/mms.12218/suppinfo as supplementary material for the article: Cantor, M., Whitehead, H. 2015. How does social behavior vary among sperm whale clans? Marine Mammal Science. doi: 10.1111/mms.12218*

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Published article:
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Ph.D. Thesis:
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APPENDIX D: SUPPLEMENTARY MATERIAL FOR CHAPTER 5[16]

D5.1 TABLE S5.1. Sampling effort summary of dedicated visual and acoustic surveys for sperm whales in the Eastern Tropical Pacific (ETP). Study areas: Galápagos Islands (1), Panamá, Ecuador, and northern Peru (2), southern Peru and Chile (3), Gulf of California (4) and Western Pacific (5). Days following whales: total days tracking and in visual contact with sperm whale groups; Photographic records: total number of pictures taken of tail flukes for photo-identification (see also [1]); Codas analyzed: total number of coda samples manually identified and included in the continuous analyses (see also [2]).

Year	Study areas	Days following whales	Photographic records	Codas analyzed
1985	1,2	32	973	1,511
1987	1	55	1,615	2,342
1988	1	15	442	0
1989	1	56	1,708	113
1991	1,2	25	962	413
1992	2,4,5	13	273	1,234
1993	2,3,4,5	26	514	1,553
1994	1	3	108	0
1995	1,2,4	23	583	660
1996	1	8	144	0
1997	1,4	20	310	0
1998	1,4	27	179	0
1999	1,2,4,5	46	811	879
2000	2,3	79	2,082	5,360
2002	1,4	35	897	0
2003	4,5	17	383	0
2004	4	6	173	0
2013	1	27	996	1,986
2014	1	41	1,113	994
Total	ETP	554	14,286	17,045

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[16] *Supplementary material for the manuscript: Cantor M, Whitehead H, Gero S, Rendell L. Cultural turnover among Galápagos sperm whales. Royal Society Open Science.*

In 2013 and 2014, we revisited the Galápagos waters, totaling 165 sampling days and 1,670 hours with visual and/or acoustic contact with 15 groups of distinctive whales photo-identified together.

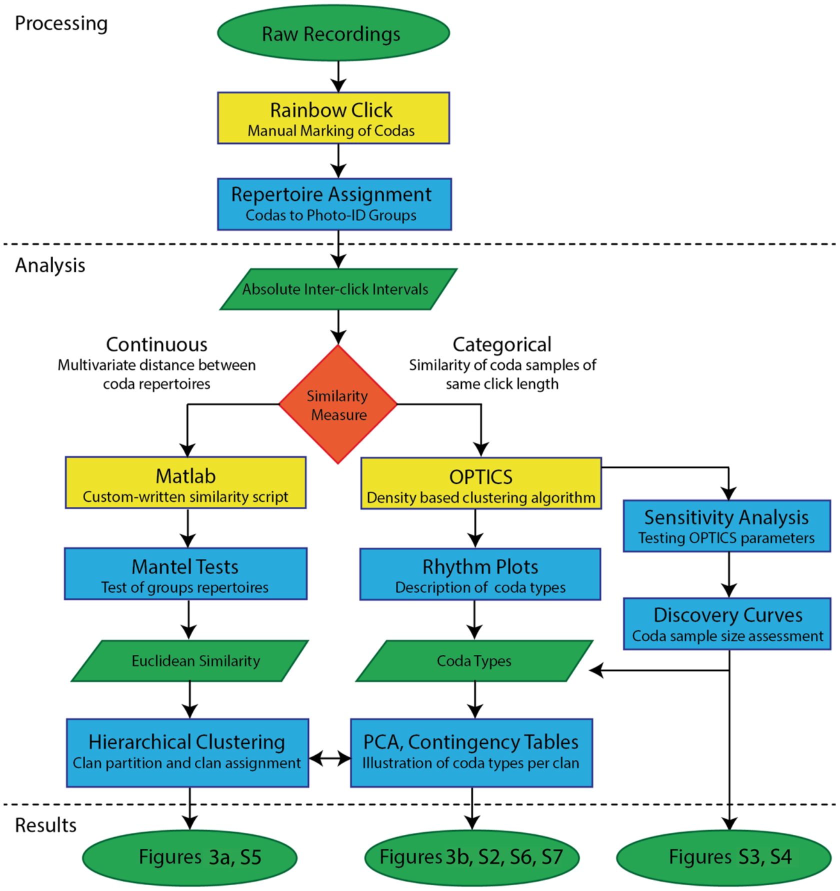
D5.2 TABLE S5.2. Number of photo-identified (quality rating $Q \geq 3$) individual adult female sperm whales and immatures of both sexes (males in parentheses) in the Tropical Pacific by study area and year. Only individuals with a recorded position are presented. Calves were not quantified. Data from 1985-2004 (3,947 individuals) came from [1].

Year	**Galápagos**	**Panamá, Ecuador, Northern Perú**	**Chile, Southern Perú**	**Gulf of California**	**Western Pacific**	**Total**
1985	344 (8)	6 (0)	0 (0)	0 (0)	0 (0)	358
1987	440 (8)	0 (0)	0 (0)	0 (0)	0 (0)	448
1988	95 (0)	0 (0)	0 (0)	0 (0)	0 (0)	95
1989	337 (4)	0 (0)	0 (0)	0 (0)	0 (0)	337
1991	94 (2)	278 (4)	0 (0)	0 (0)	0 (0)	378
1992	0 (0)	5 (0)	0 (0)	1 (0)	109 (5)	120
1993	0 (0)	116 (1)	114 (0)	2 (0)	5 (0)	238
1994	23 (0)	0 (0)	0 (0)	0 (0)	0 (0)	23
1995	91 (8)	21 (0)	0 (0)	4 (0)	0 (0)	124
1996	29 (4)	0 (0)	0 (0)	0 (0)	0 (0)	31
1997	0 (0)	0 (0)	0 (0)	5 (0)	0 (0)	5
1998	27 (6)	0 (0)	0 (0)	64 (4)	0 (0)	101
1999	9 (3)	3 (0)	0 (0)	102 (3)	1 (0)	120
2000	0 (0)	15 (0)	863 (32)	0 (0)	0 (0)	910
2002	0 (37)	0 (0)	0 (0)	280 (3)	0 (0)	420
2003	1 (0)	0 (0)	0 (0)	139 (4)	1 (0)	141
2004	0 (0)	0 (0)	0 (0)	68 (0)	0 (0)	68
2013	210 (25)	0 (0)	0 (0)	0 (0)	0 (0)	235
2014	253 (33)	0 (0)	0 (0)	0 (0)	0 (0)	286
Total	1,953 (138)	444 (5)	997 (32)	665 (16)	116 (5)	4,468

D5.3 TABLE S5.3. Number of codas analyzed from groups of female and immature sperm whales photo-identified together in the Eastern Tropical Pacific by study area and year. Year correspond to the photo-identification effort in Table S5.1. Data from 1985-1999 (14,065 codas) came from [2].

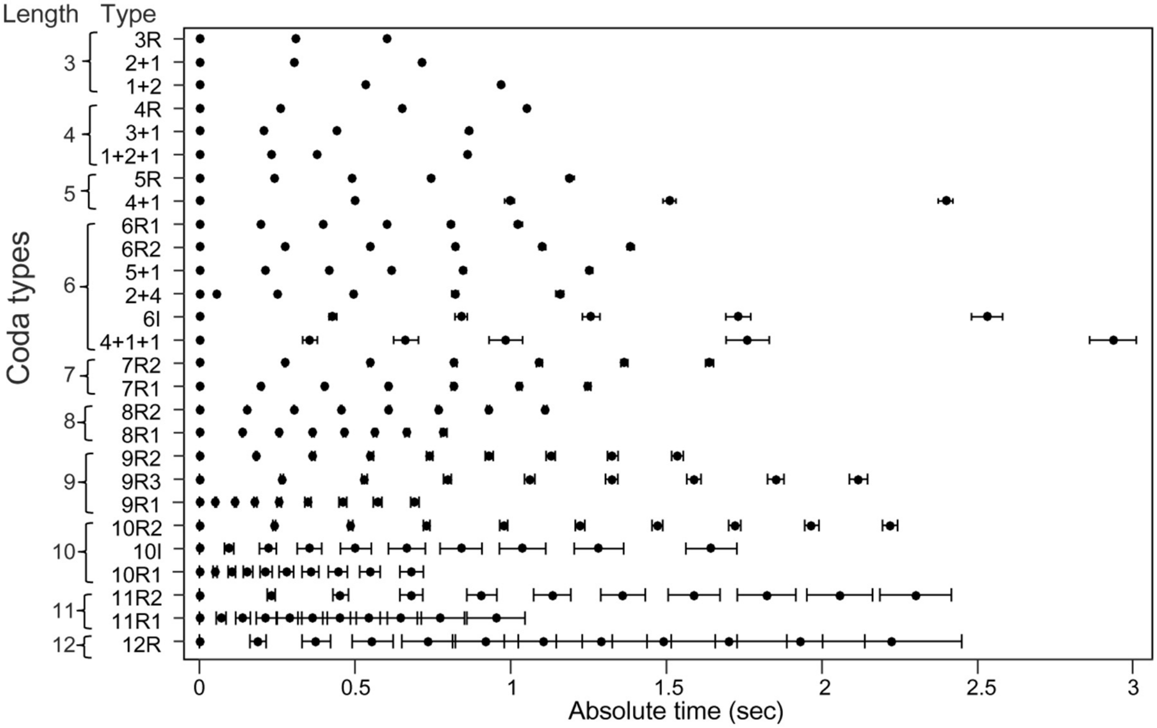
Year	**Galápagos**	**Panamá, Ecuador, Northern Perú**	**Chile, Southern Perú**	**Gulf of California**	**Western Pacific**	**Total**
1985	1,511	0	0	0	0	1,511
1987	2,342	0	0	0	0	2,342
1988	0	0	0	0	0	0
1989	113	0	0	0	0	113
1991	0	413	0	0	0	413
1992	0	293	0	941	0	1,234
1993	0	429	616	134	374	1,553
1994	0	0	0	0	0	0
1995	660	0	0	0	0	660
1996	0	0	0	0	0	0
1997	0	0	0	0	0	0
1998	0	0	0	0	0	0
1999	879	0	0	0	0	879
2000	0	0	5,360	0	0	5,360
2002	0	0	0	0	0	0
2003	0	0	0	0	0	0
2004	0	0	0	0	0	0
2013	1,986	0	0	0	0	1,986
2014	994	0	0	0	0	994
Total	8,485	1,135	5,976	1,075	374	17,045

D5.4 SUPPLEMENTARY FIGURE S5.1.



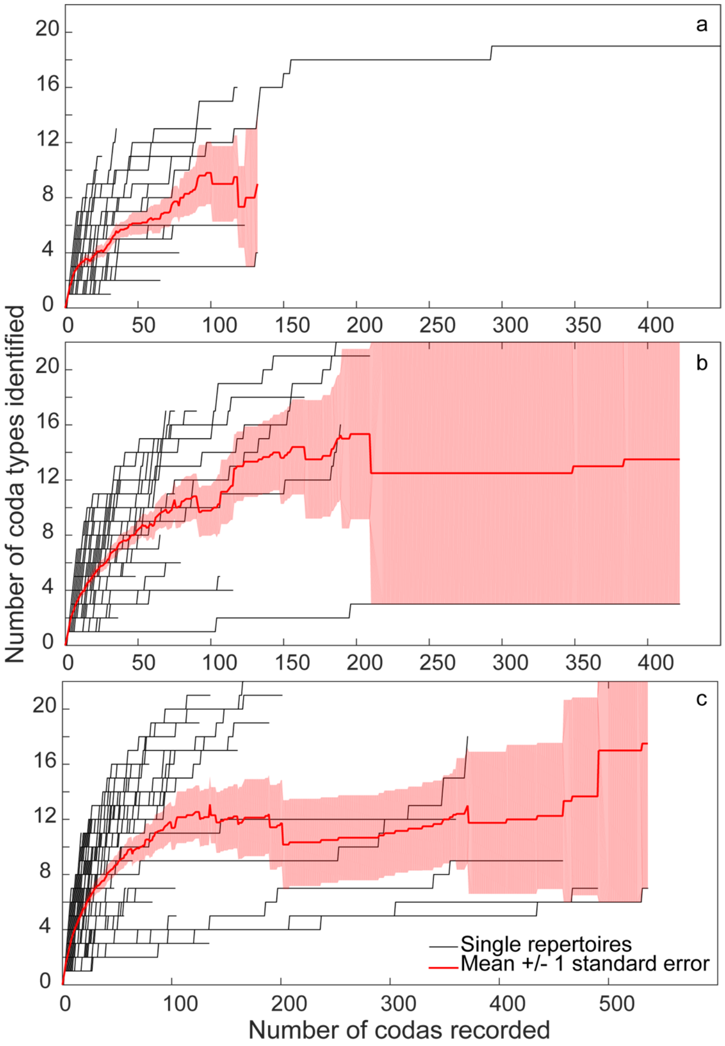
Supplementary Figure S5.1. Schematic of the analyses of acoustic recordings and coda repertoires to define vocal clans of sperm whales. In the processing phase, raw acoustic recordings were listened at ¼ speed and codas were marked in the Rainbow Click software. Coda repertoires were composed of coda recordings assigned to groups of whales photo-identified together. In the analysis phase, we used the absolute inter-click intervals (ICI, the actual time between the onset of one click to another in a coda sequence) to characterize the temporal structure of the codas. We then used two complementary analyses, continuous and categorical. With the continuous measure, we compared coda repertoires similarity among groups of whales, using customized MATLAB routines to calculate the multivariate Euclidean distance between repertoires and hierarchical clustering algorithm (supported by a bootstrap procedure) to define the partition of groups into clans of whales (Figure 5.3a). With the categorical measure, we qualitatively described the differences between clan repertoires. We used the OPTICS algorithm to identify clusters of very similar coda samples, with stereotyped rhythm and tempo (Figure S5.2), which we called coda types. We performed a sensitivity analysis to define the most parsimonious initial parameters for the OPTICS algorithm (Figure S5.4). Many coda samples were disregarded as 'noise' and not included in a coda type cluster; however nearly asymptotic discovery curves suggested that nearly all coda types made by the sampled groups were represented (Figure S5.3). We then used contingency tables (Figure 5.3B) to illustrate the principal differences between the repertoires of the different clans (Figure 5.3A), and Principal Component Analysis (Figures S5.6, S5.7) to visualize with more details these differences in coda type usage by different clans. This schematic was adapted from [3].

D5.5 SUPPLEMENTARY FIGURE S5.2.



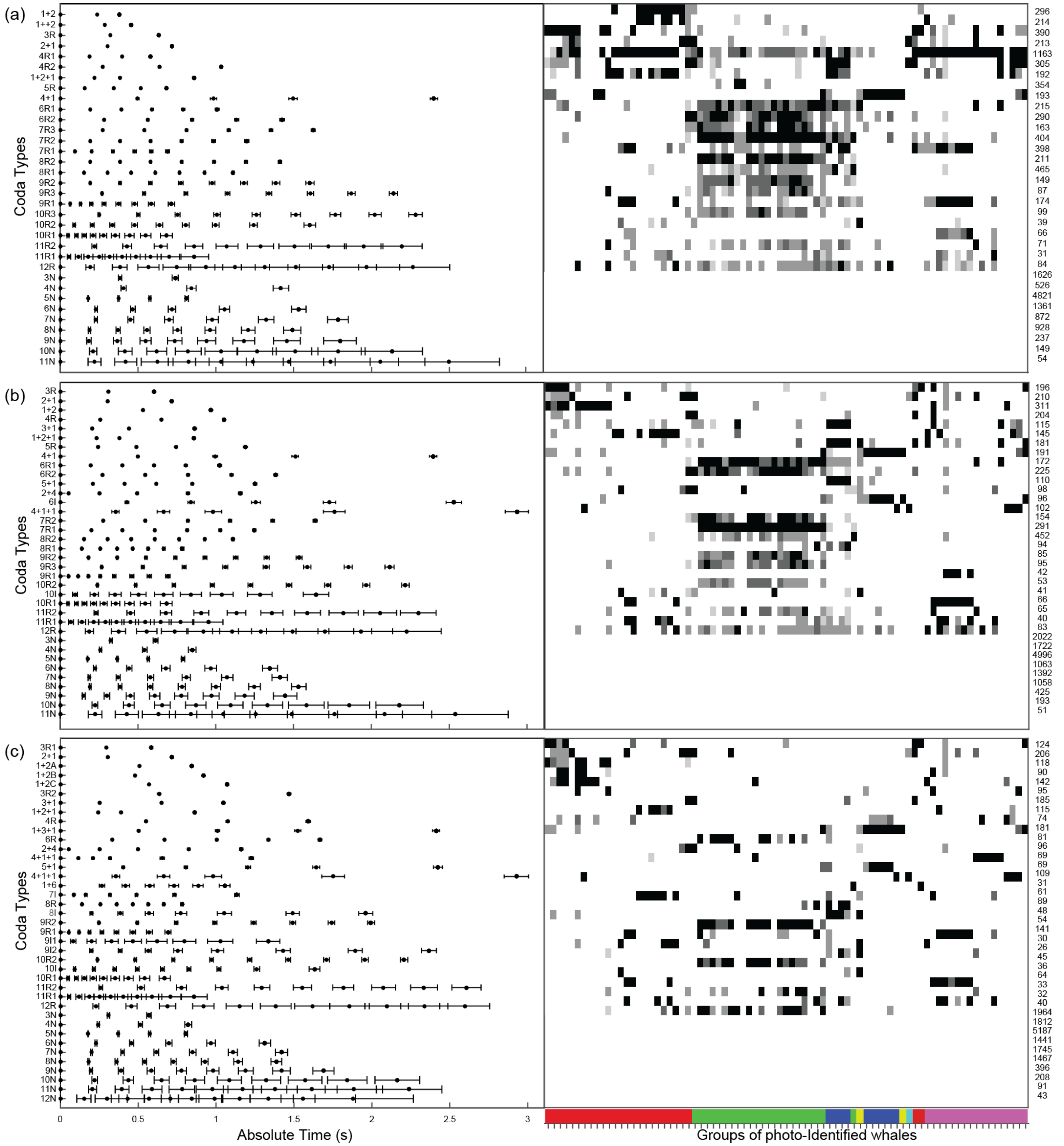
Supplementary Figure S5.2. Codas up to 12 clicks produced by sperm whales across the Eastern Tropical Pacific and classified into discrete types. Coda types (y-axis) were defined by the OPTICS algorithm (fixed ξ=0.025 and *minpts* ~4% of the sample size) based on absolute time (x-axis) between inter-click intervals (ICIs). Dots represent mean time of each click in the coda, and whiskers represent 95% Confidence Intervals around the mean time. Coda type labels were based on the rhythm, where the first number indicates the number of clicks; "R" indicates regularly spaced clicks; "I" indicates increasing click intervals along the coda; "+" indicates extended interval between clicks; and the sequential number distinguishes between codas with the same number of clicks and rhythm but of increasing duration (*e.g.* 9R1, 9R2, 9R3).

D5.6 SUPPLEMENTARY FIGURE S5.3.



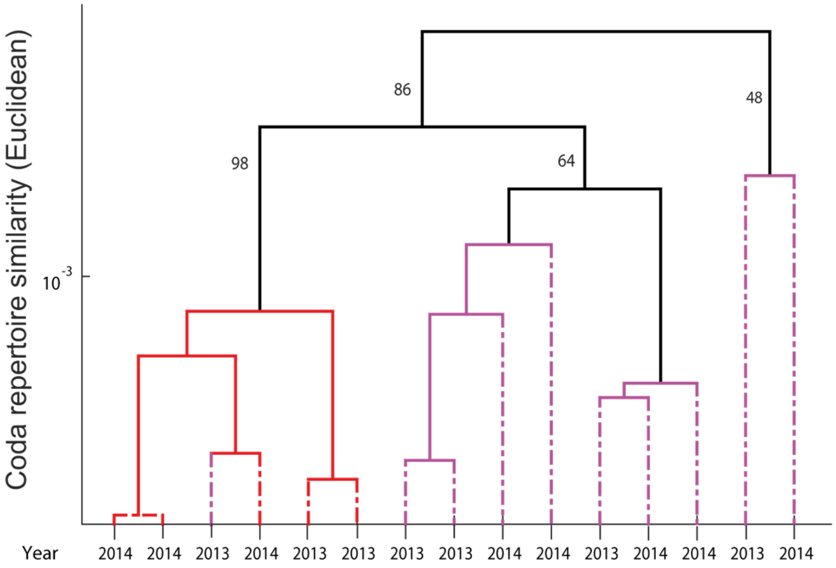
Supplementary Figure S5.3. Discovery curves for coda types per photo-identified group of sperm whales across the Eastern Tropical Pacific. Coda types were identified using the OPTICSxi algorithm, under three initial values for the key parameters ξ (drop in sample density) and *minpts* (number of minimum points): a) low $\xi = 0.005$, high *minpts* = 8% sample size; b) intermediate $\xi = 0.025$, intermediate *minpts* = 4% sample size; and c) high $\xi = 0.050$, low *minpts* = 2%. Black lines represent a repertoire of a photo-identified group of whales, red lines represent the mean discovery curve and red shades represent the standard errors for the mean curve.

D5.7 SUPPLEMENTARY FIGURE S5.4.



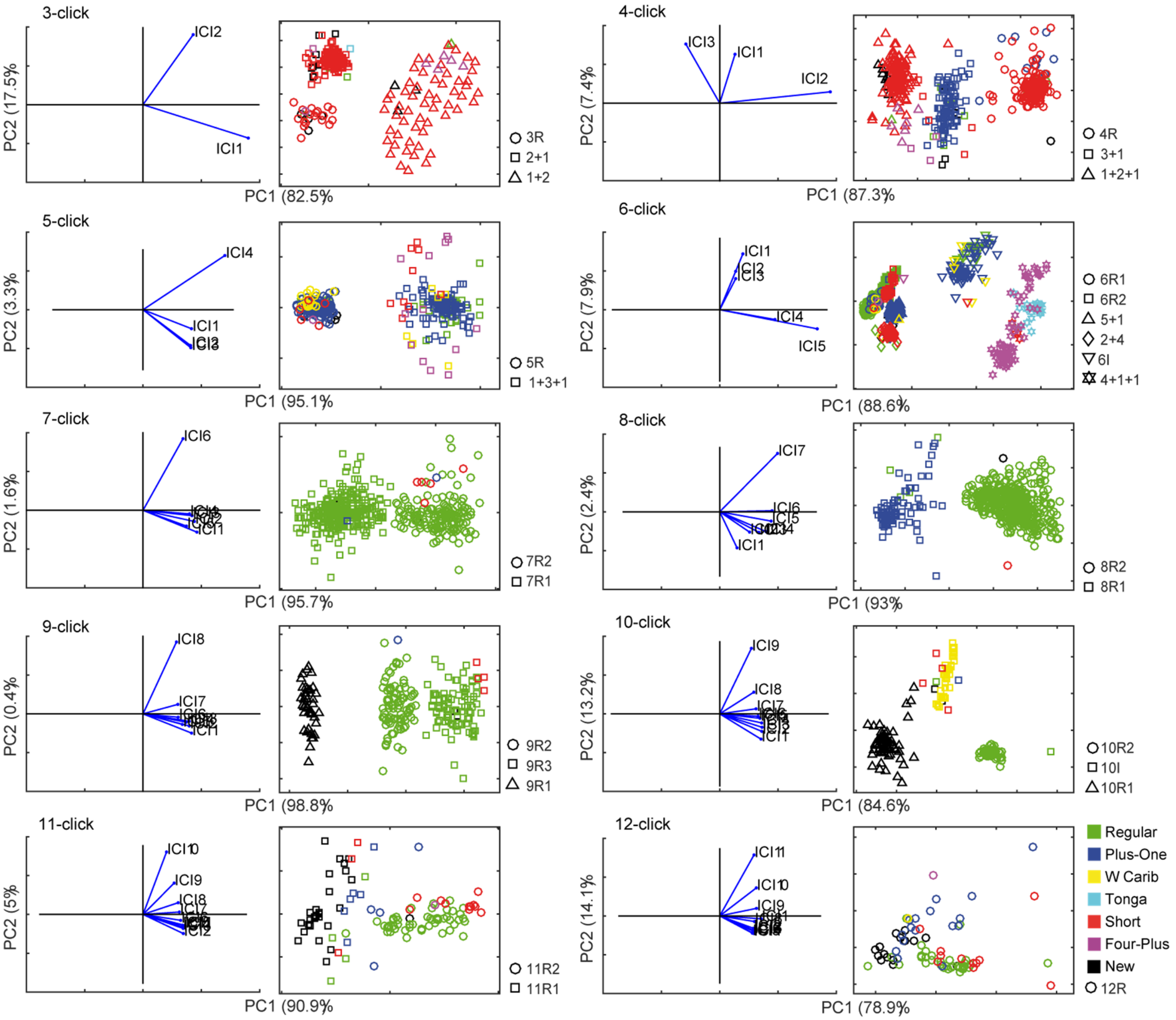
Supplementary Figure S5.4. Codas classified into discrete types according to rhythm, produced by photo-identified groups of sperm whales across the Eastern Tropical Pacific. Coda types up to 12 clicks (y-axis) were based on absolute time (x-axis) between inter-click intervals (ICIs). Dots represent mean time of each click in the coda, and whiskers represent 95% Confidence Intervals around the mean time. Coda types were defined by the OPTICSxi algorithm, under three alternative initial parameterization, varying contrast parameter ξ (threshold in reachability distance drop, establishing the relative decrease in density within clusters) and *minpts* (defines the minimum number of samples that can be considered a cluster) but fixing ξ (maximum reachability distance within which clusters will be searched for): (a) $\xi = 0.025$, *minpts* ~ 4% of sample size; (b) $\xi = 0.005$, *minpts* = about 8% of sample size; (c) $\xi = 0.05$, *minpts* ~ 2% of sample size. Coda type labels (y-axis) were based on the rhythm, where the first number indicates number of clicks, “R” indicates regularly spaced clicks; “I” indicates increasing click intervals along the coda; “+” indicates extended interval between clicks; and the sequential number or letters distinguishes between coda with same length and rhythm but of increasing duration (*e.g.* 9R1, 9R2; 2+1A, 2+1B). “N” indicate the coda samples regarded as ‘noise’ by the OPTICS algorithm (note low accuracy, i.e. large 95% confidence intervals) and so discarded from the categorical analyses. The matrices illustrate coda types (rows) for each photo-identified group (columns). Shades of grey indicate the frequency of occurrence of coda types in a given group repertoire (x>10%: black; 5%<x<=10%: dark grey; 1%<x <=5%: grey; 0<x<=1%: light grey; 0: white). Color code for photo-identified groups follow original clan partition in [2] and in the Figure 5.3 (main text). Numbers on the right indicate the total codas per type used in the categorical analysis. Note the high number of coda samples discarded as noise ("N"). Overall, there were some variations across the three parameterization schemes. For instance, the number of coda types would be 25 for the restrictive (a) or 29 for the permissive (c) parameterization schemes, mainly because some 3- and 6-click codas were merged into the same or split into more types. The intermediate parameterization (b) described more clearly the clan segregation based on the continuous analysis data.

D5.8 SUPPLEMENTARY FIGURE S5.5.



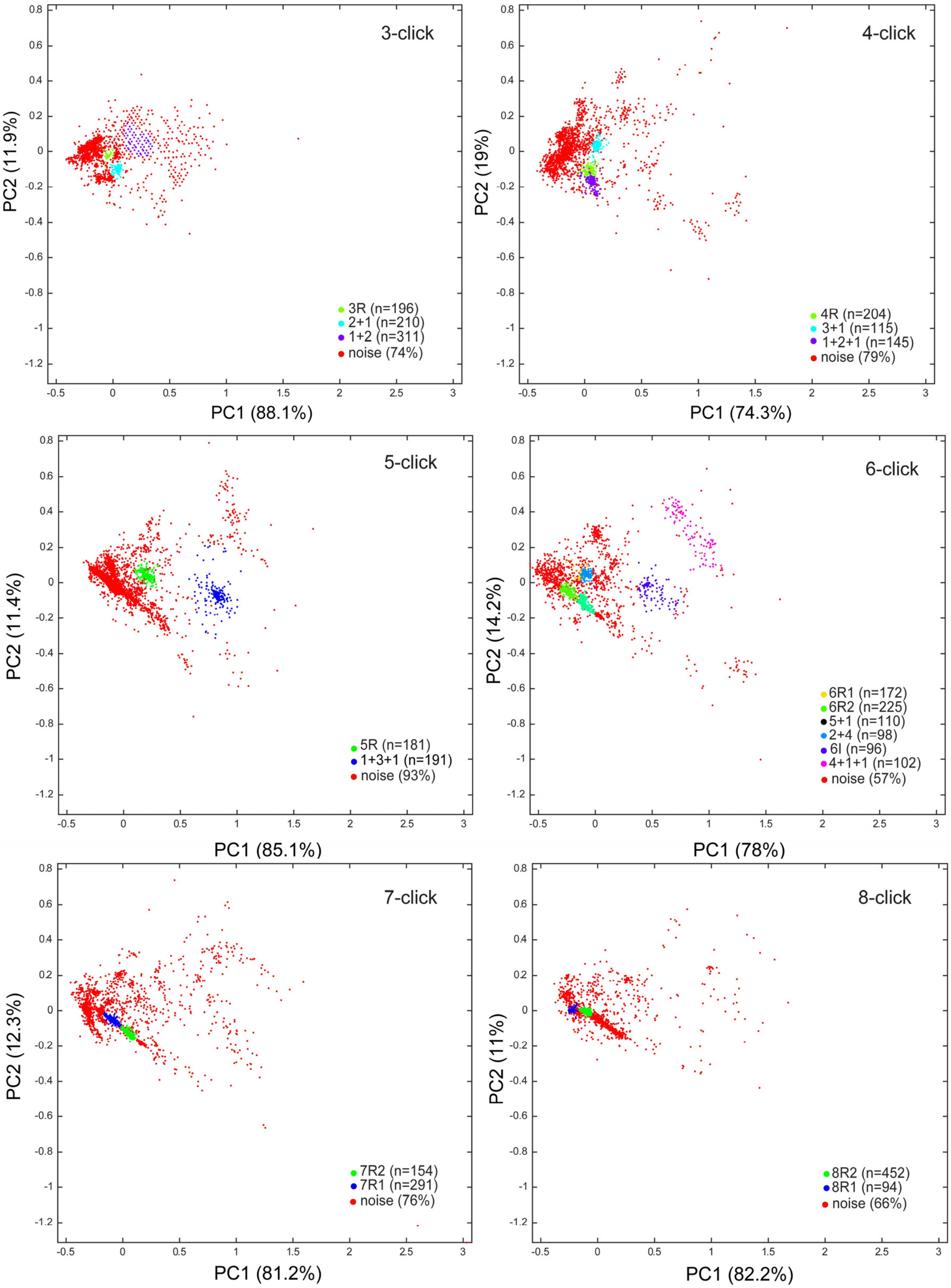
Supplementary Figure S5.5. Coda repertoire similarity among only the groups of sperm whales recorded off the Galápagos Islands in 2013 and 2014. The hierarchical clustering dendrogram (average linkage, CCC=0.89) depicts the multivariate similarity (Euclidean distances on absolute inter-click intervals) among coda repertoires of groups of whales (branches), colored by clans (as in [2]; see also Figure 5.3A). Numbers besides the clustering branches indicated the number of times (out of 100) they were replicated by in bootstrap analyses; numbers underneath are the year of recording.

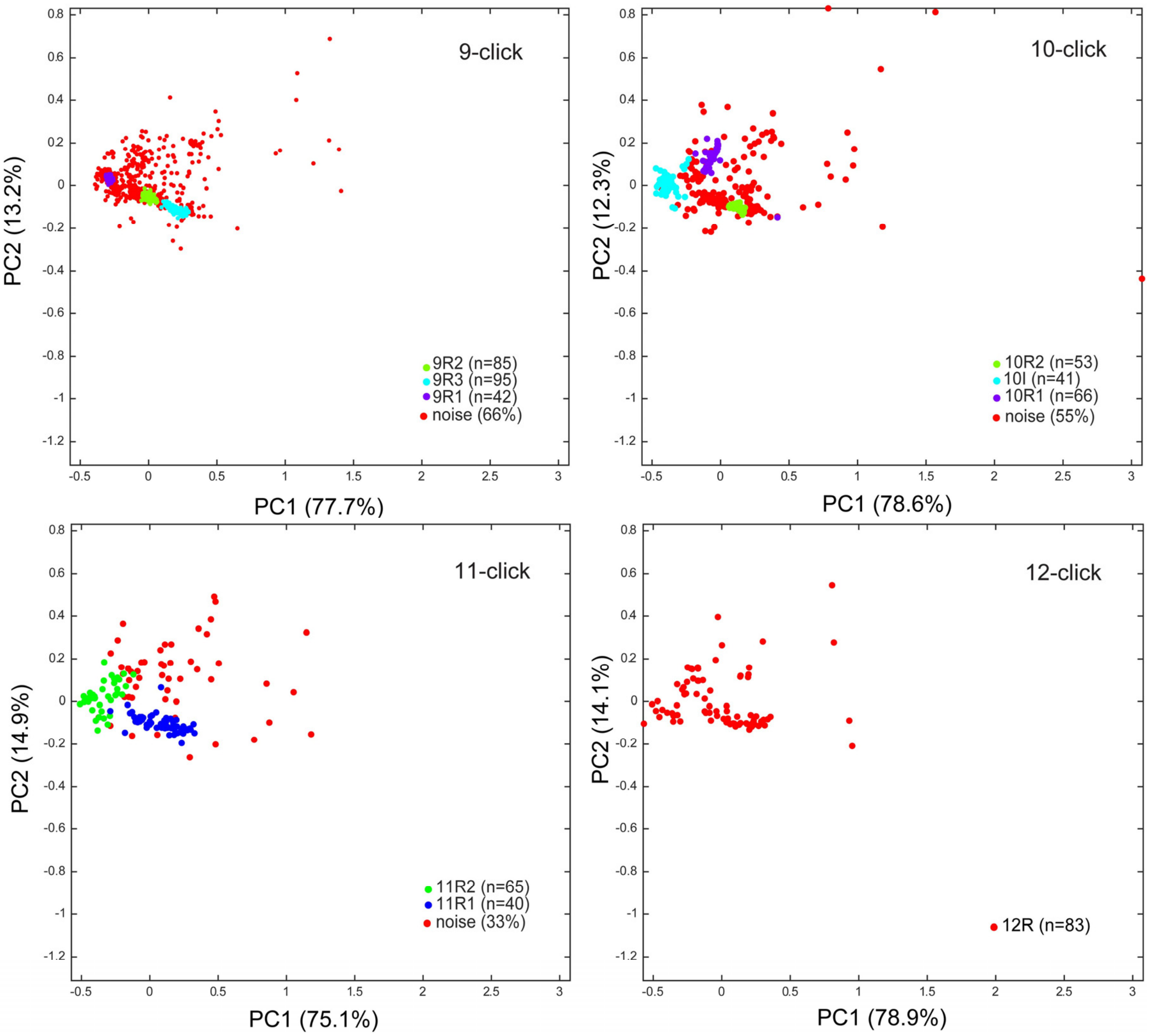
D5.9 SUPPLEMENTARY FIGURE S5.6.



Supplementary Figure S5.6. Coda types used by vocal clans of the sperm whales. Principal component analysis was used to reduce the dimensionality of the raw absolute inter-click intervals (ICI) for each coda length (number of clicks) for better visualization of the clusters of codas classified by OPTICSxi into categorical types (Figure S5.2, represented by icon shape) using the intermediate parameterization scheme (Figures 5.3B, S5.2, S5.4B). Coda samples are colored by clans, a categorical variable defined by hierarchical clustering analysis (Figure 5.3A; as in [2]). Loading plots indicate the direction of variation according to each ICI. The amount of variance explained by the first two principal components (PC) is given at the axes. The new data set recorded off Galápagos in 2013 and 2014 is marked in black. For clarity, all coda samples regarded as 'noise' by the OPTICSxi algorithm (Figure S5.4) were not plotted. Overall, coda types (here, defined by distinct clusters) were usually defined by the presence/absence of extended pauses ('+'), as suggested by the direction of loadings of the longer ICIs. Note that clans shared some coda types (e.g. 5R, 11R, 12R) but also produced coda types which were nearly exclusive of their own clan. For instance, the *Regular* clan mainly produced regularly-spaced codas from 6 to 12 clicks (e.g. 6-12R); the *Short* clan mainly produced codas with 3 to 5 clicks; *Plus-One* groups produced mainly short codas with an extended pause before the final click (*e.g.* 3+1, 1+3+1, 5+1, 4+1+1); *Four-Plus* groups produced codas with four regular clicks (*e.g.* 4R, 4+1+1, 2+4). These characteristic codas used more frequently by specific clans (Figure 5.3B) appears to have driven the clan partitions in the dendrogram presented in the main text (Figure 5.3A).

D5.10 SUPPLEMENTARY FIGURE S5.7.





Supplementary Figure S5.7. All codas sampled from sperm whales in the Eastern Tropical Pacific as categorized by OPTICSxi including unclassified samples ('noise'). Principal component analysis on the inter-click intervals (ICI) for each coda length (number of clicks) was used here to reduce the dimensionality of the data for better visualization and interpretation. The amount of variance explained by the first two principal components (PC) is given at the axes. Codas are colored by type, as defined by the OPTICSxi algorithm using the intermediate parameterization scheme (Figure S5.4B). Samples sizes by type and proportion of unclassified samples ('noise') by coda length are presented. Note our classification analysis was conservative and discarded a large portion of the samples regarded as ‘noise’ by the OPTICSxi algorithm. This creates a scenario in which we only define new coda types when there exists many, highly similar codas.

D5.11 SUPPLEMENTARY METHODS 5.1: Acoustic recordings

Recordings of sperm whale acoustic repertoires were made when whales were socializing or resting at the surface, and at the beginning of foraging dives [4], using a variety of hydrophone arrays (frequency responses: 6 Hz–10 kHz, ±3 dB; 1–10 kHz, ±3 dB) connected to different recorders and amplifiers (details in Rendell & Whitehead 2003a). In 2013 and 2014, we switched to a custom-built 100m long towed hydrophone array consisting of two Benthos AQ-4 elements (frequency response of 0.1-30kHz) spaced by 3m connected via Magrec HP02 preamplifiers to a Magrec HP27ST amplifying and conditioning box which imposed an analogue high-pass filter at 1kHz or less, and recorded using a laptop PC running PAMGUARD software [5], sampling at 96kHz. To analyze codas, we only use the temporal patterning of their clicks; thus the variation in the sampling or frequency responses of the recording systems used does not impact our analysis.

D5.12 SUPPLEMENTARY METHODS 5.2**:** Permutation tests for differences between group repertoires

All coda recordings on a given day from a given group represented a single repertoire, and repertoires from different days were treated as replicates of a group’s repertoire [3]. To test for differences in repertoire between groups, we tested the null hypothesis that the coda repertoire similarity between recordings of the same group on two different days (same group, different days: SGDD) is the same as that between recordings of different groups on different days (different groups, different days: DGDD) [3]. We performed Mantel tests (1,000 permutations, Spearman correlation) [6] to test correlations between matrices of multivariate similarity (see below) between sets of codas recorded on pairs of days and a binary matrix in which SGDD=1 and DGDD=0. If different groups have different repertoires, then we would expect greater similarity within a group than between different groups, and so significantly positive correlation between these matrices.

D5.13 Supplementary Methods 5.3: Details on continuous similarity of coda repertoires

To quantify the similarity between coda repertoires of groups of whales, we used two complementary approaches: continuous and categorical. The continuous approach is classification-free (disregards coda types) and based on the multivariate similarity of two codas with the same number of clicks using the Euclidean distances between their inter-click interval vectors [7]. We quantified the similarity between entire coda repertoires as [2,7]:

$$S_{AB} = \frac{\sum_{i=1}^{n_A} \sum_{\substack{j=1 \\ l_j = l_i}}^{n_B} \frac{b}{b+d_{ij}}}{n_A \cdot n_B} \qquad (1)$$

where S_{AB} is the similarity between repertoires A with n_A codas and repertoire B with n_B codas; l_i and l_j are the number of clicks in coda i from repertoire A and the number of clicks in coda *j* in repertoire *B*; *b* is the basal similarity (*b*=0.001) representing a very fine comparison at the order of 1 ms (repertoire similarities are in any case generally robust to variation in *b*) [7]; and d_{ij} is the Euclidean distance between the inter-click interval vectors of codas *i* and *j* [2,7]. Codas with different numbers of clicks were assigned a zero multivariate similarity [2,7,8].

D5.14 SUPPLEMENTARY METHODS 5.4: Details on categorical analysis of coda repertoires

With the categorical approach to analyze coda repertoires, we classified codas into discrete types to illustrate thematic patterning differences in the repertoires among clans of whales. We assigned categorical types based on the distribution of the absolute ICIs using the OPTICSxi hierarchical clustering [9] in the ELKI framework [10]. We ran OPTICSxi on the absolute inter-click intervals independently for all coda samples of same number of clicks. Long codas (>12 clicks) were rare (0.9% of 17,045 codas recorded, Table S5.1) and were not considered for the categorical analysis, but used only in the continuous analysis. We then named discrete codas types based on their rhythm and tempo—following previous nomenclature [2,11]: first number indicates number of clicks, "R" indicates regularly spaced clicks; "I" indicates increasing click intervals; "+" indicates extended interval; and the last number distinguishes between two similar coda types.

OPTICS is a density-based algorithm that orders samples linearly according to their distances apart in the multivariate space; distances are used to calculate "reachability" between samples and then define clusters. OPTICS defines clusters based on the following parameters: the contrast parameter ξ defines the threshold in reachability distance drop, establishing the relative decrease in density between versus within clusters; *minpts* defines the minimum number of samples that can be considered a cluster (details in [9]). The key advantage of OPTICSxi relative to other clustering algorithms is the ability to distinguish clustered samples in multivariate space (i.e. codas with low reachability, or distance in the ordered list) from sparser, outlier samples (i.e. codas with high reachability, located far away from dense clusters). The latter are regarded as 'noise' instead of being forced into a cluster, as in other clustering algorithms (*e.g.* k-means) [2,7]. Therefore, the clusters defined by OPTICSxi (here, coda types) are conservative in membership, since only coda samples with high similarity are considered and any uncertain sample (i.e. the 'noise', with low similarity, between clusters) is discarded. OPTICS density-based algorithm is more successful and accurate in identifying natural clusters in large datasets [12], and so is superior to the k-means algorithm previously used to define coda types [2,7,11] that attempted to classify every sample into a coda type, among other clear limitations [7]. We emphasize that here we used coda classification for descriptive purposes: to illustrate the thematic patterning of codas driving clan segregation given by the continuous analysis that includes all codas.

There are no rules of thumb to define the OPTICSxi initial parameterization. Therefore, we then ran a sensitivity analysis to find parsimonious parameter values. We first ran the classification algorithm with two extreme conditions: with low drop in sample density and high number of minimum points (low $\xi = 0.005$, high *minpts* = 8% sample size); and high drop in sample density and low minimum points ($\xi = 0.050$, *minpts* = 2%). The two extreme conditions yielded slightly different coda type classifications (Figure S5.3). The former produced many coda types (larger clusters were typically split into many small ones) and the latter produced only a few (visually discrete clusters were not split). Therefore, for our final analyses we used intermediate values for ξ and *minpts*.

For the final classification of codas, we fixed the ξ parameter across all independent analyses of codas of different lengths (i.e. number of clicks), but we adjusted the *minpts* parameter to the corresponding sample sizes. We used $\xi = 0.025$ (i.e. 2.5% drop in sample density defined a new cluster), so considered that the differences between coda types of different lengths are the same [3]. We adjusted *minpts* according to the sample size of each coda length to be around 4% because shorter codas are usually more numerous than longer ones. In all cases, we were very conservative and considered a coda type only the terminal branches in the hierarchical classification discarding all sample that was not in the core of the clusters.

D5.15 SUPPLEMENTARY METHODS 5.5: Social level definitions

Sperm whale societies contain multiple social levels [4,13]. The fundamental one is the nearly-permanent *social unit*, defined as sets of individuals that live and move together for long periods, from several months to several years [14]. Social units form temporary *groups* among themselves, defining sets of animals that move together in a coordinated manner for periods of few hours to few days [4]. These groups are formed among social units of the same *vocal clan* [2], defined by sets of social units with high similarity in their coda repertoires [2]. To delineate a social unit, long-term photo-identification data is therefore required (see methodological details in [14]). While this was possible for previous years off the Galápagos [14], there were not enough data available to reliably delineate social units across the Eastern Pacific (see [2]), neither off Galápagos in 2013 and 2014. Therefore, our analyses focused on acoustic repertoires of groups of sperm whales photo-identified together [2]. Social units are known to form these briefer groupings with one another [4], thus in our analysis we may have recorded the acoustic repertoire of more than one social unit. However, this would not affect our analysis because social units are known to group only with other units of the same clan [2].

D5.16 SUPPLEMENTARY REFERENCES

1. Whitehead H, Coakes A, Jaquet N, Lusseau S. 2008 Movements of sperm whales in the tropical Pacific. *Mar. Ecol. Prog. Ser.* **361**, 291-300.
2. Rendell L, Whitehead H. 2003 Vocal clans in sperm whales (*Physeter macrocephalus*). *Proc. R. Soc. B* **270**, 225-231. (doi: 10.1098/rspb.2002.2239)
3. Gero S, Whitehead H, Rendell L. 2016 Individual, unit, and vocal clan level identity cues in sperm whale codas. *R. Soc. Open Sci.* **3**, 150372. (doi: http://dx.doi.org/10.1098/rsos.150372)
4. Whitehead H. 2003 *Sperm whale societies: Social evolution in the ocean*. Chicago, IL: University of Chicago Press.
5. Gillespie D, Mellinger DK, Gordon J, Mclaren D, Redmond P, McHugh R, Trinder PW, Deng XY, Thode A. 2009 PAMGUARD: Semiautomated, open source software

for real-time acoustic detection and localisation of cetaceans. *J. Acoust. Soc. Am.* **125**, 2547 (doi: http://dx.doi.org/10.1121/1.4808713)

6. Schnell GD, Watt DJ, Douglas ME. 1985 Statistical comparison of proximity matrices: applications in animal behaviour. *An. Behav*. **33**, 239–253.
7. Rendell L, Whitehead H. 2003 Comparing repertoires of sperm whale codas: A multiple methods approach. *Bioacoustics* **14**, 61–81.
8. Antunes R, Schulz T, Gero S, Whitehead H, Gordon J, Rendell L. 2011 Individually distinctive acoustic features in sperm whale codas. *An. Behav.* **81**, 723-730. (doi:10.1016/j.anbehav.2010.12.019)
9. Ankerst M, Breunig MM, Kriegel H-P, Sander J. 1999 OPTICS: ordering points to identify the clustering structure. *Proc. SIGMOD'99. Intl. Conf. Manag. Data* **28**, 49–60. (doi:10.1145/304181.304187)
10. Achtert E, Kriegel HP, Schubert E, Zimek A. 2013 Interactive data mining with 3D-parallel-coordinate-trees. *Proc. 2013 ACM SIGMOD Int. Conf. Manag. Data* 1009–1012. (doi:10.1145/2463676.2463696)
11. Weilgart L, Whitehead H. 1997 Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behav. Ecol. Sociobiol.* **40**, 277-285.
12. Nanni M, Pedreschi D. 2006 Time-focused clustering of trajectories of moving objects. *J. Intell. Inf. Syst.* **27**, 267–289. (doi:10.1007/s10844-006-9953-7)
13. Whitehead H, Antunes R, Gero S, Wong SN, Engelhaupt D, Rendell L. 2012 Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: why are they so different? *Intl. J. Primatol.* **33**, 1142-1164. (doi: 10.1007/s10764-012-9598-z)

14. Christal J, Whitehead H, Lettevall E. 1998 Sperm whale social units: variation and change. *Can. J. Zool.* **76**, 1431-1440.