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Individualized social preferences and long-term social fidelity between social units of sperm whales

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Long-lived animals across a range of taxa display substantial social complexity that often includes hierarchical modularity of their social structures. A complete understanding of how their social systems function is achieved by understanding not only how individuals interact with each other, but also how their social groups relate to one another. Here, we examine social relationships across two levels of the hierarchical social structure of sperm whales, *Physeter macrocephalus*. Using an unparalleled data set of nine social units collected across a 6-year study (2005–2010), we calculate social differentiation (0 when relationships are completely homogeneous, and greater than 1 when there is considerable diversity among the relationships) to focus on the diversity of social relationships between the fundamental level of social structure, the unit. We contrast these patterns by comparing patterns between individuals within these units. Social relationships within units are diverse, with a mean social differentiation (S) ± SE of 0.80 ± 0.05 among adult females and 0.91 ± 0.05 when calves are included. Social differentiation was also high between units (1.11 ± 0.06). In addition, we identified long-term patterns of association between units that appear consistent over time, in two cases across more than a decade. Among the nine units, there were three strongly bonded pairs. Social preferences create complexity and diversity in the types of relationships formed at multiple levels of sperm whale social structure and across various timescales. Individuals show preferences for each other across hours, days and years; units form strong long-term bonds across decades; and vocal dialects mark social segregations between sperm whale cultures across generations.

Long-lived, cognitively complex animals across a range of taxa display substantial social complexity that often includes hierarchical modularity of their social structures (Byrne & Whiten, 1988; Dunbar, 1998; de Waal & Tyack, 2003). Mammalian species as ecologically different and phylogenetically remote as primates (e.g. Grueter, Chapais, & Zinner, 2012; Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987; Strier, 2007), elephants (e.g. Moss & Poole, 1983; Wittemyer, Douglas-Hamilton, & Getz, 2005) and bats (Boughman & Wilkinson, 1998; Kerth, Perony, & Schweitzer, 2011; Vonhof, Whitehead, & Fenton, 2004) have societies that involve both long-term cooperative relationships within defined groups and a high degree of social fluidity and movement. In such societies, these core social groups have the opportunity to aggregate over various spatial and temporal scales into higher-level social tiers. As a result, individuals encounter and interact with conspecifics outside their core social groups that they know very little or not at all, while maintaining their strong relationships with their long-term associates. The challenges of interacting not only within stable social groups, but also between them, leads to a diversity of social interactions, more complex communicative signals to mediate them, hierarchical recognition to facilitate them and, potentially, to large-scale cooperative societies (Boyd & Richerson, 1987; Freeberg, 2010; Grueter, Chapais, et al., 2012; Grueter, Matsuda, Zhang, & Zinner, 2012; McComb & Semple, 2005; Richerson & Boyd, 1998).

The cetaceans are thought to have cognitive capacities (Marino et al., 2007), communication systems (Janik & Slater, 1997; Tyack & Sayigh, 1997) and societies (Connor, Mann, Tyack, & Whitehead, 1998) that rival their terrestrial counterparts in complexity (summarized in Mann, Connor, Tyack, & Whitehead, 2000). The sperm whale, *Physeter macrocephalus*, has a particularly interesting multileveled social structure including what may be the largest mammalian cooperative groups outside of humans (Rendell &

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Whitehead, 2003; Whitehead et al., 2012). While there is some evidence of social relationships among mature males (Christal & Whitehead, 1997; Schakner, Lunsford, Straley, Eguchi, & Mesnick, 2014; Whitehead, 1993), the majority of their lives is relatively solitary. In contrast, there are several hierarchically organized tiers of female social structure. Several adult females, their dependent calves and immature offspring form the fundamental tier of female social structure, the 'unit'. Units are made up of one or more matrilines (Gero, Engelhaupt, & Whitehead, 2008; Mesnick, 2001; Whitehead et al., 2012). Most females will live out their life as members of their natal units, care for each other's calves and defend themselves against predators communally (Gero, Engelhaupt, Rendell, & Whitehead, 2009; Gero, Gordon, & Whitehead, 2013; Pitman, Ballance, Mesnick, & Chivers, 2001; Whitehead, 1996). Units can temporarily assemble into 'groups' whose associations last from a few hours to a few days (Whitehead, Waters, & Lyrholm, 1991). When in groups, however, association between individuals in clusters at the surface still remains stronger among unit members than between members of different units gathered within a group (Christal & Whitehead, 2001). Units can be classified into vocal 'clans' based on the similarity of their vocal dialect. Clans may contain thousands of individuals in hundreds of units and span thousands of kilometres (Rendell & Whitehead, 2003). Where two sympatric clans exist, units associate only with those who share a similar vocal dialect (Rendell & Whitehead, 2003).

Historically, knowledge of cetaceans has lagged behind that of their terrestrial mammalian counterparts primarily because of the difficulties of working at sea at the large spatial (Stevick et al., 2011) and temporal (George et al., 1999) scales over which these species operate. As a result, the long-term data sets on individual relationships connected to fully known demography needed to properly address these questions are only available in a few species (Connor, 2000). Using an unparalleled data set of nine social units collected across a 6-year study on the sperm whale population in the Caribbean, we examine fine-scale social relationships across two levels of sperm whale social structure. We focus on the diversity of social relationships between units and contrast those with relationships within them. Specifically, we ask how structured are relationships between social units? We then compare and contrast this with measures of association within units. Finally, using supplementary data collected over a decade prior to this study, we also examine whether associations between units persist over decadal timescales. Cetaceans inhabit a drastically different environment than terrestrial mammals and are therefore an important taxon for studying the evolutionary pathway that gave rise to vocally marked, large-scale cooperative groups.

METHODS

Field Methods

Social units of female and immature sperm whales were located and followed both acoustically and visually by observers on one of three platforms (a dedicated 12 m auxiliary sailing vessel, a dedicated 5 m outboard skiff, or an 18 m whale watch vessel) in an area that covered the entire west (leeward) coast of the island of Dominica (15°18′N, 61°23′59″W), in waters sheltered from the trade winds. Research was conducted in the winters of 2005 through 2010 for a total of 2549 h with whales across 320 days of effort (Table 1). However, opportunistic data collected throughout the year demonstrates that the same social units of whales use these waters year round (Gero et al., 2014). During outboard skiff seasons, the skiff was unable to operate on heavier weather days and the research team worked from the larger whale watch vessel. Whale watch tours focused their search effort on sperm whales. As a result, methods remained the same across all three platforms, with the work on those days being restricted only by the length of time spent at sea by the whale watch vessel.

Table 1
Effort across years

Year	Start date	End date	Effort (days)	Platform
2005	14 Jan	13 April	62	Sailing only
2006	17 Jan	11 Feb	21	Whale watch only
2007	28 Jan	28 Feb	30	Skiff and whale watch
2008	8 Feb	8 May	75	All
2009	11 Jan	29 Mar	64	Skiff and whale watch
2010	20 Jan	18 Apr	72	Sailing only

During daylight hours, clusters of individuals visible at the surface were approached and photographs were taken to identify individuals. If a calf was present in a given cluster, priority was given to taking dorsal fin pictures of the calf from alongside the larger animals, before moving behind the adults in the cluster to photograph distinct markings on the trailing edge of their flukes for individual identification purposes (Arnbom, 1987). Sloughed skin samples, for genetic determination of sex, were collected in the slicks of individuals after identification (Amos et al., 1992; Whitehead, Gordon, Mathews, & Richard, 1990).

Additional data were collected, using similar methods, by the International Fund for Animal Welfare (IFAW) during the winters of 1995 and 1996 (13 m dedicated auxiliary sailboat, 59 days effort, see Gordon et al., 1998). The presence of calves was noted in field notes, but they were not individually identified during this fieldwork.

Analyses

Identifications

A quality rating (Q) between 1 and 5 was assigned to each photograph, where 1 indicated a very poor photograph, and 5 indicated a very high-quality photograph (Arnbom, 1987; Dufault & Whitehead, 1993). Only pictures with a $Q \geq 3$ were used for the analyses. The best picture for each individual within each encounter was assigned a temporary identification code and then matched between encounters using a computer-based matching program to the Atlantic catalogue (Whitehead, 1990). In a few cases (<5% of identifications), well-known individuals that could not be photographed when multiple animals fluked synchronously but whose flukes were observed by S.G. were recorded as having been identified and given a Q rating of 6. Calves, which do not fluke, were individually identified using the shape of the dorsal fin and distinct markings on the dorsal fin and body. The best picture for each individual calf within each encounter was then matched between encounters by eye.

Defining units

Units were delineated as in previous work by Gero et al. (2014), in which a unit is a set of individuals for which each pair was observed associated during two different years. In this way, only animals that share a long-term companionship across years are included as members. Previous work by Whitehead et al. (1991) supports this definition by showing that the standardized lagged reassociation rate remains stable over these long lengths of time. This demonstrates that individuals are constant companions.

Social differentiation within units

Social differentiation (S) is the estimated coefficient of variation (standard deviation divided by mean) of the true association indices. This relates to the actual proportion of time associated, between members of a unit. If the social differentiation of a unit is 0, then relationships among members are completely homogeneous. Conversely, if the social differentiation is >1.0, there is considerable diversity among the relationships among the pairs of individuals within a unit (Whitehead, 2008a). Individuals were considered to be associating when they were within the same cluster at the surface. An individual was considered part of a cluster if it was within approximately three adult body lengths of any other cluster member (~40 m 'chain rule') and their behaviour was coordinated (Whitehead, 2003). The 'gambit-of-the-group' or the assumption that association really indicates behavioural interaction between members is satisfied here by the fact that this high degree of synchronization and coordination in space and time is costly to individuals (Conradt & Roper, 2000) and these individuals often interact socially through physical contact or by exchanging social calls (Schulz, Whitehead, Gero, & Rendell, 2008). In general, clusters were small (mean ± SD = 1.75 ± 1.24 individuals) and were visually distinct at sea being separated by hundreds to thousands of metres based on GPS locations of identification photographs (Gero et al., 2014). Social differentiation within units was estimated, using a half-weight index (HWI) of association (Cairns & Schwager, 1987), defining association as being sighted in the same cluster, and using 2 h sampling periods as in previous work in this species (Christal, Whitehead, & Lettevall, 1998; Christal & Whitehead, 2001; Gero et al., 2009, 2008, 2013). The likelihood method described by Whitehead (2008a) was used to calculate values of social differentiation and its standard error (SE) was estimated using the nonparametric bootstrap with sampling periods chosen randomly with replacement for each of 1000 bootstrap samples. Social differentiation within units was calculated within yearly data sets, thus avoiding heterogeneity that could be due to recruitment, mortality, emigration or immigration. We then used the unit-year estimates of S in a one-way ANOVA to test whether units had consistently different social differentiation across years. Overall means across units for all years were then calculated only for those units with an estimated SE <0.2.

Defining associations between units

Given that it is more difficult to determine the spatial range and behavioural cues that may indicate interactions between members of different units of sperm whales, we quantified associations between members of different units using three different metrics for association of increasing spatiotemporal coordination: 'date' (identified on the same day), '2 h' (identified within 2 h of one another) and 'clustered' (identified within the same cluster, as used for within-unit associations). We also used three sampling periods: (1) 'year', a yearly sampling period that focuses on long-term associations between units and eliminates autocorrelation between sequential days when units are sighted together for short periods; (2) 'day', sampling was actually done diurnally in the field with identifications taken only during daylight hours. The use of a daily sampling interval removes demographic effects (Whitehead & Dufault, 1999); and (3) '2 h', the approximate duration of two dive cycles in this species, which provides more samples while maintaining independence, and has proven useful in previous work on this species (Christal & Whitehead, 2001; Christal et al., 1998). Three combinations of sampling period and association measure are uninformative: 'date–date' and '2 h–2 h', in which the sampling period is equal to the measure of association, and '2 h–date', in which the measure of association is longer than the sampling period. As a result, these were not used.

We then calculated social differentiation between units using the methods as above but using each combination of sampling period and measure of association. In addition, we used a permutation test, as in Bejder, Fletcher, and Brager (1998) with modifications described by Whitehead, Bejder, and Ottensmeyer (2005), in which observed associations among individuals were permuted within the three sampling periods, controlling for the number of associates of each individual in each period, to test for preferred/avoided associations with the null hypothesis that animals associate randomly. A further modification was to fix the number of trials (attempts to switch a part of a matrix of associations) rather than the number of actual switches (as recommended by Miklos & Podani, 2004). The association matrix between units across years (2005–2010) was permuted 10 000 times as this stabilized the P values, and each permutation included 1000 trials. Finally, we used average-linkage hierarchical clustering analysis to examine the associations between units. The cophenetic correlation coefficient (CCC) was calculated to determine how well the dendrogram represented the data. A CCC of over 0.8 is considered a 'good' representation of the associations (Bridge, 1993). We used modularity (as defined in Newman, 2004) to identify significant divisions within the population. 'Type 1' modularity or 'modularity-G' (Whitehead, 2008a, 2009) was used as it controls for differences in gregariousness. A Q value greater than 0.3 suggests that the population has a modular structure (Newman, 2004).

Matrix comparisons

Mantel Z tests (Mantel, 1967; Schnell, Watt, & Douglas, 1985) and matrix correlation coefficients between matrices of associations were calculated to determine which association matrices were correlated. A test variant, the Rr-test, was also used as it controls for individual gregariousness by replacing the values of association with their within-row ranks (i.e. within-individual ranks, Hemelrijk, 1990).

The calculation of the HWI, social differentiation, hierarchical clustering analysis, Mantel Z tests, as well as the Rr-tests described above, were carried out using SOCPROG 2.4 (Whitehead, 2009) in MatLab 7.12 (MathWorks, Natick, MA, U.S.A.).

Ethical Note

This study was entirely observational in nature. Nevertheless, our methods and protocols were approved by the Animal Ethics Committee of Dalhousie University (http://bit.ly/1uDhUY8) and the Animal Welfare and Ethics Committee of the University of St Andrews (http://bit.ly/1pghXn3). They were designed to minimize impact on the animals under study. Fieldwork within national waters was conducted in compliance with and approval from the national government of Dominica (permits listed in Acknowledgments).

RESULTS

Over the course of this study, we had spent sufficient time (>9 days) with nine units to be able to conduct these analyses: units A, D, F, J, N, R, T, U and V (Gero et al., 2014). The weighted social network of these individuals, and the units they made up, highlights the modular social structure in which there were stronger edge weights (thickness of connecting lines representing relationships) within units and weaker ones between units (Fig. 1).

Social Differentiation within Units

In most cases, adult female unit members had relatively diverse social relationships with a mean S value ± SE of 0.80 ± 0.05 (range 0.59–1.14; Table 2). Including the calves in the analysis increased values for S across all units as the strength of mother–calf bonds affect this analysis (across-unit mean ± SE = 0.91 ± 0.03, range

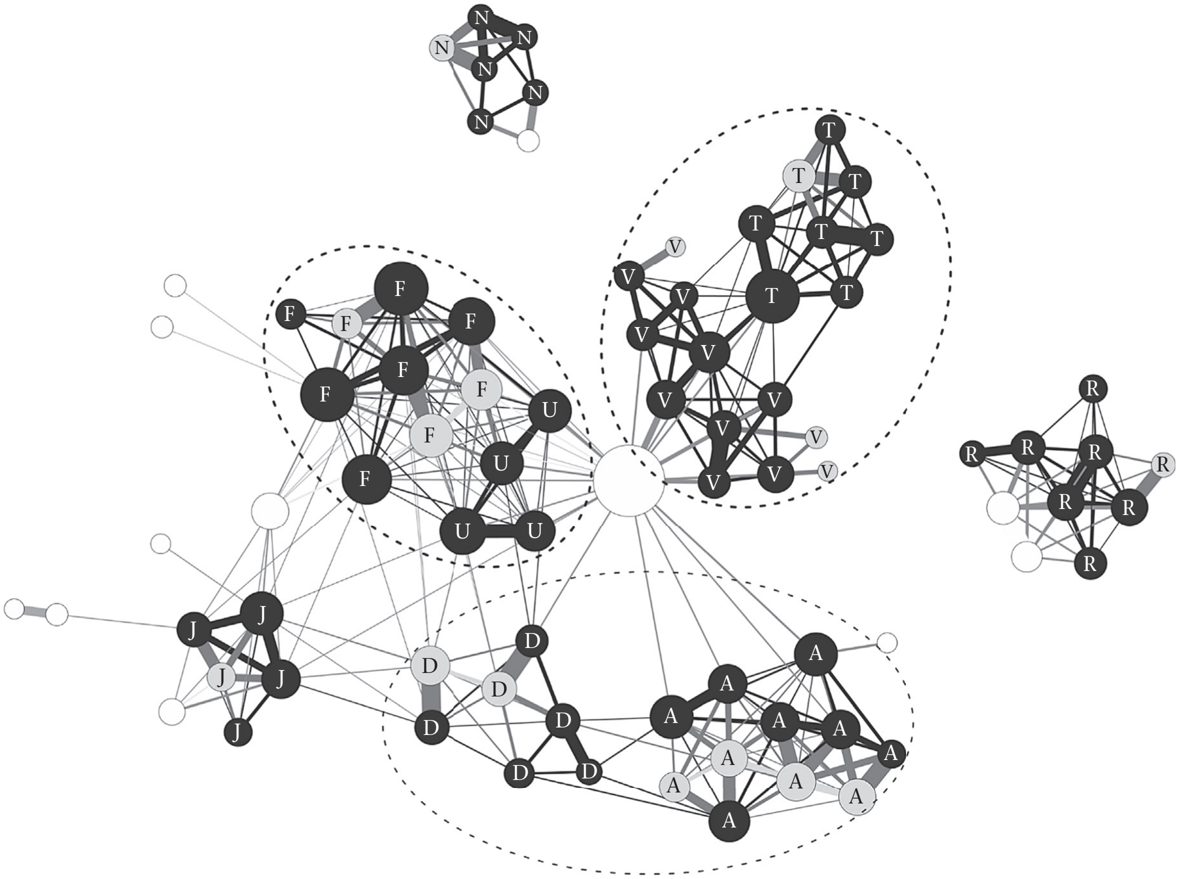

Figure 1. Individual-level social network of the nine sperm whale social units. Edges are weighted based on half-weight index (HWI) of associations using the most fine-scale, conservative measures (associated within clusters at the surface within a 2 h sampling period) between 2005 and 2010. Nodes are sized relative to their measure of degree (number of connected nodes) and coloured based on sex/age (black: females; grey: calves; white: mature male escorts). Note the modular structure in the network, with the stronger edge weight within units and the weaker edge weight between units. Dashed circles represent significant pairs of units created by a maximum modularity-G using average-linkage hierarchical clustering (see Supplementary Fig. S1), which are weighted based on HWI. Units F and U are divided into distinct methods based on quantitative methods shown in Fig. S2 and by the fact that they were often observed apart. The distance to the two unconnected units (N and R) is not proportional to association. Mature males are often the links between units by having consorted with different social units. This is particularly evident for the one male in the centre of the plot who associated with six different units. Plotted using Gephi 0.8.2beta (https://www.gephi.org) and a Force Atlas 2 layout algorithm (details: http://bit.ly/1kmVfe5). This is a force-directed layout in which nodes repel each other, while edges attract nodes they connect.

Table 2
Social differentiation between individuals within all units across all years (2005–2010), with and without calves

Unit	Mean HWI	Composition[a]	Days	IDs[b]	S	SE
Without calves						
A	0.10	7	31	992	0.706	0.113
D	0.09	5	29	620	0.955	0.127
F	0.10	6	97	1947	0.589	0.082
J	0.20	4	27	821	0.700	0.166
N	0.03	6	9	257	0.965	0.168
R	0.08	8	21	653	1.142	0.089
T	0.11	6	24	1021	0.714	0.112
U	0.13	3	27	493	0.730	0.310
V	0.13	9	10	413	0.622	0.187
With calves						
A	0.13	7A 4C	31	1911	0.891	0.102
D	0.14	5A 2C	29	1131	1.054	0.074
F	0.13	6A 3C	97	3140	0.898	0.044
J	0.20	4A 1C	27	932	0.682	0.120
N	0.08	7A 2C	9	495	1.089	0.057
R	0.08	8A 1C	21	708	1.17	0.073
T	0.15	6A 2C	24	1449	0.791	0.076
U	0.20	3A 1C	27	606	0.776	0.183
V	0.09	9A 3C	10	441	0.852	0.093

HWI: half-weight index of association; S: social differentiation.

[a] Composition with calves shows the number of adults (A) and calves (C) in each unit.

[b] Number of identifications of members of each unit.

0.68–1.17). Although units varied in size, social differentiation was not correlated with the number of individuals in a unit (Pearson correlation: without calves: $r_7 = 0.11$, $P = 0.77$; with calves: $r_7 = 0.36$, $P = 0.34$). While individuals are members of long-term, stable social units, this suggests that social preferences among unit members do exist in all units over relatively short timescales within a day and at the finest-scale spatial association of clustering at the surface together.

Social Relationships between Units

As would be expected, all of the various combinations of sampling period and association measure resulted in highly correlated matrices of association, even when comparing the most fine-scale, conservative, short-term measure of association between clusters (identified together in a cluster within 2 h, 2 h–clustered) against the most permissive, long-term ones (identified on the same day within a year, year–day; matrix correlation coefficient = 0.45). Estimates of social differentiation between units and permutation test results across sampling periods and association measures are shown in Fig. 2. Social differentiation between units was also high, with estimates ranging from 0.51 to 1.11. In most cases, permutation tests confirmed that these diverse associations differed from random and that preferred and avoided association existed

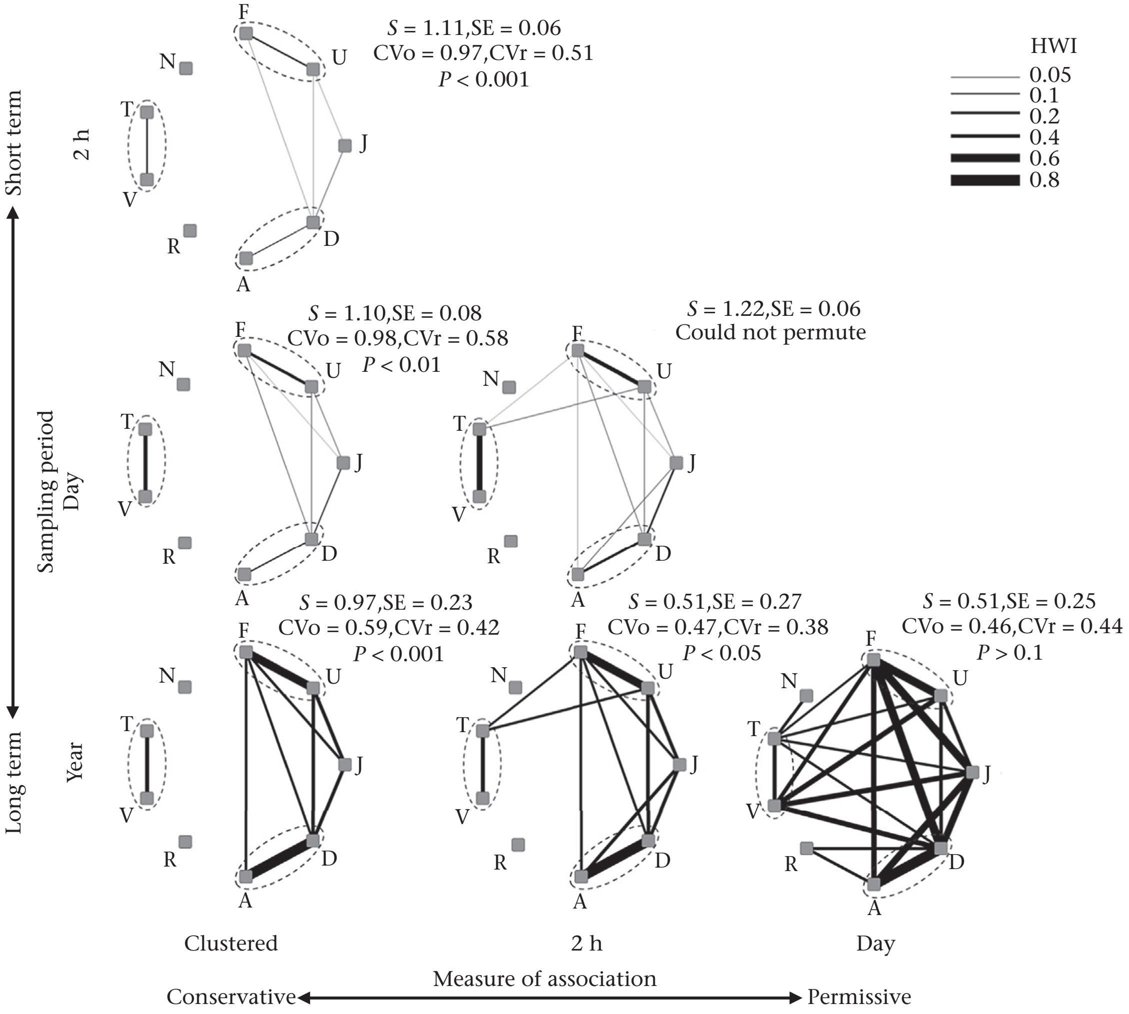

Figure 2. Sociograms portraying the relationships between the nine sperm whale social units based on half-weight index (HWI) of association across 2005–2010 using the various metrics for association and sampling interval combinations. Note that as you move down the figure, the timescale of the relationships gets longer; while moving to the right increases the permissiveness of the definition of association. Estimates for social differentiation (*S*) and results of permutation test for preferred/avoided relationships between units presented with each sociogram (CVo = CV observed data; CVr = CV randomized data). Dashed circles represent significant pairs of units created by a maximum modularity-G using average-linkage hierarchical clustering (see Fig. S1).

between units. The exceptions were the case of day–2 h, in which the sparse matrix could not be permuted using the standard algorithms and year–day, the most permissive and inclusive data set, for which the null hypothesis that units associate randomly could not be rejected. This suggests that the definition of association was too permissive and had a homogenizing effect on the measures of association. Focusing on the most fine-scale, conservative data set, 2 h–clustered (top, left of Fig. 2), there were three pairs of units with significantly stronger bonds, as delineated by hierarchical clustering and modularity-G highlights these three pairs (dashed circles in Figs 1 and 2; average-linkage dendrogram shown in Supplementary Fig. S1): units F and U, T and V, and A and D. While units F and U appeared to have a very tightly associating social network (Fig. 1), modularity within hierarchical clustering split the individuals into their respective units based on their HWI from 2005 to 2010 (Supplementary Fig. S2). Patterns of association did not differ whether Q6 identifications were included or excluded.

Long-term Patterns

For two units (F and U), data were available from a decade prior to the onset of this study, allowing us to compare patterns of association over a longer period. On 12 of 19 days in which members of unit F were sighted in 1995 and 1996, members of unit U were also sighted. On 9 of those days, members of both units were associated in the same cluster. Association matrices (2 h–clustered) including only the adult females of units F and U sighted in both time periods were not correlated (Mantel *Z* test: matrix correlation coefficient = 0.17, $P = 0.26$; Rr-test: matrix correlation coefficient = −0.08, $P = 0.63$). Patterns of association between adult unit members in the 1995–1996 seasons and during 2005–2010 fieldwork (Fig. 3) differed in some respects. The strongest bond between units in 1995–1996 was between 'Pinchy' (Female 5560) of unit F and 'Fork' (female 5151) of unit U, but was between 'Fingers' (female 5722) of unit F and 'Knife' (female 5562) of unit U in 2005–2010 (Fig. 3). While very few data were available for the other units in the 1995–1995 data set (<11 identifications for any unit), members of another strongly bonded pair of units, two individuals from unit V and one from unit T, were identified within a minute of one another in 1995, but were not clustered together.

DISCUSSION

Sperm whales have a diversity of relationships across multiple tiers of their hierarchically organized social structure. At its base are the strong mother–calf bonds, which remain strong well beyond

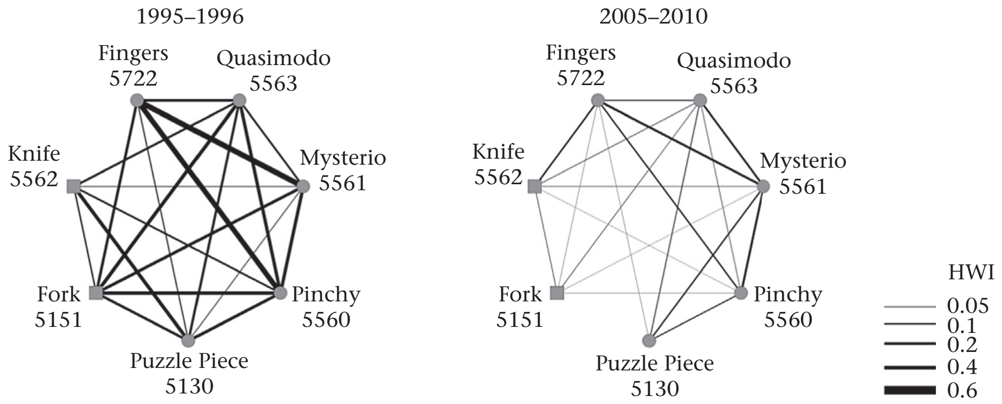

Figure 3. Sociograms portraying the relationships between the members of units F and U. Plots are based on half-weight index (HWI) of associations defined by being identified in the same cluster at the surface within a 2 h sampling period pooled across years within both the 1995–1996 and 2005–2010 time periods. Square nodes: unit U members; round nodes: unit F members.

weaning (Gero et al., 2013). These bonds along with preferred babysitters for the calves (Gero et al., 2009), and a communal, shared responsibility in protecting the young (Gero et al., 2009; Whitehead, 1996) result in a diverse social network within units (Gero et al., 2013); and here, we demonstrate that this diversity of relationships was common among all nine units studied. These units had ‘high’ levels of social differentiation among relationships within units based on existing standards (Whitehead, 2008a, 2008b). This finding shows that members of long-term, stable units show social preferences over fine-scale spatial (<1 km) and temporal (<2 h) scales. Whether units are small or large, members are not interchangeable, but are unique individuals, each with differing gregariousness and preferred associations.

Apart from rare occasions or when mature males are around (males aggregate units of females that would otherwise not be associated, Gero et al., 2014), only members of three pairs of units (F–U, A–D, and T–V) formed clusters with members of different units (Table 3). In all other cases, although multiple units might have been occupying the same area, individuals only clustered with members of their own unit. This is consistent with the finding that Pacific units prefer unit members to others when gathered in groups (Christal & Whitehead, 2001).

Perhaps most intriguingly, while patterns of association within units are diverse and appear to change over time (Gero et al., 2013), long-term patterns of association between pairs of units appear consistent over time. Members of units T and V were seen together once in 1995 and the two adult female members of unit U were seen with unit F females on 12 different days in 1995 and 1996. Unit U has been identified in 15 different years since 1990. While modularity divided the individuals into their respective social units (Fig. S2) and members of unit U were most often observed together as a separate social unit without any members of unit F, certain members of U have been sighted in clusters with members of unit F in 6 different years. This long-term preference between social units appears similar to that found in ‘bond groups’ of African elephants, *Loxodonta africana* (Moss & Lee, 2011; Moss & Poole, 1983). Elephant society is also organized into small matrilineal families that care for each other's young. These families interact over a mosaic of overlapping home ranges. Two or more elephant families that share some portion of their home range and spend much of their time together while coordinating their behaviour are called a ‘bond group’. Furthermore, relatedness predicts these temporary fusions among elephant families, such that families are more likely to fuse into bond groups if the oldest females in each group are kin (Archie, Moss, & Alberts, 2006). Unlike the elephants, however, we know very little about each of the sperm whale units' home ranges beyond our study site or to what degree they overlap with those of other units, but ongoing genetic analysis will reveal if there is any genetic relatedness between units F and U, or the other pairs of units that seem to share this ‘bonded’ long-term relationship. Much like elephants (Moss & Lee, 2011; Moss & Poole, 1983), we hypothesize that kinship may play a role in determining members of bond-group pairs among sperm whales. Such that these pairs of sperm whale units may have once been a part of the same large social unit that grew beyond an optimal size and split into two distinct but affiliate units. Furthermore, it would seem that the relationship between these bond-pair units goes beyond preferred associations among adult members. Both dependent calves from unit F, ‘Enigma’ (male calf 6068) and ‘Tweak’ (male calf 6070), were often babysat by members of unit U (Gero et al., 2014). This would suggest that the boundary for altruistic or cooperative allocare behaviour may extend beyond the stable, matrilineal social unit to members of long-term, preferred bond groups, which is common among elephants as well (Moss & Lee, 2011; Moss & Poole, 1983). Thus, there may be both mutualistic and nonmutualistic forms of groups among sperm whale units (Connor, 2000). In some cases, units come together to form groups for reasons that benefit the individuals, such as for increased numbers of babysitters, and so preferences between units exist; while at other times, groups form as a result of external influences like the presence of mature males (demonstrated by Gero et al., 2014, and as the social network in Fig. 1 demonstrates). So, while group formation is temporary,

Table 3
Associations between units in clusters and when males were present

Unit	A	D	F	J	N	R	T	U	V
A	*31/311*	**4**	0	0	0	0	0	0	0
D	**16 (3)**	*29/167*	3	3	0	0	0	3	0
F	2	4 (3)	*97/906*	2	0	0	0	**35**	0
J	3 (1)	9 (4)	5 (3)	*27/208*	0	0	0	1	0
N	0	0	0	0	*9/71*	0	0	0	0
R	1	1	0	0	0	*21/168*	0	0	0
T	0	1 (1)	1 (1)	1 (1)	1	0	*24/323*	0	**7**
U	0	3 (3)	**24 (4)**	3 (3)	0	0	1 (1)	*28/153*	0
V	0	1 (1)	2 (1)	1 (1)	0	0	**6 (3)**	2 (2)	*10/100*

Bottom-left triangle of the matrix displays the number of days on which both units were sighted followed by the number of those days in parentheses on which males were also sighted with the females or nearby. Values shown in italics (diagonally) are the total number of days on which each unit was sighted and the number of clusters across the 2005–2010 time period (days/clusters). Top-right triangle of the matrix gives the number of clusters in which at least one member of each unit was associated. Bolded cells indicate pairs of units identified by modularity-G and average-linkage hierarchical cluster analysis.

preferred membership seems to be stable across decades. More time will be needed to elucidate the details of what factors influence the patterns of formation of mutualistic bond groups and the trade-offs between ecological costs and any potential social benefits (Clutton-Brock & Harvey, 1977; Emlen & Oring, 1977).

Given the patterns of long-term social preferences identified here, sperm whales must be able to recognize units or individuals in order to associate preferentially with units across these large temporal and spatial scales. Sperm whales in the Pacific appear to use distinct culturally transmitted vocal repertoires to socially segregate their society, such that units that share a vocal repertoire associate and those that differ do not (Rendell, Mesnick, Dalebout, Burtenshaw, & Whitehead, 2012; Rendell & Whitehead, 2003). This system appears to function broadly in an 'Us' versus 'Them' fashion in that there are no preferences within acoustic clans for specific other units, simply for any unit that shares the characteristic repertoire (Rendell & Whitehead, 2003). In contrast, the data presented here suggest social preferences between units within a population in which only one dialect has been identified (all units studied in the eastern Caribbean are members of the same vocal clan, Gero, 2012). Thus, vocal markers to distinguish differing cultural groups could not serve to mediate the social complexity at the level of the unit and individual found in this study. Antunes et al. (2011) suggested that sperm whales may also have a specific coda type whose variability may function in individual identification. This type of hierarchical recognition is common in birdsong, in which the general form of the song identifies the species while variations within it identify individuals (Becker, 1982; Falls, 1982). The patterns of association between units, and the individuals within them, would indicate that female sperm whales need to identify a large number of conspecifics that are not regularly encountered and discriminate preferred units or individuals with which to associate. This type of long-term recognition of individuals and memory of past outcomes of interactions with them is also displayed in crows (Izawa & Watanabe, 2008), ants (Errard, 1994) and songbirds (Godard, 1991). Therefore, we hypothesize that female sperm whales are likely able to recognize individuals and social units, recall their interaction histories and accumulate social knowledge over long periods, drawing another parallel with African elephants, which share these abilities (McComb, Moss, Durrant, Baker, & Sayialel, 2001; McComb, Moss, Sayialel, & Baker, 2000; McComb, Reby, Baker, Moss, & Sayialel, 2003).

Should this hypothesis hold, why have bond-group pairs not been observed in the Pacific? Certainly, in the present study, we collected much more, and more fine-scaled, data over time than previous studies on any of the units in the Pacific (mean number of observation days per unit in the Caribbean ($N = 9$ units in this study): 79.6 days across 6 years, range 36–173, Gero et al., 2014; in the Pacific (all units, $N = 20$): 8.2 days across 6 years, range 2–21; Table 6.5 in Whitehead, 2003), nevertheless, broadly similar methodologies were used in both basins; both in terms of data collection and analysis. It is foreseeable, that this fine resolution of association data is needed to detect these types of patterns of association between units. However, Whitehead et al. (2012) suggested that there are a number of behavioural and ecological differences between ocean basins that could result in differences in social structure. These include oceanographic contrasts and differences in resource availability as well as more intense modern mechanized whaling, higher predation risk from killer whales, *Orcinus orca*, larger ranging patterns, larger units and a substantially lower density of units in the Pacific (Whitehead et al., 2012). Furthermore, these authors developed several scenarios in which different combinations of these factors lead to group formation being the norm in the Pacific, while group formation is rare in the Atlantic. They noted that predation by killer whales creates a situation in which commonly associating into larger groups is necessary for communal defence of calves (Whitehead et al., 2012). As movement, foraging and, potentially, predator defence behavioural norms vary between vocal clans (Marcoux, Whitehead, & Rendell, 2007; Whitehead et al., 2012; Whitehead & Rendell, 2004), the selection of group partner based on clan rather than on specific interaction histories or kin ensures grouping with other units that share similar behavioural strategies in an environment where units are farther apart, making preferred association with specific units difficult. In contrast, lower predation risk in the Atlantic allows for smaller unit sizes and predominantly travelling alone as a unit. The higher density of units and smaller ranging patterns in the Atlantic could allow for selectivity in association when forming groups. Alternatively, the devastation of social units due to intense whaling may have led to larger, less matrilineal and more socially homogenous units in the Pacific (Whitehead et al., 2012). Thus, if the bond-group pairs we have documented here are, in fact, kin based, as is observed among elephants (Archie et al., 2006), the anthropogenic destruction of genetic lineages in the Pacific may explain the absence of this level of social structure.

While playback experiments are needed to confirm the function of specific calls that might be used to mediate these various levels of recognition among sperm whales, what is clear is that social preferences create complexity and diversity in the types of relationships formed at multiple levels of sperm whale social structure and across various timescales. Individuals show preferences for each other across hours, days and years; units form strong long-term bonds across decades; and vocal dialects mark social segregations between sperm whale cultures across generations.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2015.01.008.

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