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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) $\pm$ 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.

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

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.

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