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ORIGINAL PAPER

Heterogeneous social associations within a sperm whale, *Physeter macrocephalus*, unit reflect pairwise relatedness

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Abstract A good description of a social structure in which individuals live in stable social groups must also capture individual differences in social behaviour in order to understand the selective pressures behind formation and maintenance of those groups. Depending on the evolutionary mechanism acting and the nature of the benefits incurred by individuals, we might expect different patterns of intra-group associations. Female and immature sperm whales (*Physeter macrocephalus*, Linnaeus 1758) live in stable and partially matrilineal social units. Using photo identification and sloughed skin sampling for genetic determination of sex and relatedness, we investigated patterns of association within a social unit of sperm whales from the eastern Caribbean. Focus was given to how short-term spatio-temporal associations reflect relatedness among unit members. Contrary to previous findings, we found that the patterns of association among members of this unit were heterogeneous and that individuals had preferred associations or avoidances with specific individuals. Furthermore, these preferred associations correlate with relatedness between individuals, such that individuals associated more with their close relatives when variation in sociability of the individuals is controlled. These results are inconsistent with the simple equivalence model of homogeneous associations between members of a social unit. They indicate intra-unit social complexity, a basis for which seems to be genetic relatedness.

Keywords Social structure · Associations · Relatedness · Equivalence · Kinship · Sperm whale

Introduction

The social structure of any population is built upon the interactions between pairs of individuals (Hinde 1976). A good description of a social structure captures individual differences in social behaviour but also describes the relationships among them across all relevant spatio-temporal scales. Often due to practical difficulties related to data collection, much of our current knowledge of species which live in long-term social units relates to the interactions and relationships between these units rather than the individuals themselves. However, within stable social groups, there is potential for a variety of mutualisms (Connor 1995) based upon: kin selection (Hamilton 1964), reciprocity (Trivers 1971), by-product mutualism or pseudo-reciprocity (Connor 1986). With the exception of by-product mutualism, most other forms necessitate repeated interactions between a given pair of individuals. Investigations of such social structures must focus on the level of the individuals in order

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to understand the selective mechanisms behind formation and maintenance of stable groups.

Among sperm whales (*Physeter macrocephalus*, Linnaeus 1758), the sexes have very different social lives presumably due to differences in selection pressure. Males live a much more solitary life, remaining alone or in ephemeral ‘bachelor groups’ when not breeding (Lettevall et al. 2002) and roving individually between groups of females during the breeding season (Whitehead 1993). In contrast, female and immature sperm whales live in social groupings, called units, characterised by stable long-term social relationships between individuals (Christal et al. 1998) which are often but not always matrilineally related (Richard et al. 1996a; Lyrholm and Gyllensten 1998; Mesnick 2001; Mesnick et al. 2003). Individual social units associate for periods of a few days with other units to form what are called ‘groups’ (Christal et al. 1998). Within the stable social units, there appears to be the potential for by-product cooperative benefits when foraging (Whitehead 1989) or cooperative defence against predators (Arnbom et al. 1987; Gordon 1987; Whitehead 1996; Gero 2005).

Depending on which evolutionary mechanism is acting and the nature of the benefits incurred by the individuals, we might expect different patterns of association among the individuals within a unit. The equivalence model provides an explanation of how animals classify whether things are perceptually similar or not (Sidman 1994). In this social context, sperm whales may be dividing their associates into two equivalence categories, ‘unit member’ or ‘outsider.’ If the equivalence model suffices to explain the associations within a sperm whale unit, individuals would treat each other as interchangeable members of the same equivalence category, and we would predict that no significant preferred associations or avoidances would be identified. Previous work on this species found that even when two or more units are associated in a group, at the level of the individual, animals prefer to associate in clusters with unit members over members of other units. However, the relationships among unit members appear to be generally homogeneous (Christal and Whitehead 2001), as would be predicted by an equivalence model.

Here, we present a case study of the most intensely studied social unit of sperm whales to date. The length of time spent with these animals and a complete genetic sample of the unit allows us a fortuitous opportunity to investigate the nature of associations among individuals within this social unit with an unparalleled scope. In particular, we consider whether kin selection is acting within social units by determining whether short-term association (spatio-temporal co-ordination) reflects relatedness among the individuals or whether intra-unit associations can be explained by a simple equivalence model (Sidman 1994; Schusterman et al. 2000).

Materials and methods

Field methods

Members of a well-known social unit of female and immature sperm whales were located and followed both acoustically, using a directional and towed hydrophone, and visually, by observers on a dedicated 12-m auxiliary sailing vessel. It was clear from the long-term re-sightings of the ‘Group of Seven’ (GOS) dating back to 1995 (Gero et al. 2007) that these animals consisted of just one stable unit and not an ephemeral grouping. The unit was observed on 40 days between January 16 and March 9, 2005, then again on March 26, 2005 in an area that covered approximately 1,500 km^2 along the entire west (leeward) coast of the island of Dominica, West Indies, in waters sheltered from the trade winds. During daylight hours, clusters of individuals visible at the surface were approached, and photographs were taken to identify individuals. If the calf was present in a given cluster, priority was given to taking dorsal fin pictures of the calf from alongside the animals, before moving behind the adults in the cluster in order to photograph distinct markings on the trailing edge of their flukes for individual identification purposes (Arnbom 1987). Digital pictures were taken using a Canon D10 digital SLR in full color at a resolution of 3,072×2,048 pixels and were saved in JPEG format. Slough skin samples, for genetic determination of sex, haplotype and pairwise relatedness, were collected in the slicks of individuals after identification (Whitehead et al. 1990; Amos et al. 1992; Richard et al. 1996a, b).

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). The Q value was a function of the attributes of the photograph but not the quality of the markings on the fluke (Arnbom 1987). Only pictures with $Q \geq 3$ were used for the analyses. The best picture for each individual within each encounter was assigned an identification number and then matched between encounters using a computer-based matching programme (Whitehead 1990).

The calf was individually identified using the shape of its dorsal fin and distinct markings on its dorsal fin and body. We used similar criteria as those used to assign quality ratings to fluke pictures (focus, exposure, angle of dorsal fin relative to the negative plane, percent of the dorsal fin not submerged and the proportion of the frame filled by the dorsal fin) to assign a quality rating to the calf dorsal fin photographs. The best picture of the calf within each encounter was then matched between encounters by eye.

Defining associations

To identify intra-unit associations, individuals were deemed to be associating if they were within the same cluster at the surface. The 'gambit of the group' or the assumption that membership in the same spatio-temporal grouping indicates probability of behavioural interaction (Whitehead and Dufault 1999) is likely satisfied in this case as individuals clustered together at the surface often interact vocally by matching or echoing codas, a social vocalisation, upon initiating dives (Schulz 2007). 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), although clusters were generally clearly apparent visually. A 2-h sampling period was used along with the 'half-weight index' (HWI), as this measure of association accounts best for observer biases that are usually inherent in photo identification techniques (Cairns and Schwager 1987). Dyads were considered as having a preferred association when their dyadic association index was more than twice the mean index of all dyads in the unit being considered for the analysis (Durrell et al. 2004) and avoidance when it was below half that mean. These threshold values were chosen because they were approximately twice (in the case of preferred associations) or half (in the case of avoidances) the expected value if associations were completely random. As in previous work in pigs (*Sus domestica*, e.g. Stookey and Gonyou 1998; Durrell et al. 2004), horses (*Equus callabus*, e.g. Ellard and Crowell-Davis 1989), bats (*Thyroptera tricolor*, e.g. Vonhof et al. 2004), primates (e.g. Call et al. 1999), and other cetaceans (*Tursiops truncatus*, e.g. Owen et al. 2002; *Hyperoodon ampullatus*, e.g. Gowans et al. 2001; *Stenella longirostris*, e.g. Karczmarski et al. 2005), we use the terms preferred association and avoidance. However, one must be cautious in using such terms as these analyses do not necessarily show that two individuals are actively drawn together or repelled from one another; there may be other preferences for foraging location or strategy and activity synchronisation, for example, which make a dyad more or less likely to associate. None the less, these are likely still individual preferences in so much as synchronicity is costly to individuals (Conradt and Roper 2000) and interacting with some necessarily precludes interacting with others (Newton-Fisher 1999). These preferred associations or avoidances may be of three types: (1) mutualistic, in which both parties show similar tendencies (e.g. in cooperative foraging or defense of calves), (2) unidirectional, in which only one party shows a preference or avoidance and the other shows indifference or the opposing tendency—this may be the case in which certain animals show an attraction to a class of animals or to a given social role (e.g. natal attraction in *Tursiops* sp., Mann and Smuts 1998) or when an individual incurs by-product benefits when foraging (e.g. eavesdropping in bats, Balcombe and Fenton 1988)—and (3) obligate, in which the association is necessary; such as a dependent calf and its mother.

A permutation test, as in Bejder et al. (1998) with modifications described by Whitehead et al. (2005), in which observed associations among individuals, are permuted within 2-h sampling periods, controlling for the number of associates of each individual in each period, was used 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 Miklós and Podani 2004). Each switch flips the associations among four whales in a sampling period, such that AB=1, CD=1, AC=0, BD=0 becomes AB=0, CD=0, AC=1, BD=1. The association matrix was permuted 10,000 times as this stabilised the *p* values. Each permutation included 1,000 trials, as recommended for optimising computation time in *SOCPROG* 2.3 (Whitehead 2008a) in *MATLAB* 7.4 (The Mathworks, Natick, MA, USA). A similar analysis was used to test for differences in gregariousness among individuals by permuting the cluster memberships (while maintaining the number of whales in each cluster and the number of clusters in which each whale was observed) using the standard deviation of typical cluster size (typical cluster sizes, TCS, are the cluster sizes experienced by the individual; Jarman 1974) as a test statistic (Whitehead et al. 2005).

Haplotyping and genetic determination of sex and pairwise relatedness

Whole-cell deoxyribonucleic acid (DNA) was extracted for use in subsequent polymerase chain reactions from sloughed skin samples by a standard phenol/chloroform extraction technique (Hoelzel 1998). Genetic analyses examined 13 polymorphic microsatellites from the bi-parentally inherited nuclear DNA (EV1, EV5, EV37, EV94, EV104 [Valsecchi and Amos 1996]; SW10, SW19 [Richard et al. 1996b]; FCB1, FCB14, FCB17 [Buchanan et al. 1996]; GATA28, GATA417 [Palsbøll et al. 1997]; TEXVET5 [Rooney et al. 1999]), a 399-bp sequence of the maternally inherited mitochondrial DNA control region and sex-linked markers (Bérubé and Palsbøll 1996) to determine sex of the individuals and relatedness among them according to conditions described in Engelhaupt (2004). Levels of genetic relatedness were calculated for pairs of individuals within the unit according to Queller and Goodnight's (1989) method using the programs *Relatedness* 5.0.2 (K.F. Goodnight, Rice University, Houston, TX, USA) and *Kinship* 1.3.1 (K.F. Goodnight, Rice University). See S1 for an extensive description of genetic methodology including primer and haplotype sequences, amplification conditions and a description of the regression measure of relatedness.

Associations and pairwise relatedness

Mantel tests (Mantel 1967; Schnell et al. 1985) and matrix correlation coefficients between the elements of the association matrix of the social unit and the corresponding matrix of pairwise relatedness values were calculated in order to determine whether the association indices were correlated with relatedness between unit members. Furthermore, the Hemelrijk Rr test (Hemelrijk 1990), a Mantel test variant which controls for individual differences in sociability by ranking values within rows, was then used to test for such a correlation while controlling for differences in sociability among unit members. Tests were against a null hypothesis in which the dyadic HWI was uncorrelated to the relatedness of the same dyad, using 1,000 random permutations (Schnell et al. 1985). The calculation of the HWI and Mantel tests were carried out using *SOCPROG* 2.2 (H. Whitehead, Dalhousie University, Halifax, NS, Canada) in *MATLAB* 6.5 (The Mathworks).

Results

Patterns of association

During the field work, the GOS social unit was composed of five adult females which have been identified together in the area since 1995 (Gero et al. 2007), one juvenile male (8.8 m, 8–10 years old; Schulz 2007) and one male calf (4.5 m, ~3 months old; length measurement for the calf was determined using photographs with a fixed focal length from the crow's nest on the mast of the research vessel and the age estimated from the growth curve in Figure 10 of Best et al. 1984).

Significantly high and low intra-unit associations were identified among the members of the GOS unit, since the coefficients of variation (CV) of the observed HWIs were significantly larger than the values obtained from randomly permuted data (observed CV=0.89; random CV=0.65; $p<0.0001$). Similar findings result from the test when the calf is excluded, eliminating the effects of the dependent mother–calf pair (observed CV=0.76; random CV=0.70; $p=0.023$). Of the 21 dyadic relationships within the seven animals, three are preferred associations (b, Table 1), ten are preferred avoidances (c, Table 1) and eight are of intermediate strength.

Individuals within the unit differed in their gregariousness (observed SD of TCS=0.55; random SD of TCS=0.15; $p<0.0001$), such that there was variation in the mean association index of different individuals (Table 1). When the calf is excluded from the analysis (observed SD of TCS=0.40; random SD of TCS=0.10; $p<0.0001$), its mother (identified behaviourally, Gero 2005, and genetically, see below) is the only individual with a significantly low TCS (TCS=1.36), while the primary babysitter (no. 5561; which has the highest association with the calf among adults, following the mother; Table 1) has the highest association index and a significantly high TCS (TCS=2.02). The only other individual with a significantly high TCS was the other mother in the unit (no. 5560; TCS=2.11), who had the second highest mean association index (Table 1), likely as a result of its continued association with its weaned calf (no. 5727).

Table 1 Association matrix of HWI for the 'Group of Seven' in 2005

	5703 (C)	5722 (M)	5561 (B)	5727 (J)	5560 (A)	5130 (A)	5563 (A)	Preferred associations	Intermediate strength	Avoidances	Mean HWI[a]	Mean no calf[a]
5703 (C)	1	0.97[b]	0.48[b]	0.35	0.29	0.13[c]	0.13[c]	2	2	2	0.39 (1)	n/a
5722 (M)	0.97[b]	1	0.17	0.06[c]	0.12[c]	0.04[c]	0.07[c]	1	1	4	0.23 (5)	0.09 (6)
5561 (B)	0.48[b]	0.17	1	0.32	0.29	0.27	0.33	1	5	0	0.31 (2)	0.28 (1)
5727 (J)	0.35	0.06[c]	0.32	1	0.53[b]	0.11[c]	0.07[c]	1	2	3	0.24 (4)	0.22 (3)
5560 (A)	0.29	0.12[c]	0.29	0.53[b]	1	0.18	0.07[c]	1	3	2	0.25 (3)	0.24 (2)
5130 (A)	0.13[c]	0.04[c]	0.27	0.11[c]	0.18	1	0.09[c]	0	2	4	0.14 (6)	0.14 (4)
5563 (A)	0.13[c]	0.07[c]	0.33	0.07[c]	0.07[c]	0.09[c]	1	0	1	5	0.13 (7)	0.13 (5)

Individuals are listed in order of descending strength of dyadic HWI with the calf and labelled with letters denoting their relationship with the calf or age class (*C* calf, *M* mother, *B* babysitter, *A* adult female, *J* juvenile male). A summary of the types of relationships formed by each individual is included. The final two columns denote the mean HWI, taken as an indication of gregariousness of the individual and the mean HWI for each individual when the calf is excluded. The number in parentheses ranks these values.

[a] Mean (rank)

[b] Preferential association (COA greater than twice the mean HWI)

[c] Avoidance (COA less than half the mean HWI)

Although the GOS calf was escorted by all seven unit members, it formed preferred associations with only two, its mother (no. 5722) and its primary babysitter (no. 5561, see Gero 2005 for a definition and reasoning behind this designation). Its mother showed a similar pattern of avoidance and association, avoiding all other unit members other than its calf and its calf's principal babysitter, female no. 5561. If not nursing or with the babysitter, the calf was most likely to be escorted by the only juvenile in the unit and had lowest association indices with the other adult females in the social unit.

Most associations among adult females within the GOS were avoidances (Table 1). The babysitter (no. 5561) was an exception and had the highest mean HWI of the adults. She preferentially associated with the calf but did not avoid any members of her social unit, associating approximately evenly with the other adults. Her weakest association was with the calf's mother (no. 5722), but she was the mother's strongest associate.

Patterns of relatedness

All individuals in the GOS unit share the same mitochondrial DNA haplotype (Haplotype A; as defined in Lyrholm and Gyllensten 1998; Engelhaupt 2004), which suggests that these individuals originate from the same single matriline. Table 2 summarizes the patterns of relatedness amongst the members of the GOS unit. These relatedness values confirm the identity of the calf's mother (no. 5722) and indicate that the other preferential association between the juvenile male (no. 5727) and adult female (no. 5560) is a mother–calf relationship. They also indicate that the babysitter (no. 5561) is the mother's closest relative of the adults within the unit. The calf's apparent closest relative, other than the mother (no. 5563), spends the least amount of time associating with the calf. In addition, individuals numbered 5560, 5560, 5561 and 5727 are all quite closely related. In particular, high pairwise relatedness is identified between nos. 5561 and 5560, as well as nos. 5561 and 5563, suggesting that they are first-order relatives.

There was a fairly large but non-significant correlation between association indices and relatedness for the unit as a whole (Mantel test matrix correlation=0.35, p=0.09). However, when we controlled for differences in sociability between individuals using the Rr test, the relationship was significant (Rr test matrix correlation=0.44, p=0.02). The correlation between the matrices is stronger when the calf is excluded (Rr test matrix correlation=0.67, p=0.003) and still holds true when both the calf and its mother are removed (Rr test matrix correlation=0.59, p=0.036). Figure 1 plots the strength of association against relatedness for the dyads in the group. These tests suggest that individuals tend to associate more with animals with whom they are more closely related, although some individuals within the unit are more social than others.

Discussion

The difficulties of studying marine species, especially deep-diving ones, have slowed advances in our knowledge of individual differences among sperm whales in many regards. In comparison to a socio-ecologically similar (Weilgart et al. 1996) terrestrial mammal, the elephant, we have only a basic understanding of sperm whale social behaviour. Most of our understanding stems from long-term multi-year data sets collected over large spatial and temporal scales (Whitehead 2003). Small-scale research focusing on the interactions between individuals is needed to elucidate the details of mate selection, contextual use of vocalisations and social roles.

This study begins to address one of these gaps by showing that individuals within a social unit have strong preferred associations and avoidances with calves as well as with other adult unit members and that the mother–calf bond continues well beyond weaning. These findings contrast with previous work which suggested that relationships within units were usually homogeneous (Christal and Whitehead 2001) and are inconsistent with the simple equivalence model as applied to the relationships among

Table 2 Matrix of pairwise relatedness values for the 'Group of Seven'

	5703 (C)	5722 (M)	5561 (B)	5727 (J)	5560 (A)	5130 (A)	5563 (A)
5703 (C)	1	0.43	0.00	0.04	0.00	0.00	0.25
5722 (M)	0.43	1	0.23	0.01	0.14	0.00	0.20
5561 (B)	0.00	0.23	1	0.45	0.62	0.10	0.56
5727 (J)	0.04	0.01	0.45	1	0.53	0.01	0.43
5560 (A)	0.00	0.14	0.62	0.53	1	0.07	0.44
5130 (A)	0.00	0.00	0.10	0.01	0.07	1	0.02
5563 (A)	0.25	0.20	0.56	0.43	0.44	0.02	1

Relatedness was determined using 13 microsatellite loci. Individuals are labelled with letters denoting their relationship with the calf or age class (*C* calf, *M* mother, *B* babysitter, *A* adult female, *J* juvenile male).

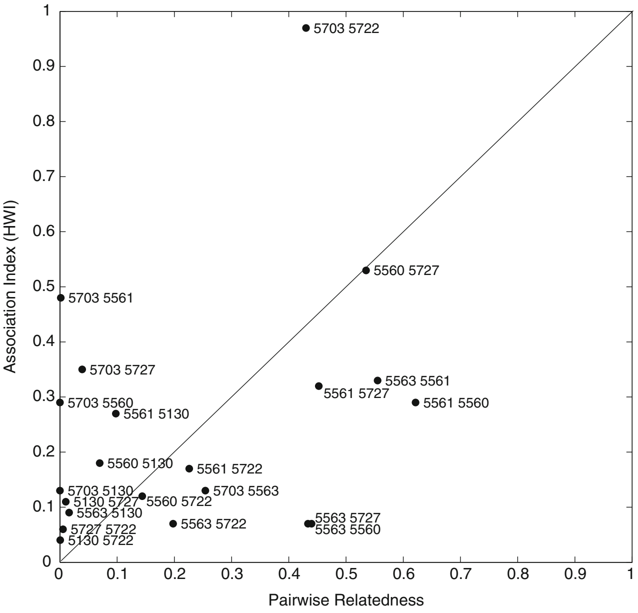

Fig. 1 Plot comparing dyadic HWI of sperm whale (*Physeter macrocephalus* Linnaeus 1758) pairs with that dyad's corresponding pairwise relatedness value. The diagonal represents the 1:1 ratio line on which points would be expected to fall if index of association was identical to the relatedness between dyad members. Note the dyads *5703–5722* and *5703–5561*, the calf (*5703*) with its mother (*5722*) and babysitter (*5561*)

adult females and immature males within sperm whale units.

There are several potential reasons that this study's findings differed from those of Christal and Whitehead (2001). First, the data in the two studies were collected from different oceans. Christal and Whitehead (2001) studied social units in the Eastern Tropical Pacific, where the impacts of modern whaling were much greater than in the Atlantic (Rice 1989; Whitehead et al. 1997; Whitehead 2003). As a result of whaling decreasing the size of matrilines in the Pacific, in order to maintain a unit size large enough to protect their young from predation, females may have formed units with shorter relationship histories and less genetic relatedness. Furthermore, the predation risk appears higher in the Pacific, where a number of attacks by killer whales, *Orcinus orca* (Linnaeus 1758), on sperm whales have been observed, at least one of which was successful, whereas there are no attacks reported for the North Atlantic, despite considerable whale-watch and scientific study of sperm whales in the North Atlantic (Jefferson et al. 1991; Pitman et al. 2001). This predation may add to the pressures of Pacific sperm whales to form units with unrelated animals with which they share weaker bonds. Thirdly and potentially as a result of the other effects, these two studies differed in the number of animals present in a unit. The average unit size in the Caribbean is around six animals (Gero 2005), while the number is almost twice that in the Pacific (~12 individuals, Christal and Whitehead 2001), likely as a result of being made up of several matrilines. With an increase in unit size, there is an accordingly large increase in social options for an individual. As such there may be a potentially greater chance that individuals choose their associates based on other potential benefits than kin selection. Finally, the two studies differed greatly in terms of the amount of data and therefore the power of their analyses. While Christal and Whitehead (2001) spent up to 21 days with a given social unit and included up to a maximum of 79 clusters in their analysis of which animals were identified in an average of nine clusters (range=3–15), this study spent 41 days with the 'GOS' and observed 491 clusters in which each of the unit members was identified in an average of 104 of these clusters (range=56–207). Thus, Christal and Whitehead's (2001) study likely suffered from a relative lack of power when examining within-unit associations among individuals (see Whitehead 2008b).

Not only do the members of the 'GOS' have strong preferences and avoidances in association, but the strength of these relationships correlates with relatedness. Among unit members, individuals generally prefer to associate with kin. This pattern is observed in other mammalian species which live in stable long-term groups. Among elephants, individuals within core social groups or 'family units' show patterns of association which can be predicted by relatedness (Archie et al. 2006). Within primate groups, individuals interact more with kin than non-kin and, further, appear to distinguish between close kin and distant kin (summarised in Silk 2005). The results of this study are drawn from a social unit in which all individuals share the same haplotype; however, these findings are also of interest when we consider the larger, often multi-matrilineal, social units found in the Eastern Tropical Pacific or North Atlantic. If relatedness creates intra-unit complexity in association within multi-matrilineal units as well, what mechanisms keep unrelated individuals within a unit?

It is believed that predation pressure is the primary factor promoting group formation in cetaceans (Connor 2000). By living in groups, individuals decrease their chance of being preyed upon through increased vigilance, protection by mobbing, predator confusion or through dilution (Connor 2000). Protection of young through babysitting is a likely candidate as a major evolutionary force driving sperm whale sociality (Best 1979; Gordon 1987; Whitehead 1996, 2003). In contrast to the generally accepted paradigm for primates, for whom intra-specific resource competition is considered the force driving the development of long-term bonds (Wrangham 1980), Whitehead (1996, 2003) suggested that in sperm whales the communal defence of the calves from predators has led to the formation of social units and the strong bonds between unrelated females.

Unlike most of their terrestrial mammalian counterparts, the pelagic sperm whales have no refuges in which to hide from predators (Whitehead 2003). A set of stable, long-term companions would grant members greater vigilance and a better ability to fight off predators (Whitehead 2003). Thus, it is likely the evolution of a babysitting system and possibly the communal care for calves that was a driving force towards sociality.

Should this evolutionary framework hold, one would expect babysitters to be unrelated, as is observed in meerkats, whose individual contributions to cooperative rearing are not correlated with kinship as some helpers are unrelated immigrants to the group (Clutton-Brock et al. 2000, 2001). In contrast, we noted the calf's babysitter was the mother's closest relative, a pattern similar to that found among primates (summarised in Nicolson 1987) and elephants (Lee 1987). This finding suggests that unrelated unit members may not be preferred providers of additional allocare in the form of babysitting but that group size during attacks from predators and increased vigilance may be the primary mechanisms maintaining multi-matrilineal social units. Future work should investigate whether kinship primarily determines which individual in sperm whale social units assumes the role of the babysitter or whether a more complex reciprocal or multi-modal system is in place.

In addition, these findings indicate that individuals differ in their sociability, such that some animals spend more time involved in social associations than others. There are likely several explanations for differences in sociability among which two are likely candidates, age and social role. With several generations of females present in a unit and the potential for some of these to be reproductively senescent (see Whitehead 2003), the grandmothering hypothesis (Hill and Hurtado 1991; Hawkes et al. 1998) would suggest that old female sperm whales may show increased gregariousness as they provide allocare for their grandchildren in the unit. Conversely, elderly female unit members may show a discernible decrease in social interactions, as in old world primates, in which older females show a trend of social withdrawal and peripheralisation (Waser 1978; Hrdy 1981; Hauser and Tyrell 1984; Nakamichi 1984), although this has been disputed (Maxim 1979; Pavelka 1991). The validity of these hypotheses can only be confirmed with accurate data on the age of these individuals which is still unavailable. Instead, variation in sociability may be an effect of social roles in sperm whale society. At the expense of their social interactions with other unit members, mothers may need to spend much of their surface time with their calf nursing and an increased amount of time at depth foraging to meet the metabolic demands of producing milk. In contrast, by definition, the role of babysitter is social, requiring the individual to associate with the calf. This might explain the patterns of avoidance and sociability observed in the mother and babysitter, respectively. Alternatively, individual differences in prey preference, dive length or activity budget could also affect the social interactions observed at the surface.

A unique series of encounters with this unit enabled the collection of an unprecedented data set, and as such, the merits and complications of these hypotheses can only be appreciated when the variability of these patterns has been examined within other units in the population. Continuing collection of data from the GOS and other units, along with changes and contrasts in patterns of association between years, as different females within the units fill the roles of babysitter or mother, should be particularly revealing.

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