# KINSHIP IN SPERM WHALE SOCIETY: EFFECTS ON ASSOCIATION, ALLOPARENTAL CARE AND VOCALIZATIONS

by

Christine M. Konrad

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To the seas and all that is in them,
particularly the sperm whale families that I've come to know and love.

And to my own family,
who raised me by the sea,
encouraged me to pursue my love of it,
and always believed I could do anything.

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## ABSTRACT

The overarching goal of my thesis is to characterize the relationship between kinship and social behaviour in a species with a cooperative, multilevel social structure – the sperm whale. To do so, I use a combination of genetic, behavioural and acoustic data collected during a longitudinal study of sperm whale social units, in the eastern Caribbean. Social units are a stable and basal component of sperm whale social structure. Associations between social units occur within large cultural groups, called vocal clans. To deal with degraded DNA from non-invasive sampling, I develop a protocol that maximizes genotyping success with degraded DNA, while quantifying and minimizing error rates. Using microsatellite loci and mitochondrial DNA haplotypes, I evaluate kinship among sperm whales, and I examine its relationship to social association, alloparental care and vocal repertoires. First, I characterize the extent and pattern of kinship in and among sperm whale social units, and test whether association is predicted by kinship. I document that social units have a clear matrilineal basis, but do not appear to be strictly matrilineal. My findings also indicate paternal relatedness between social units. Within units, I find individuals associate more with their closer relatives, but this is not the case among units. Second, I investigate calf care in relation to kinship. I demonstrate that behavioural observations are not always sufficient for assigning maternity, and that alloparental care is considerable in some cases and correlates positively with maternal kinship. Exceptions to the general pattern, however, demonstrate that, in addition to kin-selection, other factors influence alloparental care, perhaps including reciprocity, group augmentation or gaining maternal experience. Lastly, I examine acoustic repertoires of individuals and social units, in the context of kinship and social association. Variation in vocal repertoires was not explained by close kinship or social bonds. This supports the prevailing hypothesis that these vocalizations are culturally transmitted, and not determined genetically. Further, this suggests that vocal learning occurs broadly within clans, rather than preferentially from close kin or close social associates, or that biases in vocal learning at lower levels of social structure are diffused by clan-level processes. Also, by observing an absence of signals of kinship in vocalizations, my results suggest that a different mechanism, perhaps familiarity, regulates kin-selection among sperm whales. In conclusion, kinship clearly influences social unit composition, association preferences and alloparental care among sperm whales. However, I also reveal variability in social behaviour that is unexplained by kinship, which highlights the complexity of drivers behind social structure, cooperation and communication in this cultural, highly social and large-brained species.

## LIST OF ABBREVIATIONS USED

| | |
|---|---|
| bp | base pair |
| C | Celsius |
| cm | centimetre |
| DMSO | Dimethyl sulfoxide |
| DNA | deoxyribonucleic acid |
| dNTP | deoxynucleotide triphosphates |
| $\Delta r$ | difference in pairwise relatedness |
| $E_{het}$ | genotyping error rate for apparent heterozygotes |
| $E_{hom}$ | genotyping error rate for apparent homozygotes |
| hr | hour |
| HWI | half-weight index |
| ICI | inter-click intervals |
| ID | identification |
| km | kilometre |
| lb | pound |
| m | metre |
| $MgCl_2$ | Magnesium chloride |
| min | minute |
| mtDNA | mitochondrial deoxyribonucleic acid |
| mM | millimole |
| ng | nanogram |
| p | p-value |

| | |
|---|---|
| PCR | polymerase chain reaction |
| pH | potential of hydrogen |
| $P_{Ind}$ | probability of two samples originating from the same individual |
| $P_{Sib}$ | probability of the two samples being from full-siblings |
| *r* | pairwise relatedness |
| $r_s$ | Spearman's rank correlation coefficient |
| s | second |
| sd | standard deviation |
| $T_a$ | annealing temperature |
| TD | touchdown |
| µl | microlitre |
| µM | micromole |
| $ZnCl_2$ | Zinc chloride |

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# CHAPTER 1

# INTRODUCTION

"*Models that attempt to explain altruistic behaviour in terms of natural selection are models designed to take the altruism out of altruism.*"

~ R. Trivers, 1971

## 1.1 Why Cooperate?

The evolution of cooperation has been the object of much scientific thought, debate and empirical study (see reviews in Pennisi 2009; Connor 2010; Clutton-Brock 2002). Examples of cooperation range from immense 'supercolonies' of ants (Giraud, Pedersen, and Keller 2002), to food sharing among vampire bats, *Desmodus rotundus*, (Wilkinson 1984), and to the incomparably complex and cooperative society of our own species, *Homo sapiens* (Melis and Semmann 2010). There are numerous factors at work in the evolution of these cooperative social systems. This is reflected in the diversity of theories that have emerged to explain such systems (Connor 2010; Clutton-Brock 2002). However, a commonality that must be true for these systems to evolve and persist is that the benefits to cooperators must outweigh the costs.

The theory of kin selection provides one explanation for costly cooperation (Hamilton 1964a; Hamilton 1964b). Kin selection predicts that individuals maximize their 'inclusive fitness', by helping relatives when the cost of the cooperative behaviour is less than the

benefit to its relative, weighted by the degree of relatedness to the helper. Cooperation between non-relatives, however, requires a different explanation, and kin selection often fails to explain variation in cooperation among relatives (Clutton-Brock 2002).

Other theories to explain cooperation are diverse, still debated, and not mutually exclusive (Leimar and Hammerstein 2010; Clutton-Brock 2009; Connor 2007b). A popular alternative explanation is reciprocal altruism, in which individuals exchange favours, each paying a fitness cost and in turn receiving a benefit that is greater than the cost of the behaviour (Trivers 2006; Trivers 1971). In other cases, seemingly altruistic behaviours may be rewarded through by-product benefits, without requiring reciprocation from the helped individual (Connor 2007b). Group augmentation, for example, can operate if the survival or reproduction of individuals increases with group size, such that helping others raise offspring benefits the helpers by adding members to their own group (Kingma et al. 2014; Kokko, Johnstone, and Clutton-Brock 2001). Also, certain cooperative behaviours may be mutually beneficial and have no cost at all (Connor 2007b).

### 1.2 Cooperation and Complex Societies

Discussions of cooperation often highlight the apparent gap between humans and all other animals in terms of their degree and complexity of cooperation (Hauser, McAuliffe, and Blake 2009; Melis and Semmann 2010). A reason typically cited for this difference is the mental capacities and social environment required for the evolution of more advanced aspects of cooperation, such as reciprocity (Stevens and Hauser 2004; Hauser, McAuliffe, and Blake 2009). As discussed by Connor (2007a), however, outside of primates, there

are two notable peaks in the evolution of brain size: in elephants and toothed whales. A common feature of humans and these two taxa is high inter-dependence that is driven by risks from conspecifics and/or predators and that necessitated the development of social strategies (Connor 2007a). Studying the non-human taxa that come closest to the mental capacity, social complexity and degree of cooperation found in humans can improve understanding of how and why cooperative groups evolve, and, as discussed by Whitehead and Rendell (2015), such comparisons provide a context within which to consider our own evolution.

The structure and dynamics of social networks can also influence the evolution of cooperation (Ohtsuki et al. 2006; Fehl, van der Post, and Semmann 2011). Dynamic relationships, where individuals can break connections with non-cooperators, have been demonstrated to promote cooperation in humans (Fehl, van der Post, and Semmann 2011). Social structure not only affects the evolution of cooperation, but has additional ecological and evolutionary consequences. It influences numerous processes, including, but certainly not limited to, disease and information transmission and frequency-dependent selection (Kurvers et al. 2014). In a dynamic interplay, social structure can also affect, and in turn be affected by, culture (Cantor and Whitehead 2013).

As an explanation of hyper-cooperation among humans, it has also been proposed that cooperative breeding may promote prosocial behaviours more generally, a hypothesis which is supported by inter-species comparisons across primates (Burkart et al. 2014; Burkart, Hrdy, and Van Schaik 2009; Burkart and van Schaik 2010). Though the robustness of this theory has been contested (Thornton et al. 2016), the presence of alloparental care and cooperative groups also correlate with each other more generally

across mammals and birds (Riedman 1982), suggesting that cooperative breeding creates a foundation of social dependence from which cooperative societies can evolve. Thus, studying the evolution of alloparental care in a diversity of taxa, particularly those living in complex societies, develops our understanding of how socio-ecological conditions promote the evolution of cooperation and complex societies.

### 1.3 Sperm Whale Social Structure

To address questions of social structure and cooperation, the sperm whale (*Physeter macrocephalus*) presents a useful case study, as one of only a few species besides ourselves known to have a multi-level cooperative social structure (Whitehead et al. 2012). Social units form the base of this social structure, and are composed of a stable membership of female sperm whales and their dependant offspring (Gero et al. 2014; Christal, Whitehead, and Lettevall 1998). Females are generally assumed to remain within their natal unit (Whitehead 2003), while juvenile males disperse from their social units, heading poleward, and becoming increasingly more solitary until they mature and return to more equatorial waters to mate (Best 1979). Little is known of their movement patterns or the distribution of mating success among mature males, although attendance to any social unit while breeding is brief, on the order of hours (Whitehead 2003).

For hours or days at a time, social units sometimes join together to form temporary 'groups' (Whitehead 2003), but seem to only do so with units that are members of the same 'clan' (Gero, Whitehead, and Rendell 2016; Rendell and Whitehead 2003). Clans constitute a higher level of social structure, delineated using similarity of vocal repertoires (Rendell and Whitehead 2003), but also characterized by differences in non-

vocal behaviours that appear to be socially learned (Whitehead and Rendell 2004; Marcoux, Rendell, and Whitehead 2007; Cantor and Whitehead 2015; Marcoux, Whitehead, and Rendell 2007).

Agent-based modelling has suggested that clans likely evolved and persist as a result of biased social learning (Cantor et al. 2015). However, which factors contribute to the evolution and persistence of the lower levels of sperm whale social structure has been largely untested. Cooperative breeding, particularly communal defence of calves against predators, is suspected to be the primary force driving and maintaining social units (Best 1979; Gero, Gordon, and Whitehead 2013), but how this cooperative care evolved is unclear. Additionally, social preferences have been identified among individuals within social units (Gero, Engelhaupt, and Whitehead 2008; Gero et al. 2009), and among units within clans (Gero, Gordon, and Whitehead 2015). The drivers of these social preferences have rarely been explored, and only in cases restricted to few individuals or limited by coarse measures of association (Gero, Engelhaupt, and Whitehead 2008; Christal 1998; Ortega-Ortiz et al. 2012).

Sperm whale social units are frequently assumed to be matrilineally-based, though in reality this assumption has been examined in only a few units, with mixed results (Mesnick 2001; Christal 1998; Gero, Engelhaupt, and Whitehead 2008; Ortega-Ortiz et al. 2012). If this assumption proves true, however, kin selection may be able to explain cooperation among sperm whales. As a further complication, the extent of paternal relatedness and whether it contributes to inclusive fitness is essentially unknown.

Based on their social structure and life history, several other drivers of cooperation are also plausible for sperm whales. For example, given the relative stability of sperm whale social units, and the presence of long-term social preferences between social units, there is opportunity for reciprocal altruism both within and between social units (Gero, Gordon, and Whitehead 2013; Gero et al. 2009; Gero, Gordon, and Whitehead 2015). As a long-lived, slow-reproducing species that relies on communal care of calves and defence against predators, additional unit members are almost certainly valuable and difficult to replace. Thus, group augmentation is another reasonable mechanism that could be driving cooperation. Sperm whales also live in a dynamic society where social relationships within units change over time (Gero, Gordon, and Whitehead 2013) and occasionally individuals transfer between units, and units sometimes split and merge (Christal, Whitehead, and Lettevall 1998). This grants individuals the opportunity to break ties to non-cooperative individuals and seek new cooperative partners, which could lead to natural selection favouring cooperation through social network dynamics, as has been suggested by Fehl, van der Post, and Semmann (2011).

### 1.4 Thesis Objectives and Organization

The overarching goal of my thesis is to characterize kinship among sperm whales and examine its relationship with social behaviour. To achieve this, I analyze data and samples collected during a longitudinal study of sperm whale social units, in the eastern Caribbean (Gero et al. 2014), combining genetic, behavioural and acoustic data. First, I describe the congruence between genetic relatedness and sperm whale social organization, assessing the degree of matrilineality in social units, and testing whether kinship predicts social association, both within and between social units (Chapter 2).

Second, I characterize calf care within social units, comparing the relative contributions of mothers and alloparents, and assessing the extent to which alloparental care is explained kinship (Chapter 3). Third, I test for a relationship between the 'coda' vocal repertoires of sperm whales and both kinship and social association, to better understand the development and function of these vocalizations, including their potential as a kin-recognition signal (Chapter 4). In the final chapter, I conclude by considering my findings in a broader context, assessing the plausibility of different theories to explain the cooperation and multilevel social structure of sperm whales, and discussing challenges in this research and areas of interest for further investigation. This chapter is followed by two appendices, containing supplementary material for Chapters 2 and 4.

# CHAPTER 2

# KINSHIP INFLUENCES SPERM WHALE SOCIAL ORGANIZATION WITHIN, BUT NOT AMONG, SOCIAL UNITS[1]

## 2.1 Abstract

Sperm whales have a multilevel social structure based upon long-term, cooperative social units. What role kinship plays in structuring this society is poorly understood. We combined extensive association data (518 days, during 2005-2016) and genetic data (18 microsatellites and 346bp mtDNA control region sequences) for 65 individuals from 12 social units from the Eastern Caribbean to examine patterns of kinship and social behaviour. Social units were clearly matrilineally-based, evidenced by greater relatedness within social units (mean $r$=0.14) than among them (mean $r$=0.00) and uniform mtDNA haplotypes within social units. Additionally, most individuals (82.5%) had a first-degree relative in their social unit, while we found no first-degree relatives between social units. Across all spatiotemporal scales, individuals associated more with their closer relatives, even with mother-calf pairs excluded (matrix correlations: 0.13-0.36). However, excepting a highly-related pair of units that merged over the study period, associations between social units were not correlated with kinship ($p>0.1$). These results are the first to robustly demonstrate kinship's contribution to social unit composition and association

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[1] *This chapter has been submitted to the Royal Society Open Science, and is in review. Authors' contributions: Christine M. Konrad (CK), Shane Gero (SG) and Hal Whitehead (HW) participated in the collection of the field data; CK carried out all molecular laboratory work and statistical analysis, and wrote the manuscript; SG coordinated the field operations of the study, and completed the photo-identification; Tim Frasier (TF) aided sample collection efforts and supervised the molecular laboratory work; SG, TF and HW contributed funds and edited the manuscript; all authors collaborated in the conception and design of the study and gave final approval for publication. Publication history: Manuscript First Submission: 28 AUG 2017*

preferences, though they also reveal variability in association preferences that is unexplained by kinship. Parallels with kinship in elephant society suggest similar evolutionary pressures driving convergent cooperative societies.

## 2.2 Introduction

Cooperative societies are widespread in the animal kingdom (Clutton-Brock 2002; Cockburn 2006; Clutton-Brock 2009). For these systems to evolve and persist, the benefits to cooperating individuals must outweigh the costs (Clutton-Brock 2002; Axelrod and Hamilton 1981). Costly cooperative behaviours between kin are typically explained in terms of kin selection (Hamilton 1964a; Hamilton 1964b), which predicts that individuals maximize their 'inclusive fitness', by helping relatives. This theory, however, cannot explain cooperation between non-relatives, and often fails to explain observed variation in cooperation between relatives (Clutton-Brock 2002). In such cases, other mechanisms in lieu of kin selection, or in addition to it, are required to explain seemingly altruistic behaviours. Another frequently considered mechanism is reciprocal altruism, in which individuals exchange favours that have a fitness cost (Trivers 2006; Trivers 1971). However, despite much focused attention on this theory, relatively few examples have been firmly demonstrated (Hammerstein 2003). Instead, many cases of cooperation may be driven by processes involving byproduct benefits (Connor 2007b; Connor 2010), such as group augmentation (Kingma et al. 2014; Kokko, Johnstone, and Clutton-Brock 2001), which does not necessitate the reciprocation of costly investments.

To disentangle potential mechanisms driving cooperative behaviours, long-term studies of social relationships and behaviour are required, together with comprehensive genetic

sampling for kinship. These types of datasets are rare among mammals, particularly among marine mammals.

The sperm whale (*Physeter macrocephalus*) provides an interesting case study of social structure and cooperation, because it has a multi-level cooperative social structure (Whitehead et al. 2012). Female and juvenile sperm whales live in social units that are stable over a timeframe of years (Gero et al. 2014; Whitehead 2003), from which males disperse before sexual maturity to live primarily solitarily or with other males (Best 1979). Such units join together to form temporary 'groups', which can last hours to days (Whitehead 2003). Formation of these groups is mediated by a higher level of social structure: 'clans'. Units have only been observed to form groups with other units who are members of the same clan (Gero, Whitehead, and Rendell 2016; Rendell and Whitehead 2003). Clans are cultural groups, within which members share socially learned behaviours (Cantor and Whitehead 2015).

The evolution and persistence of cooperative social units and groups in sperm whales has not been explicitly examined. Calf care, specifically communal defence against predators, is hypothesized as the primary force driving and maintaining social units (Gero, Gordon, and Whitehead 2013; Best 1979), but it is unclear how these cooperative behaviours evolved. Sperm whale social units are often described as matrilineally-based, which makes kin selection a logical hypothesis for explaining cooperation. Yet, the degree to which units are matrilineal is poorly understood.

Due to the long-term observations required to confidently delineate long-term social units, kinship has typically been studied at the level of temporary social groups, which

can contain multiple units (Richard et al. 1996; Pinela et al. 2009; Mesnick 2001). Genetic data on social units have been published for only a few social units to date (Gero, Engelhaupt, and Whitehead 2008; Ortega-Ortiz et al. 2012; Mesnick 2001; Christal 1998), with little or no support for matrilineal units (Mesnick 2001; Christal 1998; Ortega-Ortiz et al. 2012), expect in one well studied social unit in the Caribbean (Gero, Engelhaupt, and Whitehead 2008). Most of these assessments of matrilineality were imprecise, however, as they lacked explicit definitions of 'matrilineal' (Gero, Engelhaupt, and Whitehead 2008; Ortega-Ortiz et al. 2012; Mesnick 2001). If kin selection is a driving force of cooperation, we would also expect individuals' interactions and associations to vary, depending on their degree of relatedness. In the few cases where social behaviour has been explicitly examined in relation to kinship, results have been mixed (Gero, Engelhaupt, and Whitehead 2008; Christal 1998; Ortega-Ortiz et al. 2012).

In this study, we explicitly define multiple possible levels of matrilineality and examine patterns of kinship and social behaviour using well-studied sperm whale social units from the Eastern Caribbean. We address three primary questions: (1) to what degree are social units matrilineal, (2) do rates of association between individuals within units correlate with relatedness, and (3) does kinship between units predict association preferences?

## 2.3 Methods

### *2.3.1 Field Methods*

Field work was carried out in an area of approximately 2,000 km$^2$, off the leeward, western coast of Dominica, in the Caribbean Sea (15.5°N; 61.5°W) from 2005-2016 as a part of a longitudinal research project on sperm whale behaviour (Gero et al. 2014).

Annual field seasons ranged from two to four months in duration, and occurred between January and June, using various research platforms (total effort: 518 days).

Sperm whales were located and followed, visually by observers on deck during daylight hours, as well as acoustically using hydrophones up to 24 hours a day (Gero et al. 2014). Photographs were taken of the trailing edge of flukes of juveniles and adults (Arnbom 1987) and of the dorsal fins of calves (Gero et al. 2009) for individual identification. In conjunction with these identification photographs, we recorded observations of associations of individuals in clusters (Gero et al., 2014). Clusters were defined as groupings of individuals at the surface in close proximity to each other (< 40 m) with coordinated behaviour (Whitehead 2003).

We used dip nets to opportunistically collect sloughed skin from the flukeprints of individual whales or clusters of whales (Whitehead et al. 1990). In 2015 and 2016, we also collected biopsy skin samples from specific individuals, to fill known gaps in our sample set. We used a 90 lb draw weight crossbow and bolts with 2.5 cm long tips with 0.5 cm circumferences (see Kowarski et al. 2014 for details). Skin samples collected from 2005 to 2010 were stored in ethanol (at a concentration of 70% or greater), and samples collected from 2011 onwards were stored in a 20% DMSO solution saturated with salt (Seutin, White, and Boag 1991).

*2.3.2 Identifications*

As in Gero et al. (2015), identification photographs were assigned quality ratings, and only high quality photographs were used for assigning final identifications.

In some cases (~6% of identifications), well-known adults and juveniles that could not be photographed when multiple animals fluked synchronously, but whose flukes were observed by S.G., were recorded as having been identified. Past analyses have demonstrated that patterns of association do not differ when including these identifications (Gero, Gordon, and Whitehead 2015). Likewise, well-known calves who were not photographed but were readily identifiable due to distinct dorsal markings that were visible by eye or because they were known to be the only calf in the social unit, were also recorded as having been identified (25% of identifications).

*2.3.3 Measuring Association and Defining Social Units*

For our analysis, we considered three definitions of association. First, as our finest spatiotemporal scale of association, individuals in clusters at the surface, and so likely within in visual contact and often in physical contact, were considered to be associated. Second, we defined association more loosely as individuals identified within two hours of each other. Individuals seen within this short timeframe are likely close enough to be in acoustic contact. Third, we defined association as being identified on the same day, to capture avoidances or behavioural coordination that may be occurring on larger spatiotemporal scales.

To examine association preferences across different time scales, we used a variety of sampling periods, chosen depending on the definition of association and the association index used. The shortest period used was two hours, which corresponds to approximately two dive cycles in sperm whales and has been applied in other studies of this species (Christal & Whitehead, 2001; Gero et al., 2015). With this sampling period, we aimed to

maximize the number of samples while minimizing autocorrelation in cluster composition. The longest period used was 'year', which has also been previously applied in this species (Gero et al., 2015) to highlight long-term associations, removing potential autocorrelation across sequential days.

Across our study period, demographic changes affected our population, as individuals were born and died. Therefore, for most analyses, we used an association index, 'both identified', that minimizes the bias of these changes on association measures. This index calculates the proportion of those sampling periods in which both individuals were identified in which they were associated (Whitehead 2008). However, this index typically requires long sampling periods to obtain enough periods within which both individuals were identified. For the analyses that would not be strongly affected by demographic changes, namely those within annual field seasons, and those at a unit-level, rather than an individual-level, we used half-weight indices (HWI) of association (Cairns and Schwager 1987). This index best corrects for the types of biases in identification rates that are typical of cetacean photo identification (Cairns and Schwager 1987; Whitehead 2008).

Social units were delineated as in Gero *et al*. (2014), so that they reflect long-term, stable social relationships. If two whales were identified within two hours of each other in at least two different years they were assigned to the same unit, except in the case of one pair of units that were also repeatedly seen apart. Calves were automatically considered members of the units they were born into.

*2.3.4 DNA Extraction, Quality Control, and Sexing*

We extracted DNA from all skin samples using standard phenol-chloroform procedures (Sambrook and Russell 2001). After extraction, DNA from all samples was quantified via spectrophotometry, using a NanoDrop 2000 (Thermo Scientific, Waltham, MA), and DNA concentrations were standardized accordingly for use in polymerase chain reactions (PCRs).

To determine the sex of individuals, we amplified a 94 base pair (bp) fragment of the ZFX/ZFY gene (Konrad et al. 2017). Within this fragment, a *Taq1* restriction site is present in the ZFX but not the ZFY sequence, due to a fixed difference between the X- and Y-chromosomes. We digested the amplicon, and we size-separated and visualized the post-restriction enzyme PCR product using ethidium bromide and agarose gel electrophoresis to distinguish females (37 and 57 bp fragments only) from males (37, 57 and 94 bp fragments) (Konrad et al. 2017).

We also used the results of this sexing reaction as a first stage of quality control, to screen for samples that were degraded beyond being useful to this study. Samples that failed to amplify at the 94 bp *ZFX/ZFY* gene fragment were deemed too degraded for subsequent attempts at genotyping or sequencing. Additionally, we used this sexing assay to determine and optimize DNA amplifiability for downstream genotyping (Konrad et al. 2017). Sperm whale sloughed skin samples vary greatly in the amount and quality of DNA they yield (Konrad et al. 2017), and DNA quantification via spectrophotometry can overestimate the amount of viable DNA in these samples, because it includes fragments that are too short to be amplified in PCRs. We adjusted DNA concentrations of sloughed

skin samples, in proportion to the brightness of the sample's amplified ZFX/ZFY gene fragments relative to those of a biopsy sample, to maximize success of amplification across microsatellite loci (Konrad et al. 2017). Samples that still genotyped poorly (genotyped at < 10 microsatellite loci; see below) were excluded from further analysis.

*2.3.5 Microsatellite Genotyping*

We screened 33 microsatellite loci for amplification success with sperm whale skin samples. We excluded microsatellite loci that failed to amplify (n = 2), amplified poorly (n = 11), or were unreliable to genotype (n = 2). For exclusion reasons by locus, see Appendix A, Table A1. For the remaining 18 loci, we optimized PCR conditions.

All PCRs for microsatellite loci were carried out in 20 µl reactions in 1x PCR buffer, with 1.5 mM $MgCl_2$, 0.2mM of each dNTP, 0.3 µM of each primer, 0.05 U/µl of GoTaq Flexi DNA polymerase (Promega, Madison, WI) and 10 ng of template DNA (based on functional concentration). Reactions were run on an ABI Veriti 96 well thermal cycler (Applied Biosystems, Foster City, CA) with the following parameters: initial denaturing for 5 min at 94°C, then cycles of denaturation for 30 s at 94°C, annealing for 1 min, and extension for 1 min at 72°C, followed by a final elongation step, of either 10 min at 72°C or 45 min at 60°C. For locus-specific annealing temperatures and numbers of cycle, see Appendix A, Table A2. We included a no-template negative control with all reactions.

For four loci that did not amplify well with this standard procedure, a biphasic touchdown (TD) PCR protocol was used, to maximize amplification of low quality DNA while minimizing spurious amplification. This protocol consisted of a phase of TD-PCR (Korbie and Mattick 2008), where annealing temperature ($T_a$) was started at 10°C above

the final $T_a$ and dropped by 0.5°C with each cycle, for 20 cycles, followed by 10 cycles at the final $T_a$. In a second phase of PCR, 2 µl of this first PCR product was used as template DNA, and the same cycle parameters were used as for the standard procedure.

To genotype the samples, we performed capillary electrophoresis to size separate and visualize the PCR product, using an ABI 3500xl Genetic Analyzer (Applied Biosystems, Foster City, CA). Before loading samples for genotyping, PCR products for some loci were diluted in distilled water (see Appendix A, Table A2 for dilution ratios), and up to three loci (that were labelled with different fluorescent molecules and had been amplified in separate PCRs) were combined. We used the program GeneMarker (SoftGenetics, State College, PA) to automatically score fluorescence peaks, and all allele calls were confirmed manually by eye and then manually re-inspected a second time.

To address issues associated with low quality DNA, particularly allelic dropout (Gagneux, Boesch, and Woodruff 1997), we applied a multiple-tubes PCR approach. This allowed us to determine rates of genotyping errors and improve confidence in genotypes. For 17 samples, selected at random with respect to DNA quality and quantity, seven of which were also used in duplicate as blind controls, we performed at least two independent PCRs for apparent heterozygotes and seven independent PCRs for apparent homozygotes. These numbers of replicate PCRs were selected based on the conservative approach described by Taberlet *et al.* (1996). We determined genotyping error rates by comparing the genotypes of the blind controls to their counterparts and calculating the rate of discrepancies. Using these rates, we determined the number of reactions required to reach a minimum desired level of confidence in genotypes of 99% per locus, and we performed this number of reactions to achieve this level of confidence. If scores from

replicate reactions for an individual were inconsistent, additional reactions were performed until one genotype score emerged as at least 100 times more likely (based on above error rates) than the other observed scores. If this likelihood ratio was not achieved in a reasonable number of reactions, no data were included in the analysis for that individual at that locus.

Previous work on sperm whales has demonstrated the absence of significant population differentiation at microsatellite loci within the North Atlantic (Engelhaupt et al. 2009). Therefore, all genetic individuals sampled off Dominica were considered to be from a single population for the purposes of calculating the population's allele frequencies.

We tested for linkage disequilibrium using GENEPOP v. 4.2 (Raymond and Rousset 1995), and tested for null alleles and deviation from Hardy–Weinberg equilibrium using Cervus 3.0.7 (Kalinowski, Taper, and Marshall 2007).

*2.3.6 mtDNA Haplotype Sequencing*

To determine mtDNA haplotypes, we amplified and sequenced 346 bp at the 5' end of the mtDNA control region, using the primers t-Pro and Primer 2 (Yoshida et al. 2001). Mitogenomic diversity is relatively low in sperm whales, compared to estimates for other mammalian species, but out of partitions of the sperm whale mitogenome that have been compared, nucleotide diversity was greatest in the control region (A. Alexander et al. 2013).

For the majority (80%) of sequencing reactions, initial PCRs were carried out in 20 µl reactions in 1x PCR buffer, with 1.5 mM $MgCl_2$, 0.2mM of each dNTP, 0.3 µM of each

primer, 0.05 U/µl of GoTaq Flexi DNA polymerase and 10 ng of template DNA (based on functional concentration). Reactions were run on an ABI Veriti 96 well thermal cycler with the following parameters: initial denaturing for 5 min at 94°C, then cycles of denaturation for 30 s at 94°C, annealing for 1 min at 55°C, and extension for 1 min at 72°C, followed by a final elongation step, of 45 min at 60°C. Excess dNTPs and primers were digested in an enzymatic reaction containing 5 µl PCR product, 0.65µl Antarctic phosphatase buffer (50 mM Bis-Tris-Propane-HCl, 1 mM $MgCl_2$, 0.1 mM $ZnCl_2$, pH 6.0), 0.1µl Antarctic phosphatase (New England Biolabs, Ipswich, MA), and 0.03µl exonuclease I (New England Biolabs, Ipswich, MA). For this reaction, samples were incubated for 15 min at 37°C, followed by 15 min at 80°C. Sequencing reactions, using the product from the preceding reaction, were then carried out in 15µl reactions using the BigDye Terminator v3.1 Cycle Sequencing kit (Applied Biosystems, Foster City, CA), containing 1.5µl of Reaction Mix, 3µl of Sequencing Buffer, and 1µl (at 10 µM) of the primer t-Pro (Yoshida et al. 2001). Reactions were run on an ABI Veriti 96 well thermal cycler with the following parameters: initial denaturing for 2 min at 96°C, then cycles of denaturation for 20 s at 96°C, annealing for 20 sec at 50°C, and extension for 4 min at 60°C.

The remaining 20% of reactions were carried out using a BigDye® Direct Cycle Sequencing Kit and the accompanying protocol (Applied Biosystems, Foster City, CA), which used M13 tailed primers.

After the sequencing reaction, salts, nucleotides and primers were removed via ethanol precipitation (Irwin, Mitchelson, and Findlay 2003) and resuspended in 10µl of HiDi formamide (Applied Biosystems, Foster City, CA). We included a no-template negative

control with all reactions, and 14 samples were duplicated as blind replicates to estimate the consistency of haplotype sequencing. To size-separate and visualize the PCR products, we performed capillary electrophoresis using an ABI 3500xl Genetic Analyzer. Sequences were manually trimmed and edited using 4Peaks (nucleoytes.com) and were manually aligned using BioEdit 7.2.5 (Hall 1999).

*2.3.7 Identification of Genetic Individuals*

To assign whether or not samples with the same or very similar microsatellite genotypes were from the same individual, we estimated the probability of the samples originating from the same individual ($P_{Ind}$), while incorporating genotyping errors (as determined above), and the probability of the two samples being from full-siblings ($P_{Sib}$; *sensu* Woods et al. 1999, Evett & Weir 1998). We classified samples as from the same individual if $\log_{10}(P_{Ind} / P_{Sib}) > 3$, and we classified them as from different individuals if $\log_{10}(P_{Sib} / P_{Ind}) > 3$. For pairs of samples where neither criterion was met, the sample with the less complete genotype was excluded from further analysis. We also checked the conclusions of this analysis for consistency with mtDNA haplotypes, sex, and photographic field identifications.

Genetic identities were linked to photo-identities directly when a biopsy sample was collected from a photo-identified whale or a sloughed skin sample was collected from a cluster made up of a single photo-identified whale. When sloughed skin samples were collected from clusters containing multiple individuals, the sample was assumed to be from any of the whales in the cluster. If all individuals in the cluster except one could be excluded as providers of the skin (based on sex or mismatching microsatellite genotypes

with other known samples) then the sample was deduced to be from the remaining individual. If multiple samples collected from different clusters were matched as the same genetic individual, the photo-identities of the whales that were present in all of these clusters were used to aid deduction. For some genetic individuals, more than one photo-identified individual remained non-excluded. These genetic individuals were not used in individual-level analyses, but if all non-excluded photo-identified individuals were from the same social unit, the genetic individual was assigned to this social unit and used in unit-level analyses. Individuals were also excluded from further analyses if they were not members of known social units or if the photo-identity of the genetic individual could not be deduced, such as when clusters contained unidentified individuals.

*2.3.8 Age Class*

Age classification of social unit members was accomplished based on observations of size and nursing in the field, as in Gero et al. (2014), combined with inference based on sex assignment. Individuals were classified as either adult females, juveniles, or dependant calves. The category 'juveniles' included individuals that were noticeably smaller than adult females, but no longer nursing. Additionally, because mature males are notably larger than adult females (Best, Canham, and Macleod 1984; Best 1979), individuals that were indistinguishable from adult females based on size but sexed as male were also classified as juveniles. Dependant calves were small individuals that were observed nursing. Some individuals that were initially classified as dependant calves were re-classified as juveniles in subsequent years if they were no longer observed nursing.

*2.3.9 Assigning Maternity and Determining Likely Genetic Relationships*

To infer maternity of juveniles and dependant calves, we used a full-maximum likelihood method for polygamous diploids implemented in Colony 2.0.6.2 (Jones and Wang 2010). We based error rates on the final genotyping error rates estimated for our multiple-tubes PCR approach (0.16% for allelic dropout rate and 0.1% for other errors). We performed a set of three runs, to increase the chances of finding the maximum likelihood configuration, and repeated these runs with two different random seed numbers, to confirm the reliability of the results. All adult females were included as putative mothers, and individuals classified as juveniles or dependant calves were included as offspring. No putative fathers were included. One juvenile female observed throughout the 12-year study period was assumed to be mature by the end of the study period (based on pregnancy ages reported in Best et al. (1984)). Therefore, the runs were performed in replicate with this individual as a putative mother instead of an offspring, but maternity assignment results did not change. We assigned maternity if the female had a mean probability > 90% across all runs. Maternity assignments were checked for consistency with mtDNA haplotypes. Individuals were classified as maternal half-siblings if they were assigned the same mother.

To test hypotheses about relationships between adult females, where relative age is unknown, we used the program ML-Relate (Kalinowski, Wagner, and Taper 2006). We evaluated which relationships (out of parent-offspring, half-sibling/grandmother-granddaughter, full-sibling and unrelated) were consistent with the genetic data at the 0.05 level of significance, by calculating likelihood ratios and using simulations to reject

unlikely relationships. If multiple relationships were consistent with the genetic data, this method was also used to identify the most likely relationship.

### *2.3.10 Determining Pairwise Relatedness*

To estimate relatedness between individuals, we used the R package *related* (Pew et al. 2015). Performance of different relatedness estimators varies depending on the relatedness structure of the population, and no single estimator performs best across all relatedness structures (Van De Casteele, Galbusera, and Matthysen 2001; Csilléry et al. 2006). Therefore, to select the best estimator for our dataset, we used a comparative function in *related* that uses our population allele frequencies to generate pairs of individuals with known relationships, and to estimate the relatedness of these pairs using four different relatedness estimators (Li, Weeks, and Chakravarti 1993; Lynch and Ritland 1999; Queller and Goodnight 1989; Wang 2002). For use in subsequent analysis, we selected the estimator with the highest correlation between observed and expected relatedness values, which was Wang's (2002) estimator. We used this estimator to calculate pairwise relatedness values for all pairs of individuals.

### *2.3.11 Relationships Between Haplotype Sharing, Pairwise Relatedness and Association*

Across all identified individuals from known social units, we tested for matrix correlations between measures of genetic similarity and social association. A large proportion of pairs of individuals were never both identified in the same time period, leading to many cells with no data in the matrices of social association, which rendered Mantel tests (Mantel 1967) inappropriate for obtaining reliable p-values. Instead, we calculated standard analytical p-values based on matrix correlation values (excluding

dyads with missing data in the association matrix), which, while not strictly valid for matrix data (the assumption of independent observations is not met), provide an approximate indication of statistical significance. The measures of genetic similarity used were mtDNA haplotype sharing (0 or 1) and pairwise relatedness. The measures of association used were: (1) same cluster, in 6-hr sampling period, (2) same cluster, in a year sampling period, (3) identified within two hours, in a 10-day sampling period, and (4) same day, in a year sampling period. To remove the effect of mothers associating with their dependant calves, we repeated the analyses with the pairwise data for these pairs omitted. We also repeated the analyses with only data for pairs of individuals in the same social unit included.

Additionally, across all genetic individuals that were assigned to a known unit, we tested for a matrix correlation between pairwise relatedness and shared unit membership (0 or 1), by performing Mantel tests (Mantel 1967), using SOCPROG2.7 (Whitehead 2009). We also examined the distributions of pairwise relatedness values within and between social units.

*2.3.12 Composition of Well-Sampled Social Units*

For well-sampled social units, we examined kinship patterns more closely. We defined well-sampled social units as those for which all adult females and at least 70% of all unit members were included in the genetic analysis. These were also the social units that we included for subsequent analyses examining within-unit association preferences and interactions relative to kinship.

For these units, we determined the proportions of relationships classified as mother-offspring, second-degree relatives (half-sibling or grandparent-grandoffspring), or more distantly related. We classified individuals as a mother-offspring pairs if they were assigned as such based on maternity assignment in Colony or if parent-offspring was the most probable relationship in ML-Relate. We classified individuals as second-degree relatives if they could be inferred as such based on mother-offspring relationships or if second-degree was the most probable relationship in ML-Relate. All other pairs were classified as more distantly related, which could also include unrelated individuals.

*2.3.13 Defining Matrilineality*

In conventional wisdom, 'matrilineal' would refer to groups where most females remain, for life, with their mothers and other close female relatives. But for meaningful discussion of matrilineality, it is helpful to define 'matrilineal' more specifically, and at several levels. At a coarse scale, a social unit could be defined as 'generally matrilineal' if members have a relatively recent common maternal ancestor, who need not be alive. In such cases, units should have a common mitochondrial DNA (mtDNA) haplotype and an average genetic relatedness that is above that of the population. Alternatively, a social unit could be considered 'strictly matrilineal' if all members have a common maternal ancestor who is still living in the social unit. Both definitions would be violated if unrelated individuals are members of the same social unit, and the strict definition would also be violated if units do not split after the death of their common maternal ancestor. A social unit that is not strictly or generally matrilineal could still be considered 'matrilineally-based' if it is made up of two or more strictly or generally matrilineal

families. We assessed which of these definitions were consistent with the social and genetic data for the social units in this study.

*2.3.14 Within-Unit Association*

Within each well-sampled social unit, we performed Mantel tests (Mantel 1967), using SOCPROG2.7 (Whitehead 2009) to test for significant matrix correlations between pairwise relatedness and association in clusters, at two sampling periods – 2-hr and a day. To remove the effect of mothers associating with their dependant calves, we repeated the analyses with the pairwise data for these pairs omitted.

Within the social unit with the most sampled members (Unit A), we also examined social modularity in relation to within-unit genetic structure. To account for demographic changes, we examined modularity within three different years that span the study period (2005, 2010, and 2015). We measured association as clusters in a daily sampling period, and we used an eigenvector-based method, as suggested by Newman (2006), and implemented in SOCPROG2.7 (Whitehead 2009). We examined the congruence between the social clusters identified by this method and the matrilineal clusters defined by mother-offspring relationships.

*2.3.15 Between-Unit Association*

For social units for which at least three members were included in the genetic analysis, we tested for relationships between social association and genetic similarity.

If at least one member of each of two social units were associated in a sampling period, then those individual's social units were considered associated in that sampling period.

We used four measures of association: (1) same cluster, in 2-hr, (2) same cluster, in a year, (3) identified within two hours, in a day, and (4) same day, in a year. For measures of genetic similarity, we classified each pair of units' mtDNA haplotypes as same or different, and calculated mean relatedness values. To calculate mean relatedness values between social units, we averaged the pairwise relatedness values between all pairs of individuals across each pairwise combination of social units.

We performed Mantel tests (Mantel 1967), using SOCPROG2.7 (Whitehead 2009) to test for matrix correlations between each index of association and each measure of genetic similarity. One pair of units appeared to be contributing strongly to correlations, and so the tests were repeated with pairwise data for that dyad omitted.

## 2.4 Results

### *2.4.1 Microsatellite Dataset and Quality Control*

Out of 153 samples (94.8% sloughed skin and 5.2% biopsy samples), 30 were excluded by quality control (23 failed to sex, 7 failed to genotype at a minimum of 10 microsatellite loci). After consolidating duplicates and excluding three likely duplicate samples that did not meet the log-likelihood ratio criteria, 95 unique individuals remained, 88.4% of which were scored at all 18 microsatellites, and all of which were scored at no fewer than 16 microsatellites. Mean allelic diversity was 9.3 (range: 3-17) and mean observed heterozygosity was 0.75 (range: 0.52-0.93). See Appendix A, Table A2 for locus-specific allelic diversity and heterozygosity.

We calculated the total genotyping error rate for apparent heterozygotes ($E_{het}$) to be 1.1%, incorporating contamination and spurious alleles (1.0% collectively) and manual scoring errors (< 0.1%). For apparent homozygotes ($E_{hom}$), the mean error rate was 2.9%, incorporating allele dropout (2.82%) and manual scoring errors (< 0.1%), but dropout rate varied widely across samples (max = 11.6%). Thus, for apparent heterozygotes, a minimum desired level of confidence in genotypes of 99% per locus was reached with two tubes (compound error rate = 0.013%). For apparent homozygotes, this level was reached with two tubes based on the average dropout rate (compound error rate = 0.085%), but three tubes were required based on the sample with the highest dropout rate (compound error rate = 0.16%). Thus, we performed a second reaction for loci at which an individual appeared heterozygous, and, to account for low quality samples, we performed at least three reactions for loci at which an individual appeared homozygous.

No loci showed strong indications of null alleles (all frequencies < 0.05) and we detected no evidence of deviations from Hardy–Weinberg equilibrium. Two pairs of loci had evidence of linkage disequilibrium after a Bonferroni correction, but given that our dataset is composed of social units of related individuals, this was not unexpected, and it would be difficult to distinguish true linkage from effects of the similarity of genotypes of relatives. Therefore, we did not exclude any loci from the analysis.

After exclusion of unidentified individuals and individuals that were not members of known social units, 65 genetic individuals remained which could be assigned to 12 known social units and were used in the unit-level analyses (Table 2.1). Of these, 55 could be linked to single photographically identified individuals from those social units, and were used in the individual-level analyses (Table 2.1). Six social units qualified as

well-sampled, with genetic data for all adult females and at least 70% of all unit members, and these social units were included in the within-unit analyses (Table 2.1).

**Table 2.1** Composition and mitochondrial haplotype (mtHap) of 12 social units sampled off Dominica. Social units were delineated as in Gero et al. (2014). Well-sampled social units, which were used for intra-unit analyses, are indicated by an asterisk. The number of sampled unit members includes only those linked to a single identified individual. The number listed in parentheses counts all sampled unit members, including samples for which individual identity was unknown.

| | | Unit Members | | | | |
|---|---|---|---|---|---|---|
| | Social Unit | Known | Sampled | | mtHap | Sex |
| * | A | 12 | | 12 | BB | 9F 3M |
| | C | 6 | | 1 | A | 1F |
| | D | 7 | (4) | 2 | A | 3F 1M |
| * | F | 10 | | 9 | A | 5F 4M |
| * | J | 6 | | 5 | A | 5F |
| | N | 9 | (8) | 5 | A[1] | 7F 1M |
| | P | 9 | (3) | 1 | BB | 1F 2M |
| * | R | 10 | | 7 | A | 6F 1M |
| * | S | 4 | | 3 | A | 3F |
| | T | 9 | (6) | 4 | A | 6F |
| * | U | 4 | | 4 | A | 3F 1M |
| | V | 12 | (3) | 2 | A | 3M |
| | Total | 98 | (65) | 55 | 49A 15BB | 49F 16M |

[1] Haplotypes for this unit were obtained for 7 of 8 samples

*2.4.2 Mitochondrial Haplotypes*

For mtDNA haplotype assignment, no errors were detected in blind replicates (n = 14) nor any inconsistencies for pairs of samples determined to be from the same individuals based on multi-locus microsatellite genotypes (n = 7). Haplotypes were successfully sequenced for 61 of 65 sampled unit members. For samples from three calves, which failed to sequence successfully, haplotypes were inferred based on the haplotypes of their mothers.

Two mtDNA haplotypes (A and BB) were identified in individuals from known social units, both of which have been previously observed in the Western North Atlantic Ocean (A. Alexander et al. 2016). These haplotypes differ by a single nucleotide substitution. This low level of mitochondrial diversity is consistent with previous observations on a global and mitogenome-wide scale (A. Alexander et al. 2016).

Mitochondrial haplotypes were consistent within social units, though each haplotype was shared by multiple units. Haplotype A was much more common, being shared by 10 out of 12 social units (Table 2.1).

*2.4.3 First- and Second-Degree Relationships*

We classified 30 individuals as adult females and the remaining 25 individuals as offspring. Thirteen of these females were assigned as the mothers of 18 offspring; in all cases the assigned mother was from the same social unit as the offspring. Ten females were assigned to a single offspring each, two were assigned to two offspring each, and one to four offspring. These maternity assignments were supported by agreement in the mtDNA haplotypes of mothers and their offspring, when both were known. Seven offspring did not have mothers identified from the sampled females. Average pairwise relatedness between identified mother-offspring pairs was 0.52 (range: 0.42-0.67, n = 18) and for half-siblings inferred based on shared maternity average pairwise relatedness was 0.32 (range: 0.12-0.50, n = 8).

Out of the adult females, we identified eight pairs of individuals for which parent-offspring was the relationship with the highest likelihood. For six of these pairs, parent-offspring was the only relationship consistent with the genetic data at the 0.05 level of

significance, but for two pairs, sibling relationships also met this level of significance. All of these parent-offspring pairs were within social units, rather than between them (Figure 2.1). Average pairwise relatedness between mother-offspring pairs identified among adults was 0.50 (range: 0.43-0.59)

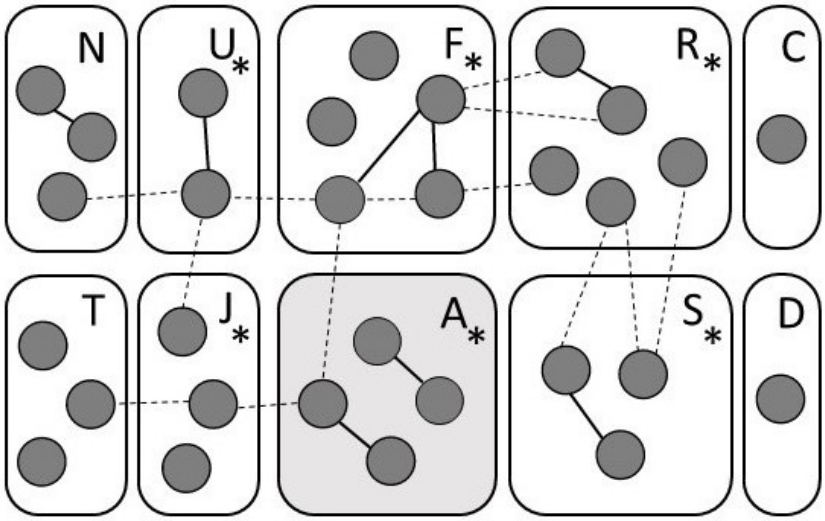


**Figure 2.1** Genetic relationships between adult females, within and between social units. Letters indicate social unit. Shading of unit block indicates mitochondrial haplotype. Solid edges between individuals denote mother-offspring relationships, and dashed edges indicate second-degree relationships, as determined using ML-Relate, including only those relationships for which 'unrelated' was not also a likely option. Nodes are arranged randomly, with no information conveyed by edge length. Social units with no missing members are indicated by an asterisk.

Pairs of adult females for which the most likely relationship was second degree (half-siblings/ grandmother-granddaughter) were much more common (n = 43), but for the majority of these (74.4 %) the genotypes were also consistent with the individuals being unrelated. For two pairs of individuals, full-siblings was the most likely relationship, but in both cases the genotypes were also consistent with the individuals being second-degree relatives. Of these putative second-degree relationships, 88.9% were split across different

social units. For the subset of 13 pairs for which 'unrelated' was not a probable relationship, all but one were between social units (Figure 2.1). In two of these cases the putative second-degree relatives had different mtDNA haplotypes, suggesting that any kinship between these individuals is paternal. For the remaining 10 well-supported sibling pairs between units, it could not be readily distinguished whether they resulted from shared paternity or from maternal relatives (half-siblings or grandmother-granddaughter) splitting into separate social units. Average pairwise relatedness between putative second-degree relatives for which 'unrelated' was not a plausible option was 0.32 (range: 0.20-0.54).

*2.4.4 Relatedness and Haplotype Sharing Predicting Association Across All Individuals*

Across all known unit members, association was significantly positively correlated with pairwise relatedness and with mtDNA haplotype sharing for all four measures of association examined, regardless of whether the pairwise data for mothers and their dependant calves were omitted (Table 2.2). The correlation strength, however, was reduced in all cases when the mother-calf pairs were omitted, with the reduction in correlation strength being most substantial for pairwise relatedness, rather than for haplotype sharing, and for the association measure with the finest resolution (clusters in six-hour sampling periods; Table 2.2).

When the dataset was restricted to pairs of individuals in the same social unit (still excluding mother-calf pairs), the correlations between pairwise relatedness and all scales of social association were significant (Table 2.2), though only marginally so for long-term close associations (i.e. clusters in a yearly sampling period).

**Table 2.2** Correlation between measures of social association and pairwise relatedness (Rel) or mtDNA haplotype sharing (Hap) across all individuals (n = 55). This relationship was also tested after omitting pairwise values for mother-calf pairs (- MCs), and restricting to members of the same social unit (mother-calf pairs excluded). Association measures were calculated using 'both identified' as the association index.

| | | | | - MCs | | Same unit; -MCs | |
|---|---|---|---|---|---|---|---|
| Association Measure | Predictor | Matrix corr. | p-value | Matrix corr. | p-value | Matrix corr. | p-value |
| Day/year | Rel | 0.260 | < 0.001 | 0.200 | < 0.001 | 0.221 | < 0.001 |
| | Hap | 0.260 | < 0.001 | 0.248 | < 0.001 | – | |
| 2 hr/10 day | Rel | 0.290 | < 0.001 | 0.217 | < 0.001 | 0.187 | 0.003 |
| | Hap | 0.265 | < 0.001 | 0.251 | < 0.001 | – | |
| Cluster/year | Rel | 0.311 | < 0.001 | 0.218 | < 0.001 | 0.130 | 0.035 |
| | Hap | 0.257 | < 0.001 | 0.244 | < 0.001 | – | |
| Cluster/6 hr | Rel | 0.362 | < 0.001 | 0.206 | < 0.001 | 0.197 | 0.001 |
| | Hap | 0.203 | < 0.001 | 0.175 | < 0.001 | – | |

Members of the same unit were also more closely related to each other than expected by chance (matrix correlation = 0.273, $p < 0.001$, n = 65). Mean relatedness between individuals in the same social unit was 0.139 (sd: 0.221, n = 200) whereas between individuals in different social units it was 0.004 (sd: 0.132, n = 1880). Relatedness values within units were bimodally distributed, with a local maximum at approximately 0.5, and a global maximum just above zero (Figure 2.2).

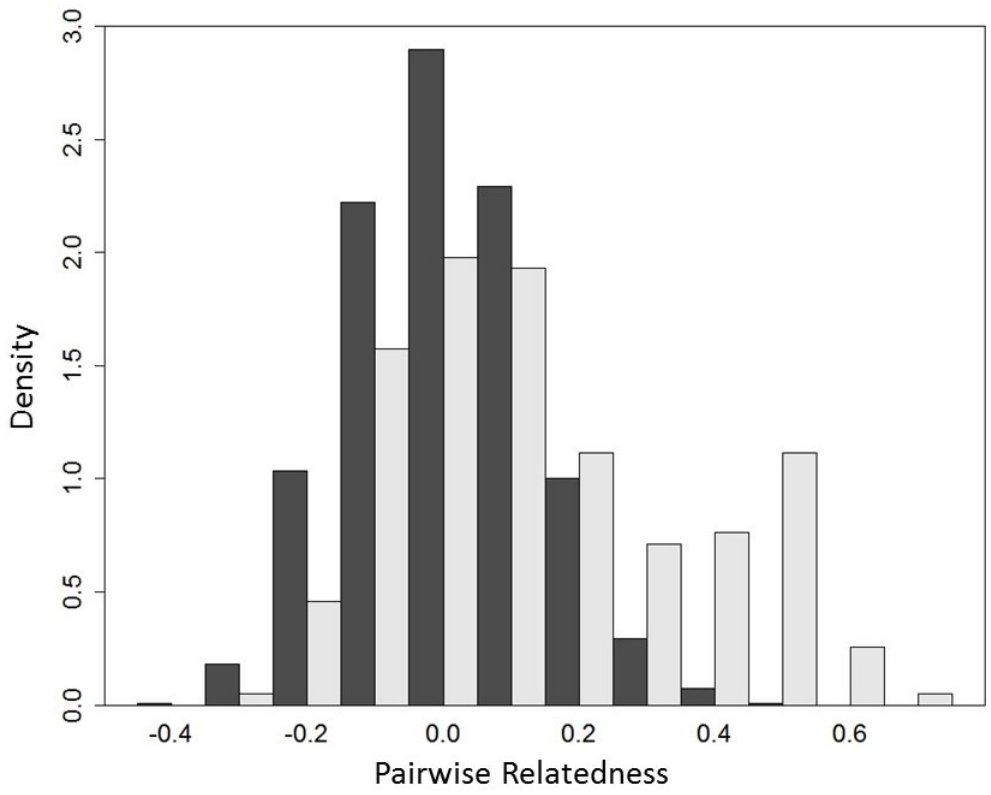


**Figure 2.2** Distributions of pairwise relatedness values within (light grey) and among (dark grey) sperm whale social units. Relatedness values were calculated using Wang's (2002) estimator.

*2.4.5 Relationships Within Social Units*

Within social units, parent-offspring relationships made up between 14.3 and 33.3% of relationships (16.9% overall), and between 0 and 33.3% of relationships were defined as second degree relationships (15.5% overall), leaving between 33.3 and 80% of relationships as more distant than second degree, potentially including unrelated individuals (Table 2.3). Most individuals (82.5%) had a mother or offspring in their social unit, and out of those who did not, the majority (57.1%) had a second degree relative (Figure 2.3). The remaining 7.5% of individuals had no relatives deemed to be first or second degree relatives sampled from their social unit.

**Table 2.3** Composition of well-sampled social units. Mean relatedness (Mean r) was calculated according to Wang (2002). Composition includes past and present sampled members, categorized as adult females (F) or offspring (O). Mother-offspring (1˚) relationships were determined using Colony and ML-Relate. Second degree (2˚) relationships were determined using ML-Relate, or inferred based shared 1˚ relatives.

| Social Unit | Sampled (%) | Mean *r* | Composition | | Relationships (%) | | |
|---|---|---|---|---|---|---|---|
| | | | F | O | 1˚ | 2˚ | > 2˚ |
| A | 100 | 0.137 | 4 | 8 | 15.2 | 12.1 | 72.7 |
| F | 90 | 0.232 | 5 | 4 | 16.7 | 25.0 | 58.3 |
| J | 83 | 0.136 | 3 | 2 | 20.0 | 0 | 80.0 |
| R | 70 | 0.106 | 5 | 2 | 14.3 | 14.3 | 71.4 |
| S | 75 | 0.212 | 3 | | 33.3 | 0 | 66.7 |
| U | 100 | 0.333 | 2 | 2 | 33.3 | 33.3 | 33.3 |
| Total | 87.0 | | 22 | 18 | 16.9 | 15.5 | 67.6 |

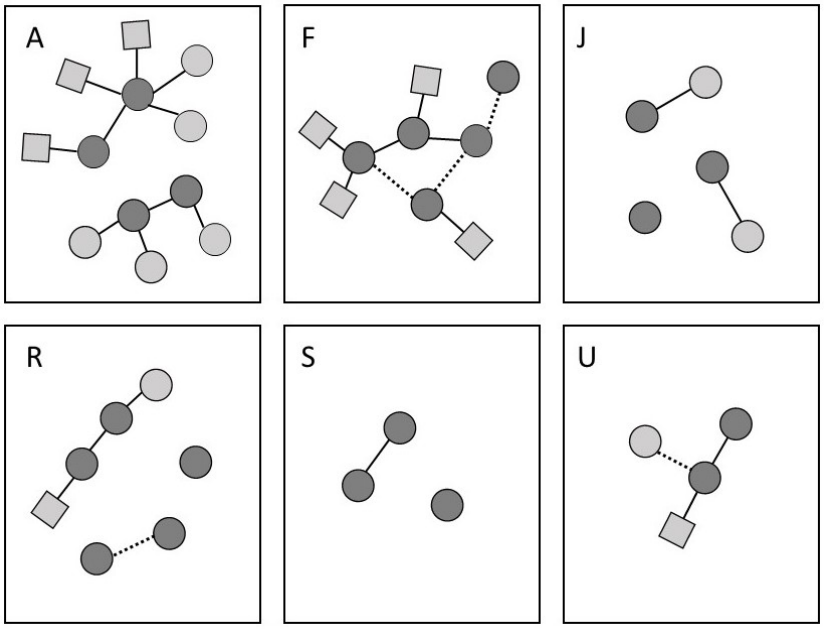


**Figure 2.3** Relationship networks of well-sampled social units, based on genetic data. Females are indicated by circles and males by squares. Dark grey indicates adults and light grey indicates offspring. Solid lines denote mother-offspring relationships, as determined using Colony or ML-Relate. Dotted lines indicate pairs that were most likely second-degree relatives, but for which 'unrelated' was also a likely option (as determined using ML-Relate). Nodes are arranged randomly, with no information is conveyed by edge length. Genetic data was unavailable for six offspring; these individuals are not shown.

For no unit could all members be connected in a single network using only parent-offspring relationships, but for two units all members could be connected when second degree relationships were included (Figure 2.3). The remaining four units had one or two missing connections between members, even when second degree relationships were included (Figure 2.3). In these social units, all unsampled members were calves, whose mothers were assumed (based on social data) to be among the sampled individuals, and so breaks in the genetic network are not likely due to the omission of these individuals, but could be due to deceased, unknown relatives.

*2.4.6 Kinship Predicting Association Within Social Units*

**Table 2.4** Intra-unit social association preferences predicted by pairwise relatedness. Association was defined as identification in the same cluster, using 'both identified' as the association index. The test was repeated with the pairwise values for mother-dependant calf pairs (MC) omitted, except for unit S, for which no dependant calves had been sampled. Mantel tests were performed with 10,000 permutations.

| | | | All individuals | | | MC pairs removed | | |
|---|---|---|---|---|---|---|---|---|
| Unit | N | Sampling Interval | Matrix correlation | p-value | | Matrix correlation | p-value | |
| A | 12 | 2 hr | 0.41 | 0.001 | *** | 0.26 | 0.010 | ** |
| | | Day | 0.54 | <0.001 | *** | 0.45 | <0.001 | *** |
| F | 9 | 2 hr | 0.42 | 0.001 | *** | 0.17 | 0.006 | ** |
| | | Day | 0.40 | 0.002 | ** | 0.11 | 0.012 | * |
| J | 5 | 2 hr | 0.12 | 0.701 | | -0.05 | 0.740 | |
| | | Day | 0.20 | 0.446 | | 0.12 | 0.529 | |
| R | 7 | 2 hr | 0.50 | 0.025 | * | -0.12 | 0.836 | |
| | | Day | 0.52 | 0.017 | * | -0.10 | 0.896 | |
| S | 3 | 2hr | 0.90 | 0.505 | | - | - | |
| | | Day | 0.99 | 0.164 | | - | - | |
| U | 4 | 2 hr | 0.34 | 0.122 | | -0.75 | 0.882 | |
| | | Day | 0.15 | 0.793 | | -0.63 | 0.961 | |

Within each of six well-sampled social units, association was positively correlated with pairwise relatedness, at both sampling intervals (Table 2.4; Appendix A, Figure A1). For the three largest social units, these correlations were statistically significant (Table 2.4). For the five units with dependant calves, effect size of the correlations dropped when pairwise values for mother-calf pairs were omitted, but the correlations remained significant for the two social units with the most sampled individuals (Table 2.4).

**Table 2.5** Social clusters and strict matrilines in social unit A across time. Strict matrilines defined based on mother-offspring relationships (see Figure 2.3). Social clusters are based on association as clusters in a daily sampling period, using half-weight indices. Cluster composition is indicated by block shade, stippled shading indicates uncertainty in cluster assignment (|eigenvector| < 0.1), and missing blocks indicates the individual was not seen (and presumably was not alive) in that year. Good divisions are generally indicated by modularity values of roughly 0.3 or greater (Newman 2004). Percent agreement with matrilineal clusters (% agreement) does not include uncertain cluster assignments.

| | | Social cluster | | |
|---|---|---|---|---|
| Individual | Matriline | 2005 | 2010 | 2015 |
| Soursop | | | | |
| Fruit Salad | | | | |
| Oryx | | | | |
| Crake | | | | |
| Snowman | | | | |
| Atwood | | | | |
| SLBC | | | | |
| Handmaid | | | | |
| Lady Oracle | | | | |
| Rounder | | | | |
| Allan | | | | |
| Modularity | | 0.51 | 0.26 | 0.13 |
| N (days) | | 3 | 12 | 13 |
| % agreement | | 87.5 | 100 | 100 |

Social modularity within Unit A decreased substantially across the years examined, but social cluster composition was similar across years and was well related to the unit's two matrilineal clusters of mother-offspring pairs in all years (Table 2.5).

*2.4.7 Kinship Predicting Association Between Social Units*

Association between units was not significantly correlated with having a shared mtDNA haplotype at any level tested ($p \geq 0.17$ for all four measures of association; Table 2.6). Some pairs of units with the same mtDNA haplotype never associated (e.g. units P & A, and units S & T) while units A and D, with opposing haplotypes frequently associated.

Association between units, defined as being in a cluster together, was weakly correlated with mean relatedness for both sampling periods (Table 2.6). For the coarser measures of association, association and mean relatedness between units were not significantly correlated.

**Table 2.6** Correlation between measures of inter-unit social association and mean pairwise relatedness (Rel) or mtDNA haplotype sharing (Hap). Association measures were calculated using half-weight indices. The tests were repeated with the pairwise values for units U and F omitted (No UF). Mantel tests were performed with 10,000 permutations (n = 11).

| Association Measure | Sampling Interval | Predictor | All units | | No UF | |
|---|---|---|---|---|---|---|
| | | | Correlation | p-value | Correlation | p-value |
| Day | Year | Hap | 0.33 | 0.17 | 0.32 | 0.11 |
| | | Rel | 0.23 | 0.15 | 0.12 | 0.43 |
| 2 hours | Day | Hap | 0.14 | 0.31 | 0.11 | 0.42 |
| | | Rel | 0.13 | 0.33 | -0.06 | 0.71 |
| Cluster | Year | Hap | 0.07 | 0.60 | 0.02 | 0.71 |
| | | Rel | 0.25 | 0.09 | 0.09 | 0.48 |
| Cluster | 2hr | Hap | 0.13 | 0.24 | 0.09 | 0.38 |
| | | Rel | 0.26 | 0.06 | 0.03 | 0.78 |

The marginally non-significant correlations between relatedness and fine-scale association were primarily driven by one pair of social units, U and F, which had the highest mean relatedness value of any pair of units (mean relatedness = 0.112) and the highest association index at all levels of association. When the data point for this pair of social units was removed, the size and significance of all correlations dropped (Table 2.6).

## 2.5 Discussion

To date, this study is the most detailed exploration of sperm whale kinship patterns in relation to social structure, examining many more social units, with a higher genetic resolution (38%-80% more microsatellite loci), than previous studies. We found a higher degree of relatedness and matrilineality in social units than has been reported in other regions (Mesnick 2001; Christal 1998; Ortega-Ortiz et al. 2012). Even so, it is unlikely that all of the social units that we examined were strict matrilines. The presence of a living common ancestor was not conclusively demonstrated in any social unit. Rather, inference of one or two intermediary relatives that are dead or gone would be required in each unit before the presence of a living common ancestor could be assumed (Figure 2.3). Additionally, no unit splits have been observed in 96 unit-years of observation off Dominica (Gero and Whitehead 2016). This is despite a mean 4.5% per year decrease in number of adults over the study period (Gero and Whitehead 2016), which would predict the death of common living ancestors in roughly four units across the study period. The presence of second-degree relationships between units (Figure 2.1) could indicate past unit splits after the death of a common ancestor, but such relationships could also be explained by paternal relatedness. Indeed, paternal relatedness is the only explanation in

cases where the second-degree relatives have different haplotypes (e.g. relationships between Unit A and either Unit J or F). The genetic data for all social units examined were consistent with our less stringent definition, 'generally matrilineal'. However, haplotype sharing does not necessitate close matrilineal co-ancestry, especially for the very common haplotype, A. As such, we could not rule out the possibility that the units contained unrelated matrilines. Even so, units composed of multiple matrilines would still be matrilineally-based.

As with the absence of unit fission, the presence of unit fusion can undermine the degree of matrilineality, unless the merging units are from of a strict or general matriline that previously split. Over the course of our study period, we documented the merger of two social units, U and F, which were originally classified as separate units, using data as far back as 1995 (Gero et al. 2014). From 2008 onwards their association rate generally increased, such that from 2012 onwards they were scarcely seen apart (Table 2.7). These units were the most closely related pair of units in our study, suggesting that mergers may be driven by kinship, which would minimize the extent to which unit fusions breakdown matrilineality and relatedness within units.

As our resolution of social data improves, so does our ability to investigate stability and distinguish constant companions from preferred associates. This is exemplified by Unit A, which had all members genetically sampled, and was observed in seven different years between 2005 and 2016. This unit was composed of two strict matrilines (Figure 2.3), which were unrelated or separated by at least two absent intermediary relatives. Social modularity within this unit aligned well with the delineation of these two matrilines (Table 2.5). Based on our definition of social units, these individuals qualified as

**Table 2.7** Changing rate of association between social units U and F, and changing unit composition across time. Half-weight index (HWI) values used association as observation within 2h, within a daily sampling period. Members were classified as adults (A; which included juvenile males), or as calves (C). Neither social unit was observed in 2014.

| Year | Days Obs | | HWI | Unit Composition | |
|---|---|---|---|---|---|
| | F | U | | F | U |
| 2005 | 40 | 0 | -- | 6A 1C | -- |
| 2006 | 9 | 1 | 0 | 5A 1C | 3A 1C |
| 2007 | 7 | 0 | -- | 5A 1C | -- |
| 2008 | 20 | 12 | 0.69 | 5A 2C | 3A 1C |
| 2009 | 7 | 3 | 0.6 | 5A 2C | 3A 1C |
| 2010 | 14 | 11 | 0.8 | 5A 2C | 3A 1C |
| 2011 | 4 | 5 | 0.89 | 4A 1C | 4A |
| 2012 | 2 | 2 | 1 | 3A 1C | 3A |
| 2015 | 11 | 12 | 0.96 | 3A 1C | 3A |
| 2016 | 3 | 3 | 1 | 2A 1C | 3A |
| Total | 117 | 49 | 0.53 | | |

members of a single unit, but the rate at which these two matrilines associated varied substantially across the study and they were often observed apart (Table 2.8). Similarly, Units F and U, by 2009, met the criteria to be classified as a single unit, even though at that point in their gradual merger the units were still frequently seen apart (Table 2.7). This suggests that unit members, as we have defined them, are not such constant companions as previously assumed, and that there can be sub-unit social structures that may go undetected with the types of analyses often used to define constant companions. It is not clear how sub-unit social structures are actually expressed in the day-to-day life of a unit at sea, perhaps by a separation of several km between subunits, or perhaps by much greater distances.

**Table 2.8** Changing rates of association within social unit A, which was composed of two strict matrilines (A1 and A2), and changing unit composition across time. Half-weight index (HWI) values used association as observation within 2h, within a daily sampling period. Members were classified as adults (A; which included juvenile males), or as calves (C). Neither maternal family was observed in 2006, 2007, 2011 or 2012.

| Year | Days Obs | | HWI | Unit Composition | |
|---|---|---|---|---|---|
| | A1 | A2 | | A1 | A2 |
| 2005 | 3 | 2 | 0.8 | 4A | 2A 2C |
| 2008 | 5 | 9 | 0.43 | 4A 1C | 3A 1C |
| 2009 | 4 | 4 | 0.5 | 4A 1C | 3A 1C |
| 2010 | 11 | 10 | 0.86 | 4A 2C | 3A 2C |
| 2014 | 0 | 2 | -- | -- | 3A |
| 2015 | 12 | 12 | 0.75 | 4A | 3A |
| 2016 | 16 | 1 | 0.12 | 4A 1C | -- |
| Total | 51 | 40 | 0.57 | | |

Our finding that association preferences between units are, on the whole, not driven by kinship, is in line with past work that has demonstrated associations being mediated by clan membership, supporting a cultural explanation for these preferences (Gero, Whitehead, and Rendell 2016; Rendell and Whitehead 2003). However, the observed patterns of associations, below the clan level – between units, and between individuals within units – that are not explained by kinship require explanation. Several plausible and potentially complementary drivers exist, which may also work synergistically alongside non-zero relatedness between cooperators, as relatedness can erode the benefits of cheating (Kokko, Johnstone, and Clutton-Brock 2001).

In a long-lived, slow-reproducing, cooperatively breeding species, such as the sperm whale, the requisite conditions for group augmentation – that group members are valuable and difficult to replace – are almost certainly met. For tentative evidence supporting the value of unit members, we can examine the merger of units F and U,

which occurs in parallel with changes in group size and composition (Table 2.7). Notable increases in association rates correspond with the first observations of a new calf in 2008, the loss of two adult members from Unit F in 2011, and the departure of a juvenile male from each unit in 2012. This suggests that perhaps the merger was driven by the importance of adult members as alloparents and protectors of calves. In Unit A, variation in association rates between the two maternal families did not have a clear relationship with changes in unit composition, but the year with the highest rate of association did correspond with the presence of two new calves (Table 2.8).

The observed variation in association rates and preferences within social units may also relate to social role (Gero, Gordon, and Whitehead 2013). For example, Gero *et al.* (2013) reported two concurrent mothers in the same social unit babysat for each other more than other unit members did, perhaps because they had frequent opportunities for reciprocity, without long delays. Given the relative stability of sperm whale social units, there is also opportunity for reciprocal altruism that is not immediately repaid. And, as individuals with large brains living in a complex cooperative society, it is plausible that sperm whales have the mental capacity and have experienced the selective forces that Hauser *et al.* (2009) considered required for delayed reciprocity to evolve.

In species that have few offspring, and long inter-birth intervals, such as the sperm whale, individuals have relatively few close relatives, which can make it challenging to preferentially associate with kin (Connor 2007a). Our dataset, however, does not suggest that sperm whales only associate with non-kin due to a lack of close relatives. Some individuals and units that associated with non-relatives had relatives with whom they did not associate as frequently. For example, the three adult females in Unit J were not close

relatives (Figure 2.3), but two of them had second-degree relatives in different social units (Figure 2.1). Likely, some relatives that did not spend time together were paternal relatives, but it is possible that individuals had maternal relatives with whom they chose not to associate. If so, one possible explanation is that individuals break ties with non-cooperators. Dynamic social networks, where individuals can break ties to non-cooperative individuals and seek new cooperative partners, have been demonstrated to give rise to self-organizing networks of clusters of cooperators (Fehl, van der Post, and Semmann 2011).

The population reported on in this study is in a state of critical decline (Gero and Whitehead 2016). As such, understanding the genetic diversity and social dynamics of these social units becomes particularly important from a conservation perspective. Social relationships can have fitness consequences, as in baboons, where female sociality correlates with reproductive success (Silk 2003), and social structure influences processes like the transmission of disease or information (Kurvers et al. 2014). Understanding drivers of cooperation can aid our understanding of how social structure may change when individuals are lost from this population.

This work also contributes to our broader understanding of cooperative groups and complex societies. Cross-species comparison can help identify common factors driving similar cooperative societies. Sperm whales and elephants have very similar life histories and social systems (Weilgart, Whitehead, and Payne 1996), and the results of this study demonstrate further similarities. Distributions of relatedness within and among sperm whale social units (Figure 2.2) and within and among African elephant (*Loxodonta africana*) core social groups (see Archie, Moss, and Alberts 2006, Figure 2.2) are

remarkably similar, suggesting similar processes are at work in shaping the composition of these units and groups. Also as in sperm whale social units, kinship predicts association within African elephant core groups (Archie, Moss, and Alberts 2006), though to a greater degree than in sperm whale social units. In African elephants, group splits and mergers are also predicted by genetic relatedness (Archie, Moss, and Alberts 2006), similar to the merger between two related sperm whale social units (Table 2.7), and to the social modularity corresponding with kinship within one large social unit (Table 2.5).

As yet another similarity, in both elephants and sperm whales, kinship does not well-predict higher levels of association. Neither associations between sperm whale social units or between African elephant core groups (Archie, Moss, and Alberts 2006) were significantly correlated with average pairwise genetic relatedness. Among African elephant core groups, mtDNA haplotype sharing was significantly correlated with association (Archie, Moss, and Alberts 2006), while it was not among sperm whale social units, but this difference may relate to the lower diversity of mtDNA haplotypes among the sperm whales we examined (two haplotypes) than among the elephants studied by Archie et al. (2006; four haplotypes).

The degree of relatedness within social units that we observed in the Eastern Caribbean is greater than those reported in the Eastern Tropical Pacific (Mesnick 2001; Christal 1998). One potential reason for such differences in patterns of kinship and association is the degree to which populations were affected by modern whaling; sperm whales were much more heavily targeted in the Eastern Tropical Pacific than in the Caribbean (Whitehead et al. 2012). Likewise, in African elephants, the relative importance of kinship to social

structure was diminished in a more heavily poached population (Wittemyer et al. 2009). In African elephants, evidence suggests that individuals form associations with non-relatives if their relatives are poached (Wittemyer et al. 2009; Archie, Moss, and Alberts 2006), and the same is likely true for sperm whales (Whitehead et al. 2012).

This suggests that in both species, direct fitness benefits, such as effective communal defence against predators, may be sufficient to maintain their cooperative social structure, though in undisturbed conditions, social bonds and cooperation are likely cemented by kin-selection. It is also possible that, even if direct fitness benefits are sufficient to maintain the hierarchical social structures of these species, kin-selection may have been required to allow for their initial evolution. Similarly, there is evidence for kin selection in human hunter-gatherer societies, because individuals preferentially associate and cooperate with their kin (Apicella et al. 2012). However, kinship does not account for the majority of associations and cooperation in hunter-gatherer societies (Apicella et al. 2012; Hill et al. 2011). Rather, recent studies emphasize the importance of social networks and preferential associations between cooperators as evolutionary drivers of cooperation (Apicella et al. 2012; Hill et al. 2011), suggesting non-zero relatedness may play a more secondary role by stabilizing other drivers of cooperation (Kokko, Johnstone, and Clutton-Brock 2001). Variations of such a process may have similarly influenced the evolutions of the cooperative societies of sperm whales, elephants and humans, all of which include kin, but do not appear to be exclusively driven or maintained by kin-selection.

## 2.6 Conclusion

While this study demonstrates that kinship is clearly an important factor influencing sperm whale social relationships, we also see that it is not the be-all and end-all. Social units were largely composed of kin but did not appear to be rigidly delineated by matrilines. Likewise, social relationships within units were biased toward closer relatives, but as a general trend, rather than a strict rule. Other drivers of cooperation, such as group augmentation and reciprocal altruism, likely interact with kin-selection to drive the social structure we observe. Preferential cooperation between particular individuals or between particular units could be based in culture or personality, or they may be by-products of circumstance and convenience. Social and ecological context, such as the presence of dependant calves or limited resources, likely also influence social structure and may encourage flexibility in how widely cooperation is extended beyond close kin. Overall, our findings support sperm whale society as being matrilineally-based, but not strictly so; rather, it is nuanced and multifaceted, resembling other complex cooperative societies that include both kin and kith, such as among elephants and early humans.

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## 2.8 Ethics

Our data and samples were collected in Dominica under scientific research permits from the Fisheries Division of the Ministry of Agriculture and Environment: SCR 013/05-02, RP-2/12 IW-1, RP-09/014 IW-1, RP-01/079W-2, RP-03/059W-4, P-122/4W-2, P-40/2W-7, and RP-16-04/88-FIS-9. Samples were transported through CITES permits for the import and export animal parts issued by Environment Canada and the Environmental Coordinating Unit of Dominica. The field protocols for approaching, photographing and recording sperm whales were approved by the University Committee on Laboratory Animals of Dalhousie University and the Animal Welfare and Ethics Committee of the University of St Andrews. Biopsy sample collection procedures were also approved by the Saint Mary's University Animal Care Committee.

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# CHAPTER 3

# KIN SELECTION INFLUENCES RATES OF SPERM WHALE CALF CARE, BUT CANNOT FULLY EXPLAIN THEM[2]

## 3.1 Introduction

Among species that have few offspring, each offspring typically receives high levels of investment, which sometimes includes care from individuals other than the genetic parents of the offspring (Riedman 1982). Typically such alloparental care (also called allocare) occurs in species that live in groups that are highly social, cooperative or related (Riedman 1982). Within groups of related individuals, kin selection and inclusive fitness benefits (Hamilton 1964a; Hamilton 1964b) likely contribute to why individuals behave in this seemingly altruistic manner (Clutton-Brock 2002). Within groups that are unrelated, however, the costs of providing care may be compensated by other factors, including gaining parental experience (Lancaster 1971), receiving reciprocated altruistic behaviours (Trivers 2006; Trivers 1971) or benefiting from increases in group size (Kingma et al. 2014; Kokko, Johnstone, and Clutton-Brock 2001). These other mechanisms may also reinforce selection for allocare among relatives.

Among sperm whales (*Physeter macrocephalus*), allocare is thought to be foundational to the evolution their complex, cooperative social system (Gero, Gordon, and Whitehead

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[2] *This chapter has been prepared in manuscript format, with the intention to submit to the Proceedings of the Royal Society B: Biological Sciences.*
*Contributing authors: Christine M. Konrad (CK), Shane Gero (SG), Tim Frasier (TF) and Hal Whitehead. CK, SG and HW participated in the collection of the field data; CK carried out all molecular laboratory work and statistical analysis, and wrote the manuscript; SG coordinated the field operations of the study, and completed the photo-identification; Tim Frasier (TF) aided sample collection efforts and supervised the molecular laboratory work; SG, TF and HW contributed funds. CK wrote the manuscript. All authors collaborated in the conception and design of the study.*

2013; Best 1979). Female and juvenile sperm whales live in social units that are stable across years (Gero et al. 2014; Christal, Whitehead, and Lettevall 1998) and are matrilineally-based, in that females typically stay with their mothers, though social units can also contain unrelated or distantly related individuals (Chapter 2, Christal 1998; Mesnick 2001; Ortega-Ortiz, Engelhaupt, Winsor, Mate, & Hoelzel 2012). Males disperse from their natal units before sexual maturity and are thought to have only fleeting interactions with other social units after that (Best 1979). Instances of communal defence of calves against predators, such as killer whales (*Orcinus orca*) has been reported in sperm whales (Pitman et al. 2001; Weller et al. 1996), as has "babysitting", in which calves are serially accompanied by other unit members while their mothers forage at depth (Whitehead 1996). Babysitting likely increases the calves' safety in the case of an attack by predators, and appears to result from a behavioural change by the babysitter, not just association driven by the calf's behaviour (Whitehead 1996). The fitness cost of babysitting is likely low (Whitehead 1996), but sperm whales may also provide more costly allocare in the form of allonursing (Best, Canham, and Macleod 1984; Gero et al. 2014; Gero et al. 2009; Gordon 1987).

Given the kin-based social system of sperm whales, a likely functional driver of these behaviours is kin selection. Within social units, association generally correlates with kinship (Chapter 2), but whether provision of allocare is related to kinship has only ever been examined for a single calf, in which case the primary babysitter was the mother's closest relative (Gero, Engelhaupt, and Whitehead 2008).

Studying allocare requires the ability to distinguish between parents and non-parents. In the absence of genetic information, mother identity is often assigned based on social

observations, under the assumption that the adult that the calf spends the most time with is its mother (Whitehead 1996; Gordon 1987). The reliability of this assumption in sperm whales, however, has only ever been validated for one calf (Gero, Engelhaupt, and Whitehead 2008), and it is not strictly valid among all odontocetes (Augusto, Frasier, and Whitehead 2017).

In this study, we explicitly examine patterns of kinship and social behaviour using well-studied sperm whale social units from the Eastern Caribbean, to test two primary hypotheses: (1) that genetic mothers can be identified based on behavioural data, and (2) that rates of allocare within units are correlated with kinship.

## 3.2 Methods

### *3.2.1 Field Methods*

Field work was carried out in an area of approximately 2,000 $km^2$, off the leeward, western coast of Dominica, in the Caribbean Sea (15.5°N; 61.5°W) from 2005-2016 as a part of a longitudinal research project on sperm whale behaviour (Gero et al. 2014). Annual field seasons ranged from two to four months in duration, and occurred between January and June, using various research platforms (total effort: 518 days).

Sperm whales were located and followed, visually by observers on deck during daylight hours, as well as acoustically using hydrophones up to 24 hours a day (Whitehead 2003). Photographs were taken of the trailing edge of flukes of juveniles and adults (Arnbom 1987) and of the dorsal fins of calves (Gero et al. 2009) for individual identification. In conjunction with these identification photographs, we recorded observations of peduncle

dives and of associations of individuals in clusters (Gero et al., 2014). Peduncle dives are shallow dives made by a calf, beside an adult, during which the calf performs what appear to be mammary bumps to stimulates milk letdown (G. Johnson et al. 2010; Gero and Whitehead 2007). Clusters were defined as groupings of individuals at the surface in close proximity to each other (< 40 m) with coordinated behaviour (Whitehead 2003).

We used dip nets to opportunistically collect sloughed skin from the flukeprints of individual whales or clusters of whales (Whitehead et al. 1990). In 2015 and 2016, we also collected biopsy skin samples using a 90 lb draw weight crossbow and bolts with 2.5 cm long tips with 0.5 cm circumferences (see Kowarski et al. 2014 for details). Skin samples collected from 2005 to 2010 were stored in ethanol (at a concentration of 70% or greater), and samples collected from 2011 onwards were stored in a 20% DMSO solution saturated with salt (Seutin, White, and Boag 1991).

### *3.2.2 Identifications and Defining Social Units*

As in Gero et al. (2015), identification photographs were assigned quality ratings, and only high quality photographs were used for assigning final identifications. In some cases (~6% of adult/juvenile identifications), well-known adults and juveniles that could not be photographed when multiple animals fluked synchronously but whose flukes were observed by S.G. were recorded as having been identified. Past analyses have demonstrated that patterns of association do not differ when including these identifications (Gero, Gordon, and Whitehead 2015). Likewise, well-known calves who were not photographed but were readily identifiable due to distinct dorsal markings that

were visible by eye or because they were known to be the only calf in the social unit, were also recorded as having been identified (25% of calf identifications).

Social units were delineated as in Gero *et al*. (2014), so that they reflect long-term, stable social relationships. If two whales were identified within two hours of each other in at least two different years they were assigned to the same unit. Calves were automatically considered members of the units that they were born into. Two social units merged in the second half of the study period (Chapter 2), but they were treated as separate units in this study.

### *3.2.3 Genetic Laboratory Methods and Analysis*

For genetic laboratory methods, determination of age class (adult, juvenile or calf) and sex, analysis of microsatellite genotypes and mitochondrial DNA (mtDNA) sequence data, calculation of pairwise relatedness values, and determination of mother-offspring relationships see Chapter 2.

### *3.2.4 Measuring Association*

We defined association at a fine spatiotemporal scale, individuals identified in the same cluster, as this spatiotemporal scale is presumably the most relevant for defence and care of calves. Across our study period, social unit compositions were affected by births and deaths. Therefore, we used an association index, 'both identified', that minimizes the bias of these demographic changes on association measures. The index calculates the proportion of those sampling periods in which both individuals were identified, in which they were associated (Whitehead 2008). To examine the effect of temporal resolution, we

calculated association rates using two sampling periods: 2-hr and one day. Two hours corresponds to approximately two dive cycles in sperm whales and has been applied in other studies of this species (Christal & Whitehead, 2001; Gero et al., 2015). Daily sampling periods minimizes autocorrelation in cluster composition and will capture any pairs that were both identified in the same day, but not in the same 2-hr period. We calculated association rates between calves and the adults and juveniles within their social units. We restricted the dataset to only include each calf up until the last year it was observed making peduncle dives.

### *3.2.5 Approximating Nursing*

As in previous work, we used observations of peduncle dives as a proxy for nursing, because nursing cannot be directly observed from above water. We classified all adult or juvenile females on which each calf was observed performing peduncle dives as nurses of that calf. However, we acknowledge this may include some individuals from whom the calf did not receive milk; variation in factors such as suckling ability and the female's ability to produce and release milk can uncouple suckling and milk intake (Cameron 1998), such that a calf may not receive milk for every observation of peduncle diving. Nonetheless, behavioural observations suggest sperm whale calves do not perform peduncle dives on animals at random, suggesting that the behaviour is performed when necessary, or in circumstances when gaining access to milk successfully is likely.

### *3.2.6 Maternal Calf Care*

For all calves that had a genetically-determined mother or a genetically sampled primary caregiver, we examined whether the genetically-determined mothers were their calves'

primary caregivers. We assessed whether genetically-determined mothers had the highest association index with their calves of any unit member and if they were the female unit member most often observed receiving peduncle dives from their calves.

### *3.2.7 Maternal Relatedness and Allocare*

To examine the influence of kinship on allocare, we compared babysitting rates and presence or absence of allonursing to the caregiver's pairwise relatedness to the calf's mother. We used pairwise relatedness to the mother, rather than to the calf, to focus on the effect of maternal relatedness and because relatedness is harder to distinguish against background noise when there are more generations between the related individuals. These analyses were restricted to include only calves from well-sampled social units (i.e. units with genetic data for all adult females and at least 70% of all unit members).

To determine babysitting rates, we standardized the association indices (described above) to account for differential identifiability of calves, in two different ways. For one method, we standardized association indices by dividing each babysitter's index with the calf by the mother's index with the calf. For the second method, we standardized association indices and pairwise relatedness values by ranking the values for the unit members of each calf, and then scaling the ranks to fall between 0 and 1. This method also removes the effect of differences between calves in the relative level of allocare received (i.e. ignores whether certain calves receive relatively high or low levels of care from all unit members, compared to other calves) and focuses on whether, for each given calf, ordinal ranks of babysitting rate and of maternal relatedness correlate (i.e. whether the closest relatives of a given calf are that calf's most frequent babysitters).

Additionally, certain whales may preferentially associate with the calf's mother, and by extension the calf, but not associate with the calf when the mother is not present. To account for this possibility, we repeated the above calculations of association indices excluding any clusters with more than one adult (or juvenile) present, such that this index reflects clusters where the individual was the sole babysitter.

For all measures of association, we calculated Spearman's correlation coefficients between association indices of each calf with each adult and juvenile in their social unit (excluding the calf's mother and juveniles that were previously classified as calves) and the pairwise relatedness estimates of the unit members to the calves' mothers. To test the statistical significance of these correlations, we randomly permuted (50,000 times) the adult-calf association rates for each calf, and recalculated the correlation with relatedness to generate a distribution of correlations. One-sided p-values were calculated as the proportion of simulations where a correlation greater than or equal to the true correlation was generated.

We also tested whether allonurses were closer maternal relatives of the calves they nursed than were the available females who did not nurse the calves. Female unit members from which the calf did not nurse were classified as 'available' if they were observed in the same year that the calf was observed suckling, and were not calves themselves. Sperm whales can begin lactating at as young as five years old (Best, Canham, and Macleod 1984), but whether this is typical has not been determined, and the ages of most juvenile females in this study were unknown. Thus, in an attempt to exclude females that were immature and not lactating, females that transitioned from calves to

juveniles in the study period were only considered 'available' after being observed as the recipient of peduncle diving.

For each calf, we obtained the pairwise relatedness to the calf's mother for each allonurse for that calf and each available female that was not an allonurse for that calf. We calculated the difference between the average relatedness values for all nurses and for all non-nurse available females. To estimate the probability of the true difference being achieved by chance, we randomly permuted the classification of nurses and available females for each calf, while maintaining the number of each class of female for each calf. We ran 50,000 permutations (which stabilized p-values) and recalculated the relatedness difference each time, to generate a distribution of differences. A one-sided p-value was calculated as the proportion of simulations where a difference greater than or equal to the true value was generated.

## 3.3 Results

### *3.3.1 Assignment of Genetically-Determined Mothers*

Out of 18 sampled calves, 15 had genetically-determined mothers among the sampled candidate mothers. All individuals were scored at no fewer than 16 microsatellites, and all maternity assignments were consistent across runs, and had a mean probability across runs greater than 90%. Maternity assignments were supported by agreement in the mtDNA haplotypes of mothers and their offspring, when both were known.

*3.3.2 Social Indications of Genetic Mothers*

In all cases, calves associated with and nursed from their genetically-determined mothers, and in most cases, genetically-determined mothers were their calves' closest associates and primary nurses (Table 3.1). Of all clusters with a single adult or juvenile present with calves, the associate was the calf's mother 71.0% of the time. Other adult females were the next most common class of sole non-calf associates in clusters with calves (14.1%), followed by juvenile females (10.2%), and juvenile males (4.6%).

**Table 3.1** Calf care in sperm whale social units. 'Mother rank' is relative to other available unit members; a tie is indicated by '$_T$'. Association was defined as identification in the same cluster, with a daily or 2-hr sampling period, using 'both identified' as the association index. For mother rank, parenthesis indicate her rank based on the 2-hr sampling period, if it differs from her rank based on the daily sampling period. For babysitters, parenthesis indicate number (N) of available unit members observed associating with the calf while associated with no other adults, if it differs from the number when all clusters are included. Only calves from well-sampled social units (indicated by an asterisk) were included in calculations of mean relatedness values and in permutation tests.

| | | | Mother rank | | Babysitters | | Allonurses | |
|---|---|---|---|---|---|---|---|---|
| Unit | Calf ID | Mother ID | Asso. | Nursing | Avail. | N | Avail. | N |
| A* | Allan | Lady Oracle | 1 | 1 | 5 | 5 (2) | 5 | 1 |
| | Aurora | Lady Oracle | 2 | 3 | 3 | 2 | 3 | 2 |
| | Soursop | Fruit Salad | 1 (2) | 1 | 5 | 4 (1) | 5 | 0 |
| | Snowman | Oryx | $1_T$ (1) | 1 | 3 | 2 (1) | 3 | 0 |
| | Crake | Oryx | 1 | 1 | 5 | 4 (1) | 5 | 2 |
| | SLBC | Atwood | $1_T$ (2) | 1 | 5 | 5 (2) | 5 | 1 |
| D | Distinct | - | - | - | - | 1 | - | 1 |
| F* | Thumb | Fingers | 1 | 1 | 5 | 5 (3) | 4 | 0 |
| | Tweak | Pinchy | 1 | 1 | 4 | 4 (3) | 3 | 0 |
| | Enigma | Mysterio | 1 | 1 | 4 | 4 (3) | 3 | 1 |
| J* | Jonah | Sophocles | 3 (2) | 1 | 2 | 2 | 2 | 1 |
| | Oedipus | Jocasta | 1 | 1 | 2 | 1 | 2 | 0 |
| R* | Routine | Raucous | 1 | 1 | 4 | 3 (0) | 4 | 0 |
| | Rema | Rita | 1 | 1 | 4 | 2 (1) | 4 | 2 |
| T | Tusk | Tooth | $1_T$ | 1 | - | 1 (0) | - | 0 |
| U* | Spoon | Fork | 1 | 1 | 2 | 2 (1) | 2 | 0 |

For each sampling interval that was used in the calculation of association indices, 62.5% of genetically-determined mothers unambiguously had the highest association indices with their calves (Table 3.1). In three cases, the association rate of the calf with another adult was equal to the mother's value, and in two cases the mother was not the calf's closest associate (Table 3.1). Two of these ties were resolved when associations were calculated within 2-hr, rather than daily, sampling periods – one resolved in favour of the mother, and the other in favour of the other associate (Table 3.1). About half of the calves suckled on one or two adult females in addition to their mother. For all but two calves (87.5% of calves), the genetically-determined mother was the female most often observed receiving peduncle dives from their calf (Table 3.1). One calf (ID: Aurora) suckled on two other females more often than on its mother. Additionally, another calf (ID: Distinct), for whom a genetic mother was not identified, was only identified associating with and suckling on one individual, who was not the calf's mother (pairwise relatedness = 0.14).

### *3.3.3 Calf Associations and Interactions Correlated With Maternal Relatedness*

Across the calves (n = 14) from well-sampled social units, pairwise relatedness between mothers and non-calf unit members was positively correlated with association rates between calves and non-calf unit members (Table 3.2). However, the effect size and significance of the correlation varied depending on the parameters of the analysis (Table 3.2). No correlations were significant when intra-calf rank values of association and relatedness were used, and the effect sizes of most of these correlations were quite small (Table 3.2). When associations were scaled relative to the mother's value, effect sizes

**Table 3.2** Correlations between association rates and maternal relatedness across all calf-babysitter pairs. One-sided p-values for Spearman's rank correlation coefficient ($r_s$) were calculated based on 50,000 simulations. Associations and relatedness values for each calf were ranked and scaled to values from 0 to 1, or association rates were standardized relative to the mother's association rate. Association indices were calculated using all clusters, or restricted to clusters without multiple adults.

| | | Rank-standardized | | Mother-standardized | |
|---|---|---|---|---|---|
| | Sampling Period | $r_s$ | p | $r_s$ | p |
| Full | Day | 0.253 | 0.051 | 0.240 | 0.049 * |
| | 2hr | 0.063 | 0.35 | 0.147 | 0.33 |
| Restricted | Day | 0.066 | 0.34 | 0.403 | 0.019 * |
| | 2hr | 0.078 | 0.28 | 0.374 | 0.048 * |

were generally greater, particularly for the restricted dataset and the daily sampling period, and three of the correlations were statistically significant at $P<0.05$ (Table 3.2).

Almost all individuals spent at least some time associated with the calves in their social units (Figure 3.1.a), but fewer individuals associated with calves in clusters where they were the sole non-calf individual in the cluster (Figure 3.1.b). With this restriction on cluster composition in place, most unit members with a low relatedness to the calf's mother ($r <$ approximately 0.125) did not babysit the calf, while most unit members with a higher relatedness did, particularly those whose relatedness to the mother was about 0.5, likely grandmothers or maternal half-siblings to the calf (Figure 3.1.b). The average sole babysitting rate of likely first-degree relatives of the mother ($r \geq 0.35$) was roughly double that of more distant relatives ($0.1 \leq r < 0.35$), which was in turn double that of individuals who were not close relatives ($r < 0.1$). This was true regardless of whether the raw association values or the mother-standardized values were used.

Consequently, much of the sole babysitting (51.2% of the occasions with a sole babysitter whose kinship with the mother was genetically determined) was carried out by likely

grandmothers or maternal half-siblings to the calf (relatedness to the mother $\geq 0.35$; Figure 3.1.b). Likely second- or third-degree relatives of the mother ($0.10 \leq r < 0.35$) were also sole babysitters more often (29.3% of occasions) than unit members who were not close relatives (19.5%; Figure 3.1.b).

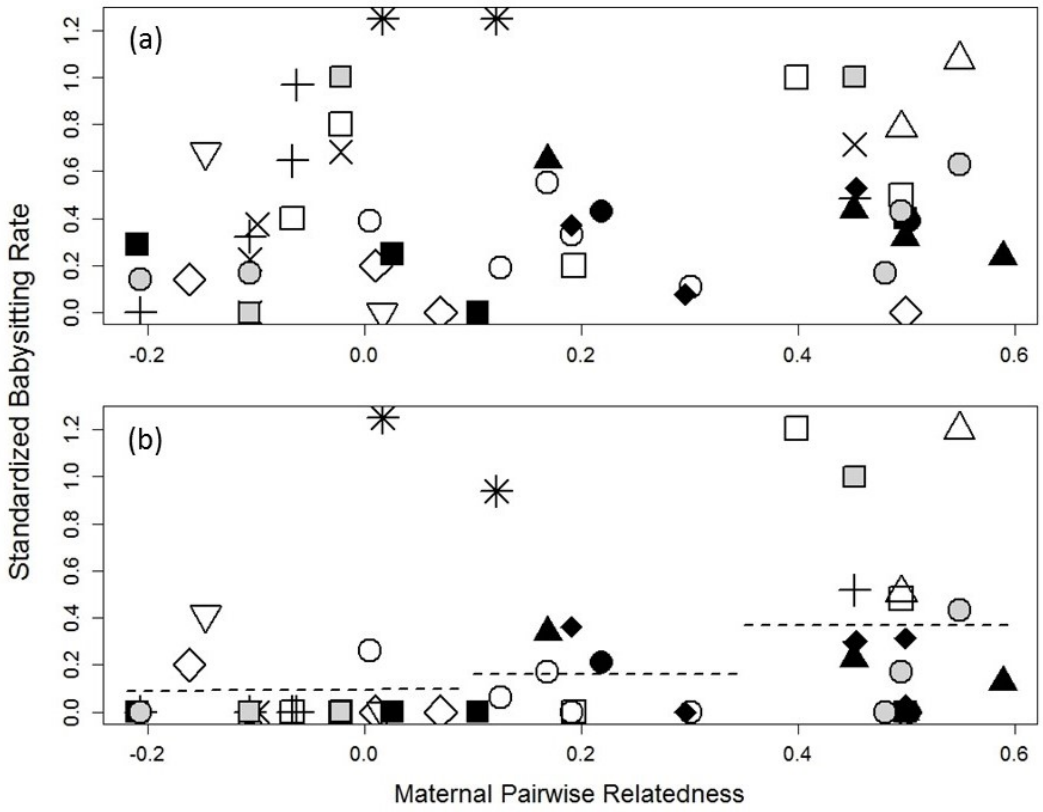


**Figure 3.1** Maternal relatedness between calves and non-calf unit members correlates with babysitting rate. Relatedness values were calculated using Wang's (2002) estimator. Babysitting rate was based on 'both identified' association indices, with a daily sampling period, and scaled by the calf's association rate with its mother, (a) with all clusters, and (b) excluding clusters with more than one adult or juvenile. Shape and shade indicate calf identity. Dashed horizontal lines indicate mean babysitting rates for likely first-degree relatives of the mother ($r \geq 0.35$), more distant relatives ($0.1 \leq r < 0.35$), and individuals who were not close relatives ($r < 0.1$).

Overall, females who nursed calves that were not their own were more closely related to the mothers of those calves than were the available females who did not nurse them ($\Delta r$ = 0.14, p = 0.0544, 50,000 simulations; Figure 3.2). The mean relatedness of nurses to the mothers of the calves they nursed was 0.287, compared to 0.147 for the available females who did not nurse the calves.

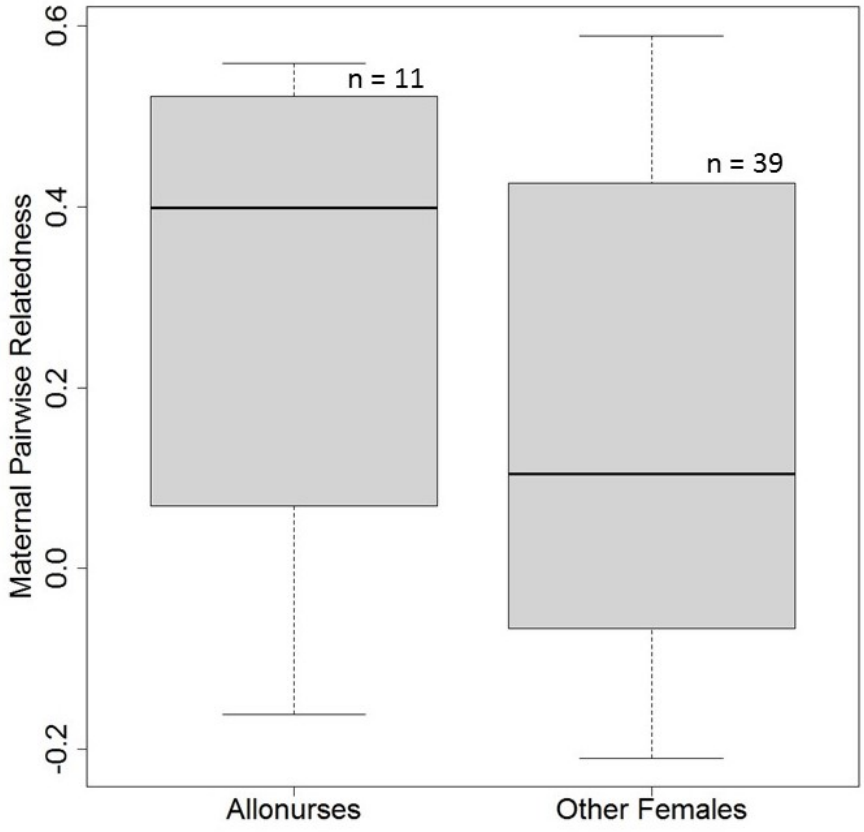


**Figure 3.2** Relatedness of allonurses and other available females to the mothers of the calves they nursed, or were available to nurse. Relatedness values were calculated using Wang's (2002) estimator.

### 3.4 Discussion

This is the first study to examine the relationship between allocare and kinship in sperm whales for more than a single calf, and thus it greatly expands our understanding of this

relationship and its variation. We demonstrated positive correlations between maternal relatedness and alloparental calf care, though notable variation around these patterns suggests that the sperm whale's system of cooperative breeding is not driven by kin-selection alone.

We also demonstrated that the commonly practiced – but previously untested – assumption that mothers can be correctly determined based purely on social data is not always valid. While in most cases, the genetically-determined mother was the same individual as would be inferred from the social data, assigning maternity based exclusively on social data is likely to be particularly unreliable if based on relatively few behavioural observations. For example, a calf who was exclusively observed peduncle diving on and associating with a female that was not his mother was a member of a poorly sampled social unit – Unit D. This could be an example of adoption or of an exceptionally dedicated babysitter, but, with only four bouts of peduncle diving observed (across two days in consecutive years), we cannot confidently exclude the possibility that it also received unobserved but substantial care from its unknown mother.

Different levels of care likely have different costs to the caregiver, which appears to affect which individuals are willing to provide care. Associating with calves while other adults or juveniles are also present would include occasions where the whole unit is socializing, and likely has little or no cost to the participating individuals, whereas being the sole escort of a calf may be costlier. The former is done by almost all unit members (Figure 3.1.a), while the latter was typically done only by those individuals who were at least third-degree relatives of the mother ($r \approx 0.125$) and most often by those who were first-degree relatives, and so a sibling or grandmother of the calf ($r \approx 0.5$; Figure 3.1.b).

Similarly, nursing, assuming milk is being provided to the calf, is likely costlier than simply associating with a calf, and it was mostly performed by close relatives of the mother ($r \geq 0.4$; Figure 3.2). For example, allonursing was prevalent in unit A, which was composed of two strict matrilines (Chapter 2), and observed allonurses were exclusively from the same strict matriline as the calves they nursed.

Consideration of allocare costs can also aid the identification of mothers based on social data. We found that calf care behaviours that were likely costlier were better indicators of maternity: peduncle diving was a more reliable indicator of maternity than social association, and restricting association data to clusters with one adult escort resolved ambiguity in the association data in one case.

To generate hypotheses about what drivers, other than kinship, may be affecting cooperative calf care among sperm whale, it is informative to consider the variation around these general trends, and examine more closely the cases that are particularly deviant. One area of variation in our results is between the two methods of standardizing calf associations. Based on rank-standardized association values, we observed that, for a given calf, ordinal ranks of babysitting were not well-predicted by ordinal ranks of maternal relatedness (Table 3.2), meaning that a calf's closest maternal relative was not necessarily its primary babysitter. In contrast, correlations were greater and generally statistically significant when associations were standardized by the mothers' values. This difference suggests that perhaps it is not the rank of unit members' genetic relatedness that matters so much as their absolute genetic relatedness. For example, it may be unimportant that an individual is the calf's closest maternal relative if that individual is still not a particularly close relative. This idea is supported by the previously-mentioned

approximate relatedness thresholds delineating which individuals provide certain types of allocare, and the increase in mean sole babysitting rates for individuals in a higher category of relatedness.

If the absolute level of relatedness is an important driver of babysitting, we would also expect social units with higher overall relatedness to have more prevalent babysitting. This was largely true among the well-sampled social unit in this study (Table 3.3). Units F and U, which had the highest intra-unit relatedness values, were the only units for which all available individuals were observed associating with all calves, and they had some of the highest percentages of unit members acting as sole babysitters (Table 3.3). Complimentarily, unit R, had the lowest intra-unit relatedness and the lowest levels of babysitting (Table 3.3). But, this trend is not universal; unit J also had a low level of relatedness, but the highest percentages of unit members acting as sole babysitters (Table 3.3).

**Table 3.3** Kinship and babysitting in sperm whale social units. Pairwise relatedness (*r*) was calculated, according to Wang (2002), and averaged among all sampled members of each social unit. Mean numbers of available babysitters were calculated as the averages across calves. Percentage of available individuals who babysat were calculated across all possible calf-caregiver pairs. Babysitters were classified using all clusters (Full), or restricted to clusters without multiple adults (Restricted).

| Social Unit | Mean *r* | Mean Available Babysitters (N) | Babysitters (%) Full | Restricted |
|---|---|---|---|---|
| A | 0.137 | 4.3 | 85 | 35 |
| F | 0.232 | 4.3 | 100 | 69 |
| J | 0.136 | 2 | 75 | 75 |
| R | 0.106 | 4 | 63 | 13 |
| U | 0.333 | 2 | 100 | 50 |

Another important difference between the two standardized metrics of calf association is that standardizing associations by per-calf ranks ignores differences between calves in the relative level of allocare received. Younger calves likely require more care, and this could involve more care from their mother as well as from alloparents. Thus, scaling association rates by the mother's value could help control for this source of variation, reducing noise, and allowing a relationship between genetic relatedness and babysitting to be detected.

Calf age may also help explain why certain calves received especially high levels of babysitting. For example, Jonah (symbolized as the asterisk on Figure 3.1) a calf from unit J was babysat extensively by two unit members who were not close maternal relatives. Jonah had no other unit members (besides its mother) and was believed to be no more than a year old. In the first year of their calves' lives, mothers are less gregarious and less socially connected (Gero, Gordon, and Whitehead 2013), perhaps due to increased energetic demands associated with lactating, which may require increased time allocated to foraging at depth (Gero, Gordon, and Whitehead 2013). This may leave calves in need of particularly high levels of babysitting in their first year, especially since they are also likely the most vulnerable to predation at this young age. Two other calves (IDs: Aurora and SLBC) that stand out as having received high levels of allocare (that matched or exceeded the level of care provided by their mothers; Table 3.1) were also less than a year old. If very young calves indeed require more allocare, in small social units without close relatives, such as Unit J, the burden of this extra care may fall on distantly related or unrelated individuals.

Personality is another source of individual variation that is important to many aspects of animal ecology (Sih et al. 2012), and which likely influences babysitting rates. More gregarious individuals, for example, whether calves or babysitters, would be expected to have higher association rates. Similarly, the boldness of a calf could affect how much time it spends with its mother, with babysitters, or alone. By adding noise around any kin-driven patterns, this individual variation could reduce the strength of observed correlations.

We also observed deviations from the overall positive relationship between maternal relatedness and allonursing. For instance, a calf from unit R (ID: Rema) made peduncle dives on two adult females from her unit who were not close maternal relatives (maternal $r = 0.0$ and -0.2), yet the calf was not observed making peduncle dives on her mother's first-degree relative (maternal $r = 0.5$). Additionally, a lack of close relatives did not explain why some calves lacked allonurses; five of the seven calves from well-sampled units who did not have observed allonurses did have available first-degree relatives of their mothers.

However, we made assumptions about the availability of females to act as allonurses based on behavioural data and approximate age, without knowledge of whether they were lactating and, if so, whether any milk was successfully obtained by the sucking calf, which is not a given (Cameron 1998). Thus, some females that were classified as 'available' may not have been so, and some females classified as nurses may not have provided any milk. Yet, sucking that does not lead to milk letdown may still have social or emotional benefits (Cameron 1998), such as among African elephants (*Loxodonta*

*africana*), where allonursing appears to relate more to providing comfort than nutrition (Lee 1987).

Observations of allocare that are disproportionate based on kinship could also relate to reciprocal altruism (Trivers 2006; Trivers 1971). Past studies have demonstrated concurrent mothers babysitting for each other, as well as a mother reciprocating babysitting after a delay of a year, when a calf was born to the past babysitter (Gero, Gordon, and Whitehead 2013; Gero et al. 2009). Compelling examples of reciprocal altruism in animals typically involve "parcelling", where the participating individuals alternate providing a costly resource or service in limited quantities that are less than what each partner needs, as a means of minimizing the risk of one partner cheating (Connor 1995). Such a mechanism could function between concurrent mothers, who could babysit each other's calves, in alternation, during the brief intervals that they spend at the surface between deep foraging dives.

Reciprocation after longer delays, such as across years, requires higher cognitive abilities, such as individual recognition and memory of past interactions (Melis and Semmann 2010). Long-term social preferences among sperm whales demonstrate their capability to recognize individuals (Gero, Gordon, and Whitehead 2015), possibly based on vocal identity signals (Gero, Whitehead, and Rendell 2016). Gero et al., (2015) also hypothesize that sperm whales can likely recall past interactions to inform these preferences. Further, considering the complex social environment in which sperm whales live (Gero, Gordon, and Whitehead 2015; Rendell and Whitehead 2003), this species may well have experienced selection for the evolution and integration of the cognitive capabilities that Hauser *et al.* (2009) deemed necessary for delayed reciprocity to evolve

in humans, namely inequity detection, future-oriented decision-making and inhibitory control.

Alternatively, as discussed by Gero et al., (2013), another possible mechanism is generalized reciprocity (Pfeiffer et al. 2005), which does not require memory of the identities of past interaction partners, but relies on repeated interactions within a small group, where decisions about cooperation are made based on the outcome of their previous interaction with any group member.

Based on the observations of allocare reported in the present study, however, reciprocity is by no means a rule. For example, in 2010, there were two new calves in unit A (IDs: Crake, and SLBC), but their mothers (IDs: Oryx and Atwood, respectively) were not observed babysitting for each other, except for when other adults or juveniles were present in the cluster. This may be a case of kin-selection outweighing reciprocal altruism; the concurrent mothers were seemingly unrelated ($r = -0.02$), while the mothers and the primary babysitters of each calf were close relatives ($r \geq 0.40$). Interestingly, Atwood had an even closer relative, Lady Oracle ($r = 0.50$), who also had concurrent calf (Allan). Yet, these closely related mothers did not compellingly reciprocate allocare. They babysat for each other occasionally, but neither mother was observed nursing the other's calf. Rather, Rounder, who was Lady Oracle's daughter and Atwood's second-degree relative, received peduncle dives from both calves and was their primary babysitter. Thus, even kin selection and reciprocal altruism together cannot fully explain this allocare arrangement.

Another factor that may influence patterns of allocare, and could explain unusually high alloparenting by Rounder, is gaining maternal experience (Lancaster 1971). Rounder was a juvenile female, who we assumed to be nulliparous based on long-term field observations since the time she was a calf. She substantially babysat three calves from her social unit and received peduncle dives from all of them. For one of these calves, Rounder was observed to provide even more care than the calf's genetically-determined mother[3]. These three calves were all from the same strict matriline as Rounder, while two other calves in unit A whom Rounder did not act as the sole babysitter of were not. This suggests that if gaining maternal experience is indeed an important factor it may operate preferentially among close kin. Similarly, the only other likely nulliparous juvenile female, Canopener from unit U, was the primary babysitter of the calf in her social unit. Both juvenile females babysat the calves in their units at a higher rate than the average for adult females, such that these two individuals accounted for 35.4% of sole babysitting observed across all calves, compared to the 22 adult females who accounted for 48.8%. There were also two juvenile males in our database, whose patterns of allocare were very different from each other. One juvenile male, Scar from unit F, acted as a sole babysitter of all three calves in his social unit at higher rates than the average rate by adult females,

[3] *Both Rounder and this calf's genetically-determined mother (Lady Oracle) share at least one allele at every locus with this calf (Aurora), and they each have a high relatedness value with Aurora (r = 0.51 and 0.50, respectively). Thus, it is genetically possible that Rounder is actually Aurora's mother, as would be suggested by the social data. However, maximum likelihood inference of maternity (see Chapter 2), implemented in Colony 2.0.6.2* (Jones and Wang 2010)*, assigned Lady Oracle as the mother of Aurora with a 99% probability in two independent runs. This suggests that, when allele frequencies are considered, it is much more likely that Lady Oracle is the mother of Aurora, and that Rounder is a close relative (either a half- or full-sibling) of Aurora who provides substantial allocare.*

while the other young male, Alan from unit A, was never observed as the sole babysitter of any calves from his unit, despite being the maternal half-brother of one of them. Perhaps, the presence of a juvenile female in Unit A, but not in Unit F, could explain this difference in rates of babysitting rates by juvenile males.

More robust assessment of the importance of gaining maternal experience will require investigation of whether individuals who provide more allocare as juveniles have higher reproductive success as adults. Given the slow life history of sperm whales, such data cannot be acquired quickly. However, among African elephants, which bear great socio-ecological similarity to sperm whales (Weilgart, Whitehead, and Payne 1996), primiparous females appeared to be less competent mothers despite juvenile females providing much of the allocare in this species and thus having the opportunity to gain maternal experience (Lee 1987).

The observation that allocare is typically found within highly social or cooperative groups of individuals (Riedman 1982) begs a question of causality: does allocare arise within these groups, or does dependence on conspecifics for the survival of young incentivize the maintenance of social relationships and provide opportunity for further cooperation? In the case of sperm whales, evidence suggests that their complex, cooperative social system is driven and maintained primarily by allocare, particularly the defence of calves (Best, 1979; Gero, Gordon, & Whitehead, 2013), rather than the other way around. The same is believed to be true of African elephants (Lee 1987), whose society bears great similarity to that of sperm whales (Weilgart, Whitehead, and Payne 1996). The importance of unit members for the defence of calves points to group augmentation (Kingma et al. 2014; Kokko, Johnstone, and Clutton-Brock 2001) as

another factor, beyond kin selection, which may strengthen allocare among both sperm whales and elephants.

Similarly, as an explanation of hyper-cooperation among humans, it has been suggested that cooperative breeding may promote further prosocial tendencies (Burkart et al. 2014). The robustness of this hypothesis has been disputed (Thornton et al. 2016), but it is commonly accepted that reducing predation risk, which often includes communal protection of offspring, motivates group living among numerous species (R. D. Alexander 1974). Groenewoud et al. (2016) argue that similar predation-driven selective pressures may have encouraged evolutionary transitions to more complex societies. In line with this idea, among lions (*Panthera leo*), defence of young against infanticide is thought to be the primary motivator behind groups formed by mothers, called crèches (Pusey and Packer 1994). Further, allocare that also occurs within crèches, namely allonursing, appears to be a by-product of this social system (Pusey and Packer 1994). Similar to what we observed among sperm whales, this allonursing was more common among close kin, suggesting that relatedness among female lions, as among sperm whales, contributes to the persistence of this potentially costly behaviour (Pusey and Packer 1994).

The sperm whale population in the Eastern Caribbean, which we reported on in this study, is in a state of critical decline, with a particularly clear decrease in the number of adults in social units (Gero and Whitehead 2016). A reduction in the number of adult social unit members will likely have implications for the quality and quantity of allocare that calves receive, which may, in turn, compound the rate of population decline if calf survival is negatively affected as a result. Thus, understanding the extent of allocare

received by calves, and from whom they receive it, can improve our understanding of the trajectory of this declining population.

### 3.5 Conclusion

Overall, we identified a positive relationship between allocare and maternal relatedness, which points to kin selection as a driver of the evolution and maintenance of allocare among sperm whales. We also observed that while mothers typically provide the majority of care for their calves, allocare can be extensive in some cases, perhaps even exceeding the mother's contribution. Since most previous studies of maternal care and allocare among sperm whales have lacked genetic data, extensive allocare may be more prevalent than previously assumed. Additionally, while kinship clearly affects the sperm whale's system of allocare, strict kin-based rules could not fully explain who provided care and to what degree, highlighting that kin selection is not the only driver involved. Deviations from the overall trends may be partially explained by variation in factors like calf age, unit size and composition, individuals' gregariousness, and sampling coverage, but we also suggest that some combination of reciprocity, group augmentation and gaining maternal experience may contribute substantially to the observed patterns. Further longitudinal studies of allocare within well-known social units are likely to be the most fruitful avenue for elucidating the contributions of other factors. By studying the mechanisms that allow allocare to evolve, we increase our understanding of a process that may be foundational to many complex cooperative societies.

# CHAPTER 4

# KINSHIP AND SOCIAL ASSOCIATION DO NOT EXPLAIN VARIATION IN VOCAL REPERTOIRE AMONG INDIVIDUAL SPERM WHALES OR THEIR SOCIAL UNITS[4]

## 4.1 Introduction

Vocal learning has been demonstrated in few lineages of mammals, but it may be more widespread than current studies show and likely serves several important purposes in animal societies (Tyack 2008). Proposed functions of learned vocalizations include sexual selection (Janik 2014), signalling individual identity (Tyack 1997), and maintaining social bonds (Poole et al. 2005), though in some cases, variation in learned vocalizations may be due to drift, rather than selection for a particular function (Andrew 1962). As a result of the limited number of studies demonstrating vocal learning among mammals, the function of vocal learning and the social processes by which it occurs have been assessed in few situations.

Among mammals, cetaceans are a taxon for which vocal learning has been relatively well-documented, and for which the function and process of vocal learning have been fruitfully examined (Janik 2014). Among sperm whales (*Physeter macrocephalus*), repertoires of vocalizations that are presumed to be socially learned are shared among

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[4] *This chapter has been prepared in manuscript format, with the intention to submit to Animal Behaviour.*
*Contributing authors: Christine M. Konrad (CK), Shane Gero (SG), Tim Frasier (TF) and Hal Whitehead. CK, SG and HW participated in the collection of the field data; CK carried out all molecular laboratory work and statistical analysis, and wrote the manuscript; SG coordinated the field operations of the study, and completed the photo-identification; Tim Frasier (TF) aided sample collection efforts and supervised the molecular laboratory work; SG, TF and HW contributed funds. CK wrote the manuscript. All authors collaborated in the conception and design of the study.*

sympatric cultural groups (Rendell and Whitehead 2003). Additionally, repertoire variation has been identified that may be used as signals of identity at nested levels of sperm whales' well-characterized multi-level social structure (Gero, Whitehead, and Rendell 2016). Thus, sperm whales are a natural choice for continued study of the function of learned vocalizations and cultural transmission of these vocalizations.

Female and juvenile sperm whales live in social units that are stable across years (Gero et al. 2014; Whitehead 2003), from which males disperse before sexual maturity (Best 1979). Within social units calves are communally cared for (Gero, Gordon, and Whitehead 2013; Whitehead 1996; Gero et al. 2009), and social preferences exist among individuals (Gero, Engelhaupt, and Whitehead 2008) and between social units (Gero, Gordon, and Whitehead 2015). Social units can contain unrelated individuals, but these units are matrilineally-based (Chapter 2, Christal, 1998; Mesnick, 2001; Ortega-Ortiz, Engelhaupt, Winsor, Mate, & Hoelzel, 2012). Association preferences within units, including patterns of alloparental care, loosely reflect kinship (Chapters 2 and 3), though association preferences among social units generally do not (Chapter 2).

Social units can be classified as members of higher level cultural groups, called vocal clans (Rendell and Whitehead 2003). Clans differ in non-vocal behavior and are socially segregated but they are defined based on repertoires of codas (Rendell and Whitehead 2003), which are stereotyped patterns of broadband clicks (Watkins and Schevill 1977) that appear to be used for communication (Schulz et al. 2008; Whitehead and Weilgart 1991). Models show that social learning, with a bias towards learning common codas from individuals with similar repertoires, can explain the evolution of sympatric vocal clans (Cantor et al. 2015). But this mechanism was not dependant on the social level

(within social units, within clans, or population-wide) at which social learning occurred (Cantor et al. 2015). This leaves ambiguity about from whom vocal repertoires are learned, the details of which will, to a large extent, determine how coda repertoire variation emerges among units and individuals.

Considering Gero, Whitehead, and Rendell's (2016) observation of shared coda types within social units, coda repertoires or specific coda types may be preferentially learned from closer social associates. Alternatively, or additionally, coda repertoires or particular coda types may be preferentially learned from kin. These codas could then serve as a kin-recognition signal, and thus could explain kin-driven patterns of association and calf care in sperm whale social units.

To investigate how social association and kinship relate to the acoustic repertoires of individual sperm whales and their social units, we compared social, genetic and vocal repertoire relationships derived from a longitudinal research project on sperm whale behaviour (Gero et al. 2014).

## 4.2 Methods

### *4.2.1 Field Methods*

From 2005 to 2016, social units of sperm whales were located and followed, visually by observers on deck during daylight hours, as well as acoustically using hydrophones up to 24 hours a day (Gero et al. 2014), in an area of approximately 2,000 $km^2$, off the leeward, western coast of Dominica, in the Caribbean Sea (15.5°N; 61.5°W). Annual field seasons

ranged from two to four months in duration, and occurred between January and June, using various research platforms (total effort: 518 days).

Photographs were taken of the trailing edge of flukes of juveniles and adults (Arnbom 1987) and of the dorsal fins of calves (Gero et al. 2009) for individual identification. In conjunction with these identification photographs, we recorded observations of associations of individuals in clusters (Gero et al., 2014). Clusters were defined as groupings of individuals at the surface in close proximity to each other (< 40 m) with coordinated behaviour (Whitehead 2003).

We used dip nets opportunistically to collect sloughed skin from the flukeprints of individual whales or clusters of whales (Whitehead et al. 1990). In 2015 and 2016, we also collected biopsy skin samples from specific individuals, to fill known gaps in our sample set. We used a 90 lb draw weight crossbow and bolts with 2.5 cm long tips with 0.5 cm circumferences (see Kowarski et al. 2014 for details). Skin samples collected from 2005 to 2010 were stored in ethanol (at a concentration of 70% or greater), and samples collected from 2011 onwards were stored in a 20% DMSO solution saturated with salt (Seutin, White, and Boag 1991).

*4.2.2 Acoustic Sampling*

Using a towed hydrophone array, codas were recorded when clusters of whales initiated dives and while the whales were socializing at the surface, as in Gero, Whitehead, and Rendell (2016). In 2014 to 2016, codas were also recorded using 3$^{rd}$ generation Dtags (M. P. Johnson and Tyack 2003). See Appendix B, Table B1, for numbers of codas recorded across years.

Codas were previously assigned to individuals and units (see Gero, Whitehead, and Rendell (2016)). For new Dtag recordings, codas were assigned to the unit which the tagged whale was a member of, if no other units were identified on the tagging day. At the individual level, Dtag codas were only assigned to the focal, tagged, whale based on consistent inter-pulse interval (as in Gero, Whitehead, and Rendell (2016)), and for which angle of arrival was consistent with tag placement.

### *4.2.3 Social Units and Defining Social Association*

Social units were delineated by Gero *et al*. (2014), so that they reflect long-term, stable social relationships. One pair of social units (Units F and U) that merged across the study period (Konrad et al., 2017) were treated as separate units, because much of the acoustic data was collected before the merger was complete.

For our analysis, we used two definitions of association. First, as a fine spatiotemporal scale of association, we considered individuals in clusters at the surface. Clustered individuals often interact vocally (Schulz et al. 2008), thus association at this scale may influence the coda repertoires of individuals. Second, we defined association more broadly as individuals identified within two hours of each other, as such individuals are likely close enough to be in acoustic contact.

To assess the influence of both short- and long-term association preferences on acoustic similarity, we used two different sampling periods to calculate association indices with our finer definition of association (i.e. clusters). The shorter period used was two hours, which corresponds to approximately two dive cycles in sperm whales and has been applied in other studies of this species (Christal & Whitehead, 2001; Gero et al., 2015).

With this sampling period, we aimed to maximize the number of samples while minimizing autocorrelation in cluster composition. The longer period used was 'year', which has also been previously applied in this species (Gero et al., 2015) to highlight long-term association preferences. With our broader definition of association (i.e. both identified within same two hours), we used a daily sampling period, to calculate an association index of intermediate temporal scale.

To calculate association indices for these three combinations of association definition and sampling period, at both the individual and unit level, we used half-weight indices (HWI) of association (Cairns and Schwager 1987). This index best corrects for the types of biases in identification rates that are typical of cetacean photo identification (Cairns and Schwager 1987; Whitehead 2008). For unit level associations, if at least one member of each of two social units were associated in a sampling period, then those individual's social units were considered associated in that sampling period.

*4.2.4 Genetic Laboratory Methods and Analysis*

For genetic laboratory methods, analysis of microsatellite genotypes and mitochondrial DNA (mtDNA) sequence data, calculation of pairwise relatedness values, and determination of mother-offspring relationships see Chapter 2.

*4.2.5 Testing for Kin Relationships Between Vocal Clans*

To test for instances of close kinship between clans, we used the program ML-Relate (Kalinowski, Wagner, and Taper 2006). Based on microsatellite genotypes across 18 loci, we tested whether the relationship between any pair of individuals in different vocal clans

was likely to be parent-offspring, half-sibling/grandparent-grandoffspring, or full-sibling, and unlikely to be unrelated. We determined which of these four relationships were consistent with the genetic data at the 0.05 level of significance, by calculating likelihood ratios and using simulations to reject unlikely relationships. If multiple relationships were consistent with the genetic data, this method was also used to identify the most likely relationship.

### *4.2.6 Measuring Similarity Between Coda Repertoires*

To quantify coda repertoire similarity among individuals or units, we used a continuous measure of similarity, as used by Gero, Whitehead, and Rendell (2016). The components of codas used to assess similarity were the absolute inter-click intervals (ICIs), which are the times between the onsets of each sequential click in a coda. ICIs were extracted from recordings from a towed hydrophone array as in Gero, Whitehead, and Rendell (2016). Additional codas were extracted from Dtag recordings, using a custom written MATLAB R2015b script (The Mathworks, Inc., MA, USA) and LabVIEW program (National Instruments, TX, USA). For pairs of codas with the same number of clicks, we calculated the multivariate similarity of the codas using the Euclidean distance between the ICI vectors of those codas. Codas with different numbers of clicks are assigned a similarity of zero. Using custom-written routines in MATLAB v. 7.12 (TheMathworks, Inc., MA, USA), we averaged these multivariate similarities to calculate a measure of similarity between pairs of coda repertoires, for both individuals and social units, following the equation in the electronic supplementary material of Gero, Whitehead, and Rendell (2016).

For an analysis of 'whole repertoire' similarity at both the unit and individual level, we included all codas with a length up to and including ten codas. We also determined the multivariate similarity of four-click coda repertoires at the unit level and multivariate similarity of 5R1 codas at the individual level, as these coda types may function as unit-level and individual-level identity cues, respectively, based on the results of Gero, Whitehead, and Rendell (2016).

*4.2.7 Unit Level Matrix Correlations*

In this analysis, we included social units for which genetic data were available for at least three individuals, and for which at least 250 codas had been recorded. Discovery curves have demonstrated that coda sample sets of this size should be representative of a unit's repertoire, including all but very rare coda types (see ESM, Figure 3, in Gero, Whitehead, and Rendell (2016)). For tests of four-click coda similarity we restricted our analysis to social units for which at least 25 four-click codas had been recorded, which is a minimum sample size that has been applied in other studies of unit coda usage in this species (Rendell and Whitehead 2005).

We performed Mantel tests (Mantel 1967), with 10,000 random permutations (which stabilized p-values), using SOCPROG2.7 (Whitehead 2009) to test for matrix correlations between each measure of acoustic similarity (whole repertoire similarity and four-click coda similarity) and each association index (clusters in two hours, clusters in a year, two hours in a day), as well as each measure of genetic similarity (mean pairwise relatedness and mtDNA haplotype sharing). The 'whole repertoire' analysis was repeated with the single unit from the EC2 vocal clan (Unit P) excluded, to examine variation between

units exclusively within the EC1 vocal clan. Similarly, we performed Mantel tests of matrix correlations between social units' clan membership (same – 1, or different – 0) and the two measures of genetic similarity. For all analyses, we conducted two-sided tests, because units or individuals may learn repertoires that are more like their kin or associates, or that are dissimilar, such as has been observed among bottlenose dolphins (*Tursiops* spp.), for which females' whistles were unlike those of their mothers (Sayigh et al. 1995).

*4.2.8 Individual Level Acoustic Analysis*

For our analysis of whole repertoires of individuals, we included individuals from known social units for which genetic data were available, and at least 25 codas had been recorded. Discovery curves have demonstrated that coda sample sets of over 75 should be representative of an individual's repertoire (see ESM, Figure 3, in (Gero, Whitehead, and Rendell 2016)), so we repeated these analyses after removing individuals who did not meet this more stringent sample size. As in a past study that identified individual differences in 5R codas (Antunes et al. 2011), we restricted our analysis of 5R1 codas to individuals with at least five 5R1 codas recorded. We also repeated this analysis with a more stringent sample size cut-off of 25, to remove possible effects of under-sampling individual variation.

Across all adequately sampled individuals, as well as within social units that had at least three adequately sampled members, we performed Mantel tests (Mantel 1967), with 10,000 random permutations, using SOCPROG2.7 (Whitehead 2009) to test the significance of matrix correlations. We tested for correlations between each measure of

acoustic similarity (whole repertoire similarity and 5R1 coda similarity) and each of two association indices: association in a cluster in a two-hour sampling period and association in a cluster in a yearly sampling period. Across all individuals, we also tested for a correlation between social unit (same or different) and each acoustic similarity measure. Likewise, we tested for matrix correlations between these acoustic similarity measures and three measures of kinship: pairwise relatedness, mtDNA haplotype sharing, and whether the pair of individuals had been genetically identified as a mother-offspring pair or not. We did not include mtDNA haplotypes as a predictor in the within-unit analyses, because haplotypes were uniform within social units. Analyses were repeated with calves omitted, to account for differences between repertoires of calves and adults, which have been reported in this species (Gero, Whitehead, and Rendell 2016).

*4.2.9 Power Analysis of Individual-Level Analysis*

To assess the Mantel tests' power to detect small effects of relatedness on individual-level acoustic similarity, we repeated Mantel tests of matrix correlations between pairwise relatedness and whole repertoire similarity across all individuals ($N_{ind} = 20 \therefore N_{pairs} = 190$) with modifications to the acoustic similarity matrix based on kinship. To simulate a situation where mothers and their offspring have more similar repertoires, we boosted the acoustic similarity of all known mother-offspring pairs ($N_{pairs} = 8$) by adding to these values a percentage of the mean acoustic similarity value, ranging from 10% to 400%. To simulate a situation where all close relatives have more similar repertoires, we boosted the acoustic similarity of all pairs with a relatedness value of at least 0.2 (i.e. roughly including first- and second-degree relatives; $N_{pairs} = 27$) by adding to these values a percentage of the mean acoustic similarity value, ranging from 10% to 200%.

## 4.3 Results

### *4.3.1 Unit-Level Analysis*

For 10 social units from the EC1 vocal clan (Units A, D, F, J, N, R, S, T, U, and V) and one social unit from the EC2 vocal clan (Unit P) genetic data were available for at least three individuals (mean: 8.4, max: 12), and at least 250 codas had been recorded (min: 296, mean: 579, max: 1443; Table 4.1). Four of these social units (Units A, F, N and V) had at least 25 four-click codas recorded (min: 54, max: 256; Table 4.1).

**Table 4.1.** Acoustic and genetic data and sample sizes for eastern Caribbean sperm whale social units, delineated as in Gero et al. (2014). Vocal clans are designated as in Gero et al. (2016). Only social units with at least 25 four-click codas recorded were included in the four-click coda analyses.

| | | | Unit members | | Coda recordings | |
|---|---|---|---|---|---|---|
| Vocal clan | Unit | mtDNA hap | known | with genetics | whole rep. | 4-click |
| EC1 | A | BB | 12 | 12 | 779 | 181 |
| | D | A | 7 | 4 | 336 | - |
| | F | A | 10 | 9 | 1443 | 256 |
| | J | A | 6 | 5 | 870 | - |
| | N | A | 9 | 8 | 296 | 74 |
| | R | A | 10 | 7 | 302 | - |
| | S | A | 4 | 3 | 464 | - |
| | T | A | 9 | 6 | 382 | - |
| | U | A | 4 | 4 | 737 | - |
| | V | A | 12 | 3 | 530 | 54 |
| EC2 | P | BB | 9 | 3 | 388 | - |

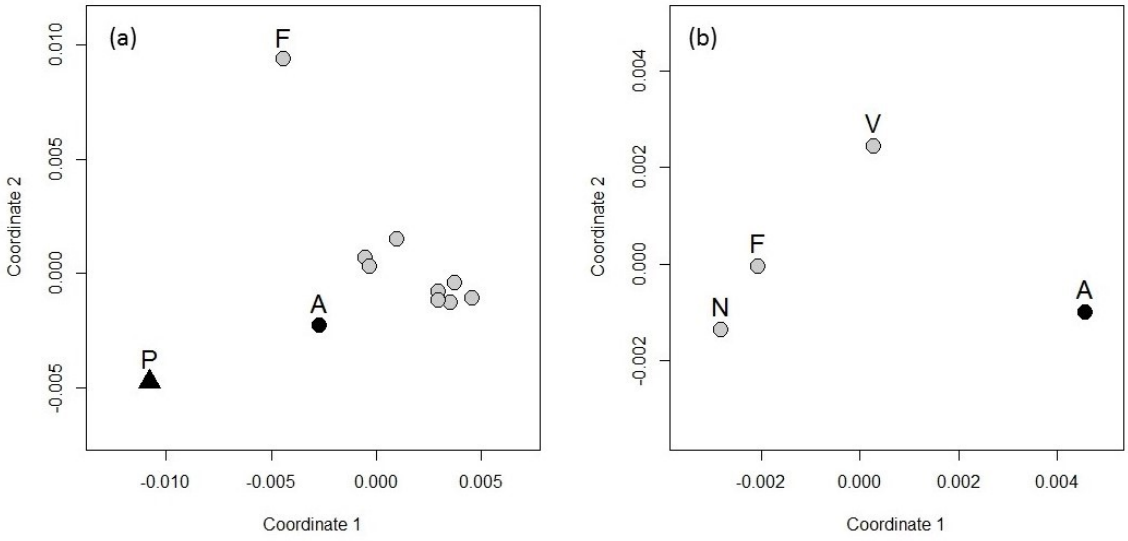
No correlations between acoustic similarity and genetic or social predictors were statistically significant at $P<0.05$, but for all three levels of analysis (whole repertoire, four-click coda repertoires, and clan membership), the correlation between acoustic similarity and mtDNA haplotype sharing was large and positive ($\geq 0.58$), with the lowest p-values of any predictor (Table 4.2). The single social unit from the EC2 vocal clan for

which genetic data were available (Unit P) had the rarer of the two mtDNA haplotypes observed in these social units, which was shared with only one other unit, Unit A. The contribution of Unit P to this positive correlation in the whole repertoire analysis is clear (Figure 4.1), but this correlation is large and positive even with this unit excluded (Table 4.2). Thus, Unit A is also relatively acoustically dissimilar from the other social units in its vocal clan, in both its whole repertoire and its four-click coda repertoire (Figure 4.1).

**Table 4.2.** Correlations between unit-level acoustic similarity and genetic and social predictors. Predictors included: mean pairwise relatedness (Mean rel), mitochondrial DNA haplotype sharing (mtDNA) and three indices of social association (Asso: definition of association/sampling period). The whole repertoire relationship was also tested after omitting the only unit from the EC2 vocal clan: Unit P (No EC2). Mantel tests were performed with 10,000 permutations.

| | | | | | No EC2 | |
|---|---|---|---|---|---|---|
| Acoustic Similarity | N | Predictor | Matrix corr. | p-value | Matrix corr. | p-value |
| Whole repertoire | 11 | Mean rel | -0.10 | 0.60 | -0.11 | 0.62 |
| | | mtDNA | 0.58 | 0.06 | 0.42 | 0.29 |
| | | Asso: clus/2hr | 0.07 | 0.51 | -0.03 | 0.88 |
| | | clus/yr | 0.01 | 0.85 | -0.15 | 0.22 |
| | | 2hr/day | 0.09 | 0.48 | -0.08 | 0.52 |
| 4-click codas | 4 | Mean rel | 0.14 | 0.89 | - | - |
| | | mtDNA | 0.78 | 0.25 | - | - |
| | | Asso: clus/2hr | 0.48 | 0.37 | - | - |
| | | clus/yr | 0.07 | 0.79 | - | - |
| | | 2hr/day | 0.33 | 0.54 | - | - |
| Clan | 11 | Mean rel | -0.03 | 0.99 | - | - |
| | | mtDNA | 0.58 | 0.18 | - | - |

**Figure 4.1.** Multidimensional scaling plots of acoustic dissimilarity among social units. Acoustic dissimilarity was assessed for (a) whole repertoires (all codas ≤ 10 clicks in length), and (b) four-click codas. Point shading indicates mitochondrial DNA haplotype (black: BB, grey: A), and shape indicates acoustic clan (circle: EC1, triangle: EC2).




*4.3.2 Individual-Level Analysis*

For analyses of whole repertoires, 20 individuals from five social units (Units A, F, J, S and U) had at least 25 codas recorded (min: 28, mean: 119, max: 300), with at least three individuals from each of these social units for intra-unit analyses. For 13 of these individuals, at least 75 codas were recorded, including at least three individuals from each of three of these social units (Units F, J and U) for intra-unit analyses. For analyses of 5R1 coda similarity, 13 individuals from five social units (Units A, F, J, S and U) had at least five 5R1 codas recorded (min: 7, mean: 35.2, max: 66), including least three individuals from each of three social units (Units A, S and U) for intra-unit analyses. For eight of these individuals at least 25 codas were recorded, but no intra-unit analyses could

**Table 4.3.** Correlation between acoustic similarity and genetic and social predictors across individual sperm whales. Predictors included: pairwise relatedness (Rel), mother-offspring relationships (MO), mitochondrial DNA haplotype sharing (mtDNA), fine social association (Asso: cluster in 2hr sampling period), coarse association (Asso: identified in the same 2hrs in a daily sampling period), and social unit membership (Unit). These relationships were also tested after omitting dependant calves. Only individuals with at least 25 codas analysed were included in this whole repertoire analysis, and only those with at least five 5R1 codas analysed were included in this 5R1 analysis. Mantel tests were performed with 10,000 permutations.

| | | | | | | No calves | | |
|---|---|---|---|---|---|---|---|---|
| Acoustic Measure | Unit | N | Predictor | Matrix corr. | p-value | N | Matrix corr. | p-value |
| Whole rep | All | 20 | Rel | -0.06 | 0.56 | 16 | -0.10 | 0.43 |
| | | | mtDNA | 0.10 | 0.52 | | 0.11 | 0.50 |
| | | | MO | -0.03 | 0.79 | | 0.00 | 0.77 |
| | | | Asso: clus/2hr | 0.06 | 0.30 | | 0.11 | 0.21 |
| | | | Asso: 2hr/day | 0.05 | 0.42 | | 0.04 | 0.56 |
| | | | Unit | 0.05 | 0.36 | | 0.06 | 0.42 |
| | A | 3 | Rel | 0.01 | 0.83 | | - | - |
| | | | Asso: clus/2hr | -0.03 | 0.83 | | - | - |
| | F | 6 | Rel | 0.29 | 0.31 | 5 | 0.18 | 0.77 |
| | | | Asso: clus/2hr | -0.34 | 0.19 | | -0.28 | 0.49 |
| | J | 4 | Rel | -0.42 | 0.38 | 3 | 0.92 | 0.51 |
| | | | Asso: clus/2hr | 0.13 | 0.61 | | -0.86 | 0.16 |
| | S | 3 | Rel | -0.59 | 0.49 | | - | - |
| | | | Asso: clus/2hr | -0.60 | 0.50 | | - | - |
| | U | 4 | Rel | -0.70 | 0.20 | 3 | -0.82 | 0.51 |
| | | | Asso: clus/2hr | 0.28 | 0.46 | | 0.99 | 0.16 |
| 5R1 | All | 13 | Rel | 0.01 | 0.95 | 11 | 0.09 | 0.54 |
| | | | mtDNA | 0.18 | 0.30 | | 0.15 | 0.50 |
| | | | MO | 0.03 | 0.70 | | 0.00 | 0.98 |
| | | | Asso: clus/2hr | 0.04 | 0.64 | | 0.00 | 0.95 |
| | | | Asso: 2hr/day | 0.04 | 0.60 | | 0.03 | 0.65 |
| | | | Unit | 0.05 | 0.51 | | 0.10 | 0.29 |
| | A | 3 | Rel | 0.56 | 0.16 | | - | - |
| | | | Asso: clus/2hr | 0.60 | 0.17 | | - | - |
| | S | 3 | Rel | -0.86 | 0.16 | | - | - |
| | | | Asso: clus/2hr | -0.85 | 0.16 | | - | - |
| | U | 3 | Rel | 0.11 | 0.84 | | - | - |
| | | | Asso: clus/2hr | -0.52 | 0.50 | | - | - |

be conducted in this case, because no social unit had at least three individuals with this minimum number or 5R1 codas.

Across all individuals and within social units there were no significant relationships between whole coda repertoire similarity or 5R1 coda similarity and any of the predictor variables that we examined (Table 4.3). These results were essentially unchanged when dependant calves were omitted (Table 4.3) or when stricter coda sample size requirements were used (Appendix B, Table B2).

Based on the power analysis, our ability to detect small effects of relatedness on acoustic similarity was relatively low. The acoustic similarity values for mother-offspring pairs had to be elevated by three times the mean value before the correlation was statistically significant at $P<0.05$ (Table 4.4). If acoustic similarity values for additional close relatives (all individuals with $r \geq 0.2$) were also elevated, this level of statistical significance was reached when the mean acoustic similarity value was added to the values for these individuals (Table 4.4).

**Table 4.4.** Power analysis for individual-level Mantel tests. Matrix correlations between pairwise genetic relatedness and whole repertoire acoustic similarity were tested for after modification of acoustic similarity values to either (1) known mother-offspring pairs or (2) all those with pairwise relatedness ≥ 0.2. Values were modified by adding a percentage of the mean acoustic similarity value.

| | Mothers-Offspring | | Relatedness ≥ 0.2 | |
|---|---|---|---|---|
| Add (% of mean) | Matrix corr. | p-value | Matrix corr. | p-value |
| unmodified | -0.06 | 0.56 | -0.06 | 0.56 |
| 10 | -0.05 | 0.63 | -0.03 | 0.74 |
| 50 | 0.00 | 0.99 | 0.07 | 0.47 |
| 100 | 0.05 | 0.57 | 0.19 | 0.05 |
| 200 | 0.15 | 0.10 | 0.38 | < 0.001 |
| 300 | 0.24 | 0.01 | - | - |
| 400 | 0.31 | < 0.001 | - | - |

*4.3.3 Relationships Between Vocal Clans*

The data were consistent with some close kin relationships between members of different vocal clans, and thus between individuals possessing fundamentally dissimilar coda repertoires. Each of the three genetically sampled individuals from the EC2 vocal clan had two potential second-degree relatives (half-sibling or grandparent-grandoffspring) that were members of the EC1 vocal clan (Table 4.5). These were cases for which half-sibling/grandparent-grandoffspring was the most likely option, based on likelihood ratios, and for which 'unrelated' was not a likely relationship at the 0.05 level of significance. The microsatellite data were also consistent with full-siblings in three of these cases, but in each case the mother of the proposed full-sibling was known and not common to the EC2 vocal clan member or the putative siblings differed in their mtDNA haplotype, excluding the possibility of full-siblingship. In no case was parent-offspring a likely relationship. Three of the potential second-degree relatives had a different mtDNA haplotype than the EC2 vocal clan members, while the remaining three had their haplotype in common with the EC2 vocal clan members (Table 4.5). Thus, these instances of close kin in different clans include paternal relatives, and may also include maternal relatives.

**Table 4.5.** Putative second-degree relatives across vocal clans.

| EC2 ind | Sex | mtDNA | EC1 ind | Unit | Mother | Sex | mtDNA | Relatedness |
|---|---|---|---|---|---|---|---|---|
| P4 | M | BB | Scar | F | Pinchy | M | A | 0.40 |
| | | | TBB | S | - | F | A | 0.13 |
| Prego/Pasta | F | BB | Tooth | T | - | F | A | 0.21 |
| | | | Fruit salad | A | - | F | BB | 0.24 |
| P9/calf | M | BB | Oryx | A | - | F | BB | 0.22 |
| | | | Snowman | A | Oryx | F | BB | 0.28 |

## 4.4 Discussion

### *4.4.1 Potential Functions of Coda Repertoires*

In this study, we did not find evidence of individual and social unit acoustic repertoires being influenced by either close kinship or social association. This is in contrast to studies across numerous species that have demonstrated convergence of calls of associated individuals (Tyack 2008), such as whistle convergence among allied male bottlenose dolphins (Smolker and Pepper 1999; Watwood, Tyack, and Wells 2004). Convergence of vocal repertoires may serve to signal group membership or to strengthen social bonds and promote group cohesion (Tyack 2008). Sperm whale coda repertoires likely function to socially delineate vocal clans (Gero et al. 2016; Rendell and Whitehead 2003), as well as perhaps to signal unit membership (Gero, Whitehead, and Rendell 2016), but we did not find that acoustic repertoires reflected social relationships at other levels of social structure. Thus, if the four-click coda types used by certain social units are unit identity signals, as suggested by Gero, Whitehead, and Rendell (2016), they appear not to carry additional information about kinship or social bonds, beyond encoding social unit membership.

In other cases, certain learned vocalizations may function as signals of individual identity, in which case selection should favour that they be unique, rather than conforming, as among bottlenose dolphins, which have individually distinctive whistles, called signature whistles (Tyack 1997). Antunes et al. (2011) and Gero, Whitehead, and Rendell (2016) suggested that signalling individual identity may be a function of the 5R1 coda type, which is a coda type with widespread use and individual variation. This coda

type, however, does not appear to carry information about kinship or social bonds. Among bottlenose dolphins, females' whistles were typically different from their mothers', while the signature whistles of males were more likely to resemble those of their mothers (Sayigh et al. 1995). Sayigh et al. (1995) proposed that this difference may be due to stronger pressure on females to maintain distinct signals, given their use of signature whistles as contact call with their calves and their frequent association with maternal kin. Additionally, there may be benefits to males if they clearly advertise their maternal kinship, for avoiding inbreeding or maintaining bonds with kin (Sayigh et al. 1995). Given that sperm whale social structure is characterized by female social philopatry and male dispersal, a similar pattern might be expected among sperm whale 5R1 codas. However, our small sample size (only one son-mother pair and two daughter-mother pairs with sufficient individual 5R1 data), did not allow us to test for sex-specific biases in vocal learning of the 5R1 coda.

### *4.4.2 Evidence for Vocal Transmission Among Broad Matrilines*

Current evidence strongly suggests that codas are socially learned, given that they are not accounted for by geography (Rendell and Whitehead 2003; Rendell et al. 2012), or, to the extent that it has been previously examined, genetic similarity (Rendell and Whitehead 2003; Rendell et al. 2012; Schulz et al. 2011). Additionally, differences between repertoires of adults and younger individuals are consistent with expectations if learning occurs (Gero, Whitehead, and Rendell 2016; Schulz et al. 2011). That coda repertoires did not correlate with genetic relatedness in the present study adds to this existing evidence that codas are socially learned rather than genetically determined.

As discussed by Rendell and Whitehead (2003), vocal clans in the Pacific are not matrilineally monophyletic; they contain individuals with multiple mtDNA haplotypes, some of which are shared between clans (Rendell and Whitehead 2003; Rendell et al. 2012), and the transfer of an individual between clans has been documented (Rendell and Whitehead 2003). Likewise, in our data, two haplotypes were detected in the EC1 vocal clan, one of which was shared with the EC2 vocal clan (Table 1). However, transfer of individuals between vocal clans appears to be rare, and correlations between mtDNA haplotype similarity and acoustic similarity, including clan membership, have been demonstrated in the Pacific Ocean (Whitehead et al. 1998; Rendell et al. 2012), and in the present study (Table 4.2). Though not statistically significant, at the unit level the correlations between mtDNA haplotype and all measures of repertoire similarity were large and positive (Table 4.2). At the individual level, the correlations between mtDNA haplotype and acoustic similarity measures were not as strong, but mtDNA haplotype sharing was still the factor with the largest effect size (Table 4.3). This suggests an element of maternal descent to vocal repertoires and clan membership.

Mitogenomic diversity is low among sperm whales (A. Alexander et al. 2013), such that haplotype sharing does not necessitate close maternal kinship, but we can still confidently designate individuals with different haplotypes as being from different matrilines. Thus, the unit from the EC2 vocal clan is not maternally related to most of the social units from the EC1 vocal clan. However, with only one social unit from the EC2 clan included in this analysis we cannot draw robust conclusions about the degree of mtDNA haplotype sharing and maternal kinship among vocal clans in the Atlantic Ocean, which appear to

differ from those in the Pacific Ocean, in terms of their degrees of repertoire similarity and sympatry (Gero et al. 2016).

That pairwise relatedness does not correlate with acoustic similarity suggests that vocal learning is not constrained to be from close family members. Rather, the correlation with mtDNA haplotype sharing suggests that the coda repertoires of social units are a product of vocal learning occurring more broadly, within large groups that contain distant maternal relatives. Presumably, these groups would be vocal clans. However, we are hesitant to conclude that finer kinship plays no role in acquiring vocal repertoires. We determined pairwise relatedness based on biparentally-inherited markers and thus cannot distinguish maternal relatedness from paternal relatedness, which we would not expect to correlate with vocal learning. Thus, in our analysis, paternal relatedness could mask or muddy trends between close maternal kinship and acoustic similarity. Additionally, as demonstrated by the power analysis, very strong effects, or moderate effects that affected a greater proportion of pairs of individuals, should have been detected, but our ability to detect subtler effects at the individual level was limited (Table 4.4).

Rendell et al. (2012) suggested a pattern of cultural transmission among sperm whales where coda repertoires are generally learned via vertical transmission from mothers to offspring, with an influence of oblique transmission from unit members other than an individual's mother. Our data do not provide evidence to support this hypothesized pattern of transmission, but, for the reasons discussed above, neither can we firmly reject it. Further, if coda repertoires are preferentially learned from mothers, other close maternal kin, or close associates, but are then horizontally transmitted more broadly among less closely-related members of social units or among social units in the same

vocal clan, this could conceal fine-scale patterns and result in the overall pattern we observed. Rendell et al. (2012) also hypothesized that horizontal transmission between vocal clans may occur through females occasionally transferring between clans, which, as discussed below, is consistent with our data.

### *4.4.3 Genetic Flow Between Vocal Clans*

Prior to the present study, genetic similarity based on biparentally-inherited markers had been examined in relation to vocal clan membership in only a single preliminary analysis based on five microsatellite markers (Whitehead 2003, p. 300). As in the present study, Whitehead (2003) found no difference in nuclear genotypes between clans. Based on the contrast of significant differentiation in mtDNA sequences between oceans versus relative homogeny of microsatellite alleles, it appears that males disperse and mate between ocean basins more than females (Lyrholm et al. 1999). Contrasting patterns between mtDNA and microsatellite-based relatedness suggest the same may be true between clans – that males mate between clans while females more typically remain within their natal clan.

As further support of male mating across clans, we detected paternal relatives between vocal clans. For three of the potential second-degree relatives between clans, relatedness must be paternal, because these individuals have a different mtDNA haplotype than the EC2 vocal clan members (Table 4.5). Thus, the pairs appear to be either paternal half-siblings or grandparent-grandoffspring pairs. The latter would require one of two scenarios: either that one individual was a mature male who grandfathered the other individual, or that one individual was the mother of a son who later fathered the other

individual. Given that none of the individuals included in this analysis were mature males (based on observations of size (Best, Canham, and Macleod 1984; Best 1979)), we can exclude the first scenario. The likelihood of the second scenario is less clear, given the relatively poor understanding of movement and mating patterns of male sperm whales; as discussed above, juvenile males disperse from their natal units, likely mating across ocean basins at least occasionally (Lyrholm et al. 1999), but there is also evidence that males in some regions return to their natal region to mate (Mesnick et al. 2011). For one pair of putative second-degree paternal relatives, however, the individuals were both juvenile males that appear to be of similar ages; for overlapping periods during which these individuals were observed (ID: Scar, observed 2005-2011; ID: P4, observed 2008-2012), both were weaned but had not yet dispersed from their respective social units. This suggests that the pair are paternal half-siblings, perhaps fathered in the same year. For the other two putative second-degree relatives with different mtDNA haplotypes, one or both individuals were females of unknown age, so either paternal grandmother-grandoffspring or half-sibling relationships are possible. Potentially, some pairs assigned as second-degree relatives based on comparisons of likelihood ratios may, in reality, be more distant relatives, because no relationships intermediate to second-degree relationships and 'unrelated' were assessed.

For other putative second-degree relatives between vocal clans, specifically between Units A and P, which have a shared mtDNA haplotype (Table 4.5), maternal kinship cannot be excluded as a possibility. Interestingly, Unit A is also the social unit with the repertoire most like Unit P, though Unit A is still more acoustically similar to the rest of its vocal clan, EC1, than to Unit P (Figure 4.1). Gero et al. (2016) suggested that the

social units in the study area that are members of the EC2 vocal clan may have recently immigrated from elsewhere in the Atlantic. If this is the case, might Unit A also have once been a part of the EC2 vocal clan that migrated into the area and gradually picked up the local dialect? While transfers of social units between vocal clans have not been documented, the patterns of mtDNA haplotype sharing observed among vocal clans suggest that such transfers may occur, at least occasionally.

### *4.4.4 Can Coda Repertoire Variation Explain Kin-Selection?*

Considering that social associations between units are not primarily driven by kinship (Chapter 2), and that mtDNA haplotype sharing does not necessarily indicate close kinship, it is unlikely that more similar repertoires between units with the same haplotype is a kin-recognition signal enabling kin-selection. This is further supported by the lack of correlation between mean pairwise relatedness (which is a finer measure of kinship than mtDNA haplotype sharing) and acoustic similarity (Table 4.2). As discussed above, paternal relatedness and low power could prevent detection of a correlation between relatedness and repertoire similarity. It is also possible that while the coda types we examined in detail (four-click codas and 5R1 codas) seemed to be likely candidates as identity signals (based on Gero, Whitehead, and Rendell 2016), they may not be the codas used for kin-recognition. Among killer whales, for example, similarities of different call types are not all correlated (Filatova, Burdin, and Hoyt 2013), and in a study of Northern Resident killer whales variation in only one out of three call types assessed correlated with kinship (Deecke et al. 2010).

Nevertheless, based on the current data, kin-biased patterns of association (Chapter 2) and alloparental care (Chapter 3) do not appear to operate by kin-recognition using vocal signals carrying kinship information. While the coda repertoires of individuals and of social units vary enough to carry identity information (Gero, Whitehead, and Rendell 2016), I did not detect a direct relationship between this variation and kinship (Chapter 4). However, there are other ways that kin-selection could be mediated by vocal identity signals. For example, sperm whales may be able to recognize each by differences in these vocalizations and have knowledge of their actual maternal relationships to close relatives, such as half-siblings. Another plausible alternative mechanism is familiarity. As discussed by Pfefferle et al. (2016), in species with extensive and long-lasting maternal care, familiarity is closely tied to maternal kinship. Among African elephants (*Loxodonta africana*), for example, known siblings associate with each other more than with distantly-related family members, likely because the older sibling maintains a bond with her mother even after the new calf's birth (Lee 1987). African elephants' ability to distinguish between and react differently to the contact calls of family and other associates may also be based in differing degrees of familiarity (McComb et al. 2000). Similarly, familiarity likely explains maternal kin recognition reported among non-human primates, such as barbary macaques (*Macaca sylvanus*) (Rendall, Rodman, and Emond 1996). The matrilineally-based social structure of sperm whales (Chapter 2) presumably involves offspring, particularly daughters, maintaining lasting bonds with their mothers, which would lead to familiarity between siblings, perhaps providing a basis and opportunity for siblings to form social bonds. Familiarity, however, could also operate

without the ability to recognize specific individuals, being instead based on categories of familiarity (McComb et al. 2000).

### 4.5 Conclusion

Beyond potentially encoding vocal clan and social unit membership (Gero, Whitehead, and Rendell 2016), individual and social unit variation in coda repertoires does not discernably relate to close kinship or social bonds. As such, kin-selection among sperm whales may be driven by familiarity with distinct vocal signals of individuals or social units, but the potential identity signals do not appear to intrinsically encode kinship information. Our results also suggest that vocal learning occurs broadly within clans, rather than preferentially from close kin or close social associates, or that any signal from biases in vocal learning at lower levels of social structure is diffused by clan-level processes. Vocal learning has been demonstrated in several mammal species (Tyack 2008), but research projects with sufficient data to assess function and transmission of learned vocalizations are rare among wild mammals. Through this study, we add to our understanding of cultural transmission among mammals, and how variation in learned vocalizations relates to patterns of genetic relatedness.

# CHAPTER 5

# DISCUSSION

## 5.1 Research Findings and Implications

My results reveal sperm whale society that is matrilineally-based, with maternal kinship influencing social structure and cooperative behaviours, but not strictly so (Chapters 2 and 3). Rather, it is nuanced and multifaceted, and resembles other complex cooperative societies that include both kin and kith, such as among elephants and humans. In particular, kinship appears to have little bearing on association between social units (Chapter 2), supporting the hypothesis that higher levels of sperm whale social structure, such as vocal clans, are based upon culture rather than kinship (Cantor et al. 2015; Rendell and Whitehead 2003). Likewise, repertoire variation that reflects these higher levels of social structure does not correlate with kinship (Chapter 4). Below I expand on and synthesize certain topics from the discussions in Chapters 2 through 4, and consider how my findings inform broader ideas and questions.

### *5.1.1 Modularity and Variation in Social and Genetic Structure*

Sperm whale social units are generally considered to be constant companions, and composed of maternal kin, but as more fine-scale data are obtained, we can begin to examine these generalities in a more nuanced way. For example, in Chapter 2, I describe intra-unit social modularity in Unit A that correlates with kinship. Unit A was composed of two families of close maternal kin (Figure 2.3), and social modularity correlated with the boundaries of these maternal families (Table 2.5). The fine-scale social data of this study suggest that these families are not 'constant companions' in the way that unit

members are typically assumed to be, as they were frequently seen apart (Table 2.8). Additionally, I observed that these two maternal families restricted the provision of allocare to members of their own family (Chapter 3). It is unclear how prevalent this type of kin-based partitioning of cooperation is within social units. Unit A was the largest social unit examined in this study, so it may be that such modularity is most typical within large social units, or it may be harder to detect in smaller social units. This is supported by the findings of Christal and Whitehead (2001), who observed strong evidence of relationship heterogeneity within only the two largest social units of 20 that they studied.

Social and ecological context, including resource availability, predation risk, unit size, and unit composition, likely affects the pressures on social units and individuals. Thus, changes in socio-ecological context should affect the costs and benefits of restricting cooperation to strictly relatives, or extending it more broadly. Between Units F and U, I observed a gradual increase in association across years, which qualitatively appeared to correspond with the loss of adult unit members and the births of calves (Table 2.7). The adult unit members lost from Unit F were close (1º or 2º) relatives of individuals that remained in the unit. So perhaps, a decrease in the availability of close relatives pressured individuals to define 'kin' more inclusively when determining whom to help and associate with. There were no close (1º or 2º) kin relationships between living members of Units F and U when their merger was completed, but the average relatedness between the units was the highest of any pair in the study, suggesting some kinship between the units. Conversely, in Unit A, inter-annual variation in the association strength between the two strict matrilines did not correlate will with changes in unit composition (Table

2.8). Rather, shifts in ecological factors, such as resource availability, may more strongly affect the relative costs and benefits of this unit spending time apart or all together. However, regardless of the year, members of Unit A consistently restricted allocare to those unit members who were close maternal kin. This suggests that different levels of cooperation may have different thresholds of social or ecological conditions before they will be extended beyond close kin.

### *5.1.2 Using Social Data to Infer Maternity*

In my thesis I explicitly examined the relatively untested assumption that mothers can be identified as the adult who spends the most time with a given calf. This assumption is not only made among sperm whales (Whitehead 1996; Gordon 1987), but also other species of cetaceans (Grellier et al. 2003; Mahaffy et al. 2015), and in studies of other wild mammals (e.g. Mabille and Berteaux 2014). For non-social species where mothers and their offspring are isolated from conspecifics, it seems unlikely that this assumption would be violated. But in social species, such as many odontocetes, this is an assumption that should be made with caution, particularly if the extent of allocare for that species is substantial or unknown. In my findings, while the genetically-identified mother typically matched expectations based on behavioural observations, there were cases of incongruence or ambiguity (Chapter 3). Similarly, this assumption was violated in another social odontocete, the long-finned pilot whale. In a study characterizing calf care in this species, several individuals who would have been assumed to be the mother of a calf based on social association rates were determined to instead be males (Augusto, Frasier, and Whitehead 2017).

In the absence of genetic data, and when the prevalence of allocare is high or unknown, the following insights can be applied to minimize the risk of incorrect maternity assignment based on social data. First, as discussed in Chapter 3, the social behaviour with the greatest fitness cost is likely to be the most reliable indicator of maternity. Additionally, examining association at two sampling intervals, or examining multiple measures of calf care, can highlight cases where there is not an uncontested primary caregiver. For example, one individual may have the highest association rate with the calf when this rate is calculated using one sampling interval, but not when it is calculated with another sampling interval (e.g. calf IDs: Soursop and SLBC, Table 3.1). However, even with these consideration, I identified cases of incongruence between social and genetic indicators of maternity. Ultimately, the above-mentioned examples of assumption violations demonstrate that researchers should be tentative with maternity assignments based solely on social data, particularly when allocare may be common.

### *5.1.3 A Synergy of Mechanisms to Explain Cooperation*

While my thesis identified significant correlations between kinship and social behaviours, including association and allocare, and a general correspondence between mtDNA haplotype and vocal repertoires, I also observed much variation that was not accounted for by kinship. Thus, I propose that kin-selection is likely important to the evolution and maintenance of sperm whales' cooperative and complex social structure, but that it is not acting in isolation.

If cooperation, driven by the benefits of kin-selection, becomes established in a group of relatives, kin-selection can then work synergistically with other drivers of cooperation,

such as group augmentation (Kokko, Johnstone, and Clutton-Brock 2001). This can result in high-levels of cooperation among kin that may be only loosely correlated with pairwise relatedness values within the kin group (Kokko, Johnstone, and Clutton-Brock 2001), which aligns with intra-unit patterns observed in this thesis. Other potential drivers that may play a role, including reciprocal altruism, generalized reciprocity and gaining maternal experience, are discussed in proceeding chapters. Obstacles to further disentangling the influence of these drivers, and potential next steps are discussed in section 5.3.

Almost certainly, culture also plays a substantial role in structuring cooperation, particularly moderating interactions between units and delineating clans. As discussed by Alvard (2011), kinship cannot create large networks as culture can – after networks grow to a certain size, unless individuals have many close relatives (as in social insects), kinship and its associated benefits become too diluted to maintain cooperation within all members of the network. With this in consideration, it is perhaps unsurprising that the higher levels of social structure among sperm whales cannot be explained by relatedness. However, the general correlation between mtDNA haplotypes and coda repertoires (Table 4.2), which are almost certainly culturally transmitted, suggests that culture among sperm whales is in part structured by maternal lineages.

### 5.2 Research Contributions

The study of the evolution of cooperation and social structure in animals is relevant to fields as diverse as behavioural ecology, cognitive psychology, sociology and anthropology. As such, I believe the research presented in this thesis will be of interest to

a wide audience of academics, as well as those members of the general public who are curious about the daily lives and family dynamics of these deep-sea denizens. As well as contributing to the scientific community's breadth of knowledge about drivers of cooperation and complex societies, this research addresses outstanding questions about the role of kinship in the society of this particular species. As such, my findings enrich the literature on sperm whale social structure and behaviour. Additionally, this thesis improves our understanding of a population under critical decline (Gero and Whitehead 2016). Cooperation and social living are fundamental components of the lives of female sperm whales and their young. As such, better understanding kin selection and other mechanisms that drive these components can allow us to better predict the consequences of the loss of individuals from this population. For example, if this population decline reduces the number of close kin that individuals have, this will likely impact aspects of social structure and allocare, and by extension reproductive rates and population resilience.

## 5. 3 Challenges and Future Directions

### *5.3.1 Challenges to This Research*

Studying kinship and the social dynamics of long-lived, far-ranging individuals that spend the majority of their time deep below the surface of the ocean has many intrinsic challenges. In addition to the challenge of locating and tracking sperm whales, much about social behaviour must be inferred or approximated based on what can be observed of the whales at the surface. Longitudinal studies are required to delineate the social units of sperm whales, and kin relationships are even harder to determine socially. Not only

can social data sometimes lead to incorrect assignment of maternity (Chapter 3), but female sperm whales can live into their eighties (Whitehead 2003), such that overlapping generations of adults of unknown relationship are to be expected, meaning that even a decade long research project falls far short of being able to construct pedigrees socially.

To supplement social observations, genetic data can be used to estimate kin relationships, but this can be complicated by issues of DNA quality and quantity if non-invasive sampling is used. Skin that is naturally sloughed by sperm whales can often be found and collected in tropical waters, but it cannot always be linked to specific individuals (Whitehead et al. 1990), and commonly provides DNA that is highly degraded (Konrad et al. 2017). Thus, genotyping success can be low, and extra care must be taken to minimize errors, particularly errors associated with allelic dropout (as described in Chapter 2).

Because of challenges such as these, the research presented in this thesis has few parallels among cetaceans (Connor and Krützen 2015; Ford, Ellis, and Balcomb 2000) and is unique among sperm whales. Thus, my findings represent a substantial contribution to the literature on the role of kinship in animal cooperation and social structure. Additional challenges, outstanding questions, and avenues for further inquiry are described below.

### *5.3.2 Matrilineality*

Low mtDNA haplotype diversity in the study population restricted my ability to distinguish between matrilines and thus to clarify patterns of relatedness within and between social units, beyond first- and second-degree relatives. However, diversity is low across the sperm whale mitogenome (A. Alexander et al. 2016; A. Alexander et al. 2013), and the most common haplotype we observed (haplotype A) only splits to a limited

extent when sequenced to 619 bp (only about 4% of the samples, based on personal communication with A. Alexander). Thus, it is likely that sequencing substantially more of the mitogenome would be required to differentiate amongst matrilines for the units we studied. Another approach would be to model expected patterns of relatedness for given matrilineal systems, and test which are most consistent with the patterns observed here. However, such models are not likely to be particularly informative or reliable until good estimates of age-specific mortality and fecundity are determined.

*5.3.3 Paternal Relatedness*

I identified evidence of paternal relatedness between social units (Chapter 2) and between clans (Chapter 3), and previous studies have noted similar evidence within sperm whale groups off mainland Ecuador (Richard et al. 1996) and between social units off the Galapagos Islands (Christal 1998). The implications of such paternal relatedness, however, remains in question, as its pervasiveness has never been thoroughly investigated. For example, if paternal relatedness is substantial within or among social units, it could influence allocare and other cooperative behaviours through kin selection. If the process driving kin selection relates to overall relatedness within social units, it would be reinforced by the presence of paternal relatives within social units. Our understanding of patterns of male movement and the distribution of male mating success is also poorly developed, but can be improved by genetic studies. Much as ocean-wide patterns of nuclear and mitochondrial genetics have revealed broad scale movement and mating patterns of males across ocean basins (Engelhaupt et al. 2009), fine-scale studies of paternal relatedness within groups and units could reveal finer details of male movement and mating success. Investigation of paternal relatedness is likely to be

particularly informative when maternal relationships are known, allowing identification of the paternal contribution to genotypes without the need for genetic data from potential fathers. As such, the social units from the eastern Caribbean population, for which I have determined maternal relationships, are excellent candidates for such study.

### *5.3.4 Evidence for Reciprocity and Group Augmentation*

In the discussion sections of proceeding chapters I have considered alternative mechanisms that are consistent with my findings and that may explain variation in association and cooperation that is not explained by kinship. Here, I discuss further the current evidence and what would be required to test rigorously particular candidate mechanisms, namely reciprocity and group augmentation.

To demonstrate whether reciprocal altruism is at work, Clutton-Brock (2009) identified several criteria: (1) that the same individuals assist each other repeatedly, (2) that the frequencies of giving and receiving help are proportional, (3) that helping has a temporary fitness cost to the helper and a fitness benefit to individual being helped, and (4) that the individuals involved are not close relatives or prospective mates. We have identified that the fourth criterion is met for at least some associating sperm whales, and the longevity of individuals and the stability of social units provides ample opportunity for the first criterion to be met. However, explicit analyses, quantifying the rates of cooperative behaviours between individuals, are required to properly assess the validity of the first and second criteria. Demonstrating fitness costs and benefits of helping behaviours is even more challenging (Clutton-Brock 2009). Taborsky et al. (2016), argue that a simpler kind of reciprocity, generalized reciprocity, should also be considered,

where individuals 'help anyone if helped by someone', without needing to recognize individuals. Continued long-term field studies of social behaviour will allow for more observations of opportunities for reciprocity. Characterizing the contexts in which individuals do and do not reciprocate will enable better evaluation of whether reciprocal altruism or generalized reciprocity are important drivers, and their level of influence, relative to kin selection.

Another potential mechanism, group augmentation can operate when members of a social group are valuable, hard to replace, and offspring remain in their social group (Kingma et al. 2014; Kokko, Johnstone, and Clutton-Brock 2001). The third criteria is generally true among female sperm whales and even males remain in their social unit into their teens and provide allocare in the form of babysitting (Gero, Gordon, and Whitehead 2013). Also, given the slow-reproductive rate of sperm whales, unit members are not readily replaceable. As described in Chapter 2, the gradual merger of Units F and U may hint at the value of unit members, because it occurred in correspondence with decreases in unit size and changes in unit composition (Table 2.7). However, to test the validity of group augmentation as a driver, future studies should explicitly examine the value of group members, such as by testing whether units with more members are quantitatively more successful (e.g. by determining per-capita reproductive success, or mortality).

Further study of the function of codas is also likely to help parse out which drivers moderate cooperation and social association. Based on the findings of Chapter 3, it seems unlikely that coda repertoires in and of themselves carry kinship information, though past research has demonstrated that they vary in such a way that individuals and units can be distinguished (Gero, Whitehead, and Rendell 2016). If coda repertoires are indeed used

as signals of individual identity, this would allow for reciprocal altruism between individuals who recognize each other as past cooperative partners. Likewise, vocal signals of unit identity could facilitate reciprocal altruism between units, or vocal signals of clan identity could facilitate generalized reciprocity among units. Vocal signals of unit membership could also be important for generalized reciprocity and group augmentation, as these mechanisms would be aided by the ability to clearly distinguish between unit members and outsiders.

### *5.3.5 Geographic and Cultural Variation*

Differences in social behaviour have been described between regions and among clans (Whitehead et al. 2012; Cantor and Whitehead 2015). It is likely that such differences also extend to the relationship between kinship and social behaviour. Therefore, I anticipate that examining this relationship more broadly, both geographically and culturally will be fruitful.

The current data suggest that the degree to which social units are matrilineally-based differs between oceans (Whitehead et al. 2012). I observed a greater degree of relatedness within the eastern Caribbean social units in this study than has been reported in the Pacific, where multiple mtDNA haplotypes are found within single units (Mesnick 2001; Christal 1998). As in my findings, however, a study of Pacific sperm whales found no mother-offspring relationships between social units (Christal 1998), while a study in the Gulf of Mexico identified a pair of likely first-order relatives did not associate at all during the period they were tracked, for the better part of a year (Ortega-Ortiz et al.

2012). This suggests that regional variation in social unit matrilineality is not exhaustively accounted for by a Pacific-Atlantic divide.

The findings of this thesis also suggest that there is geographical variation in the degree to which kinship influences social dynamics within and between social units. While I found significant correlations between relatedness and association within units (Tables 2.2 and 2.4), a study of two units in the Eastern Tropical Pacific found no such relationship (Christal 1998), nor did a study of 23 satellite-tagged sperm whales in the Gulf of Mexico (Ortega-Ortiz et al. 2012). Such differences may be, in part, due to differences in sampling or other aspects of methodology (e.g. the social units in the Gulf of Mexico, were sparsely sampled, with few close relatives in the analysis). Alternatively, these differences may represent true variation among populations or clans. Similarly, in this thesis, I described the merger of two highly related social units (Chapter 2), while in the Eastern Tropical Pacific, two individuals were observed to transfer into a social unit (Christal, Whitehead, and Lettevall 1998) in which they had not close relatives (Christal 1998). What we would expect to observe if mergers of units and transfers of unit membership are based on kinship more so in the Atlantic than the Pacific is, indeed, matched by current evidence of stronger matrilineality in social units in the Atlantic than in the Pacific. This, in turn may be a consequence of differences in predation pressure or whaling histories between the oceans (Whitehead et al. 2012).

Evidence also suggests that patterns of calf care differ regionally and between cultural clans (Gero et al. 2009; Cantor and Whitehead 2015). Thus, our understanding of allocare among sperm whales will likely be enriched if or when adequate data is collected from social units in different clans or regions that allow analyses similar to those in Chapter 3

to be repeated. Until such a time, the findings presented in this thesis represent the most thorough description of kin selection's contribution to allocare among sperm whales, but it is unknown how universal the patterns described here are.

### 5.4 Closing Remarks

The findings presented in this thesis paint a picture of sperm whale family life; and it is a life where families are close knit, where older sisters are trusted as babysitters, and where friends reconnect with one another on a regular basis. However, these friends and families live in a neighbourhood that is far from peaceful, with increasing pressures from ship traffic and underwater noise, and with risks of entanglement in fishing gear (Gero and Whitehead 2016).

In light of this, understanding the family ties of these whales is important. When a daughter spends years of her life with a rope tangled around her tail, struggling to survive, it doesn't just affect that one whale – it affects her mother, her babysitters, and her extended relatives. This is not a fabricated example, but a situation that I watched unfold over the field seasons I spent in Dominica.

So, beyond the scientific contribution of my thesis, I hope that this research helps us see these whales as individuals, that, like you or I, are part of a family and a community. And I hope that others will see value in taking the time to get to know these sperm whale families, and to be better neighbours to them, so that we don't accidentally disable their daughters and burden their societies.

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# APPENDIX A

## Supplementary material for Chapter 2

**Table A1.** Reasons for rejection of microsatellite loci that were excluded from analysis.

| Locus | Rejection Reason | Reference |
|---|---|---|
| EV14Pm | Amplified poorly | Valsecchi & Amos (1996) Mol Ecol 5:151-156 |
| FCB10 | Amplified poorly | Buchanan et al. (1996) Mol Ecol 5:571-575 |
| FCB4 | Amplified poorly | Buchanan et al. (1996) Mol Ecol 5:571-575 |
| FCB5 | Amplified poorly | Buchanan et al. (1996) Mol Ecol 5:571-575 |
| FCB6 | Amplified poorly | Buchanan et al. (1996) Mol Ecol 5:571-575 |
| GATA028 | Amplified poorly | Palsboll et al. (1997) Mol Ecol 6:893-895 |
| GATA098 | Failed to amplify | Palsboll et al. (1997) Mol Ecol 6:893-895 |
| GT023 | Amplified poorly | Berube et al. (2000) Mol Ecol 9:2181-2183 |
| IGF1 | Unreliable genotyping | Barendse et al. (1994) Nat Genet 6:227-235 |
| RW31 | Amplified poorly | Waldick et al. (1999) Mol Ecol 8:1763-1765 |
| RW48 | Amplified poorly | Waldick et al. (1999) Mol Ecol 8:1763-1765 |
| TEXVET19 | Unreliable genotyping | Rooney et al. (1999) J Heredity 90:228-231 |
| TR3A1 | Amplified poorly | Frasier et al. (2006) Mol Ecol Notes 6:1025-1029 |
| TR3F2 | Failed to amplify correct fragment | Frasier et al. (2006) Mol Ecol Notes 6:1025-1029 |
| TR3F4 | Amplified poorly | Frasier et al. (2006) Mol Ecol Notes 6:1025-1029 |

**Table A2.** Locus-specific microsatellite PCR protocols and results. For the biphasic protocol, initial annealing temperatures for the first phase started 10˚C above $T_a$ and dropped by 0.5°C with each cycle, for 20 cycles, followed by 10 cycles at the final $T_a$, and the second phase used same $T_a$ and 30 cycles. Final elongation temperature was either (A) 60˚C for 45 minutes or (B) 72˚C for 10 minutes. PCR product was diluted, in distilled water, according to dilution ratio, prior to capillary electrophoresis.

| | | | | | | | Protocol | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Locus | Na | Ho | N | Allele range (bp) | Type | Reference | $T_a$ (˚C) | Cycles | Biphasic? | Final Step | Dil. Ratio |
| D08 | 6 | 0.716 | 95 | 80-102 | Di | Shinohara et al. (1997) Mol Ecol 6:695-696 | 55 | 30 | | A | |
| D22 | 6 | 0.684 | 95 | 107-117 | Di | Shinohara et al. (1997) Mol Ecol 6:695-696 | 55 | 30 | | A | |
| EV104Mn | 5 | 0.653 | 95 | 152-160 | Di | Valsecchi & Amos (1996) Mol Ecol 5:151-156 | 55 | 30 | | B | |
| EV1Pm | 11 | 0.621 | 95 | 109-141 | Di | Valsecchi & Amos (1996) Mol Ecol 5:151-156 | 58 | 30 | | B | |
| EV5Pm | 9 | 0.691 | 94 | 146-168 | Di | Valsecchi & Amos (1996) Mol Ecol 5:151-156 | 60 | 32 | | B | |
| EV94Mn | 12 | 0.779 | 95 | 195-223 | Di | Valsecchi & Amos (1996) Mol Ecol 5:151-156 | 55 | 32 | | B | |
| FCB1 | 10 | 0.916 | 95 | 117-137 | Di | Buchanan et al. (1996) Mol Ecol 5:571-575 | 55 | 30 | Y | B | 1:9 |
| FCB14 | 12 | 0.779 | 95 | 279-311 | Di | Buchanan et al. (1996) Mol Ecol 5:571-575 | 55 | 39 | | B | |
| FCB17 | 17 | 0.926 | 95 | 135-183 | Di | Buchanan et al. (1996) Mol Ecol 5:571-575 | 55 | 35 | | B | |
| FCB3 | 11 | 0.789 | 95 | 134-154 | Di | Buchanan et al. (1996) Mol Ecol 5:571-575 | 55 | 37 | | B | |
| GATA417 | 3 | 0.516 | 93 | 169-185 | Tetra | Palsboll et al. (1997) Mol Ecol 6:893-895 | 55 | 30 | | B | |
| MK6 | 7 | 0.625 | 88 | 144-166 | Di | Krützen et al. (2001) Mol Ecol Notes 1:170-172 | 60 | 37 | | B | |
| RW34 | 13 | 0.916 | 95 | 84-110 | Di | Waldick et al. (1999) Mol Ecol 8:1763-1765 | 50 | 32 | | A | |
| SW10 | 11 | 0.853 | 95 | 136-158 | Di | Richard et al. (1996) Mol Ecol 5:313-315 | 60 | 30 | Y | B | 1:9 |
| SW13 | 10 | 0.895 | 95 | 131-171 | Di | Richard et al. (1996) Mol Ecol 5:313-315 | 50 | 30 | | A | |
| SW2 | 6 | 0.553 | 94 | 62-76 | Di | Richard et al. (1996) Mol Ecol 5:313-315 | 55 | 37 | | A | 1:24 |
| TEXVET5 | 11 | 0.809 | 94 | 192-214 | Di | Rooney et al. (1999) J Heredity 90:228-231 | 55 | 30 | Y | B; A | 1:1 |
| TR3G2 | 7 | 0.789 | 95 | 159-183 | Tetra | Frasier et al. (2006) Mol Ecol Notes 6:1025-1029 | 55 | 30 | | A | |
| Mean | 9.3 | 0.75 | 94.3 | | | | | | | | |

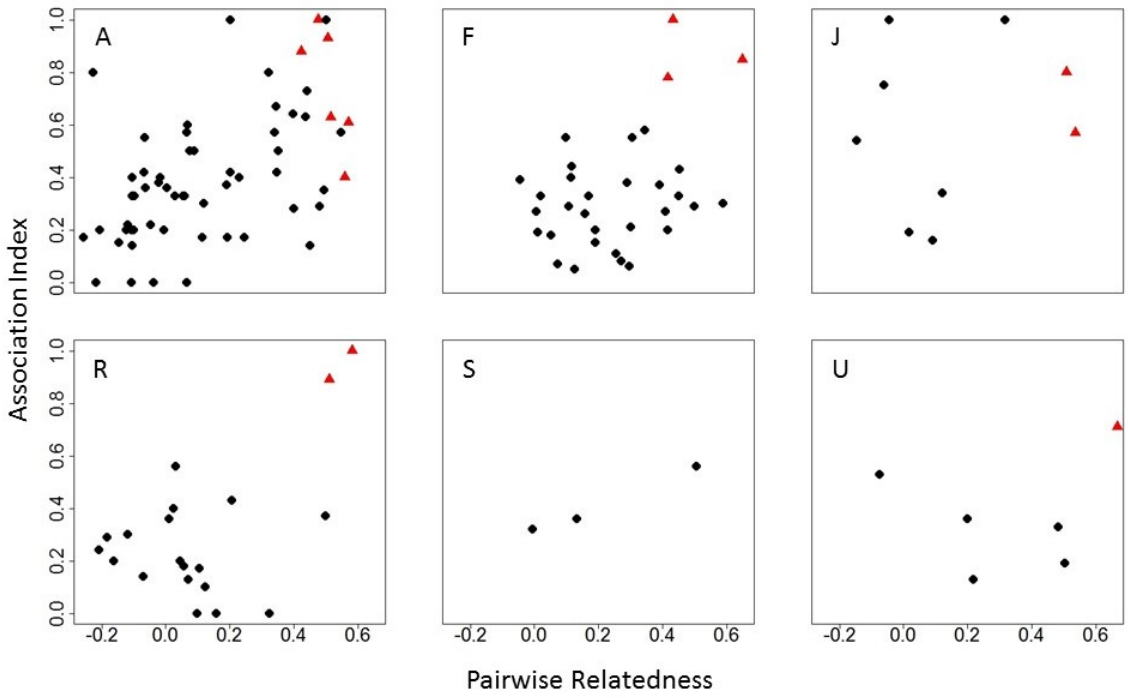


**Figure A1.** Intra-unit social association preferences predicted by pairwise relatedness. Association was defined as identification in the same cluster in a day, using 'both identified' to calculate the association index. Relatedness values were calculated using Wang's (2002) estimator. Mother-dependant calf pairs are indicated by red triangles. Letters denote social unit.

## APPENDIX B

### Supplementary material for Chapter 4

**Table B1.** Recording types across years, and the number of codas from recorded (N) that were used in this study. The number in brackets denotes only those codas that were assigned to individuals used in this study.

| Year | N | | Recording Type |
|---|---|---|---|
| 2005 | 420 | (356) | Towed |
| 2007 | 40 | (40) | Towed |
| 2008 | 1050 | (245) | Towed |
| 2009 | 304 | (190) | Towed |
| 2010 | 2574 | (716) | Towed |
| 2011 | 116 | (0) | Towed |
| 2014 | 397 | (225) | Dtag |
| 2015 | 1489 | (552) | Dtag |
| 2016 | 137 | (48) | Dtag |

**Table B2.** Correlation between acoustic similarity and genetic and social predictors across individual sperm whales, using stricter inclusion criteria. These relationships were also tested after omitting dependant calves. Predictors included: pairwise relatedness (Rel), mother-offspring relationships (MO), mitochondrial DNA haplotype sharing (mtDNA), fine social association (Asso: cluster in 2hr sampling period), coarse association (Asso: identified in the same 2hrs in a daily sampling period), and social unit membership (Unit). Only individuals with at least 75 codas analysed were included in this whole repertoire analysis, and only those with at least 25 codas analysed of the 5R1 type included in this 5R1 analysis. Mantel tests were performed with 10,000 permutations. Mantel tests were performed with 10,000 permutations.

| | | | | | | No calves | | |
|---|---|---|---|---|---|---|---|---|
| Acoustic Measure | Unit | N | Predictor | Matrix corr. | p-value | N | Matrix corr. | p-value |
| Whole rep | All | 13 | Rel | -0.11 | 0.50 | 11 | -0.10 | 0.63 |
| | | | mtDNA | -0.02 | 0.92 | | 0.00 | 0.96 |
| | | | MO | -0.08 | 0.49 | | -0.05 | 0.84 |
| | | | Asso: clus/2hr | -0.05 | 0.75 | | -0.16 | 0.21 |
| | | | Asso: 2hr/day | -0.07 | 0.58 | | -0.16 | 0.27 |
| | | | Unit | -0.04 | 0.76 | | -0.16 | 0.20 |
| | F | 4 | Rel | 0.87 | 0.29 | | - | - |
| | | | Asso: clus/2hr | 0.82 | 0.05 | | - | - |
| | J | 4 | Rel | -0.42 | 0.38 | 3 | 0.92 | 0.51 |
| | | | Asso: clus/2hr | 0.13 | 0.61 | | -0.86 | 0.16 |
| | U | 3 | Rel | -0.72 | 0.17 | | - | - |
| | | | Asso: clus/2hr | -0.67 | 0.16 | | - | - |
| 5R1 | All | 8 | Rel | 0.25 | 0.13 | | | |
| | | | mtDNA | 0.13 | 0.58 | | | |
| | | | Asso (fine) | -0.17 | 0.33 | | | |
| | | | Asso (coarse) | -0.12 | 0.37 | | | |
| | | | Unit | -0.03 | 0.95 | | | |