

## Studying marine mammal social systems

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### 12.1 Introduction

#### 12.1.1 The definition of social structure

Pinnipeds and cetaceans often aggregate, sometimes in their thousands, and on occasion in exceptional densities. Many of these gatherings are not obviously the result of attraction to environmental features. Thus, these are actively maintained groups, not passive aggregations. Groups imply social structure, and social structure can affect ecology, genetics, population biology, and thus issues of conservation and management (Wilson 1975; Sutherland 1998). Hence, both for interest in the social lives of marine mammals, as well as a general understanding of the biology of the animals, their places in ecosystems, and the effects of human activities on them, we need to study social structure. Additionally, because the habitat of marine mammals is so different from that of terrestrial species, an understanding of the social structure of marine mammals provides an important comparative perspective on the forces of mammalian social evolution (Connor *et al.* 1998).

Those who study the social structures of non-humans often use the framework of Hinde (1976) as their conceptual basis. From this perspective, social structure is fundamentally about interactions between individuals. A relationship between two individuals is the content, quality and patterning of their interactions. The social structure of a population is the nature, quality, and patterning of the relationships among its members.

A glossary of many of the terms used herein is given at the end of this chapter.

#### 12.1.2 How do we study social structure?

Many marine mammalogists who adopt Hinde's (1976) conceptual framework for the study of social structure face an immediate problem. Except when pinnipeds are hauled out on land or ice, most behavioural interactions, the basis of the framework, between aquatic mammals are unobservable. Cetologists have long circumvented this roadblock, and have made considerable progress in understanding

the social structure of whales and dolphins, by observing ‘associations’ rather than interactions (Whitehead *et al.* 2000). The ability to use visual observations as a tool for studying pinnipeds at sea is very limited. Most information gathered in the past has been restricted by the available technology, which has limited information gathering to the interactions of small numbers of individuals. However, advances in and novel uses of existing technologies have enabled pinniped scientists to begin to build a more complete picture within which associations can begin to be assessed at sea.

Formally, two animals are associated if they are in circumstances in which interactions usually take place (Whitehead 2008b). As interactions are generally mediated by communication, a definition of association should be based upon the circumstances under which individuals communicate, and thus ideally studies of communication underlie those of social structure. Using associations rather than interactions as the basis of a study of social structure might be considered to be making the best of a bad job. However, some relationships among animals are not expressed by overt interactions (Whitehead 2008b). Synchronous movement is an example of when associations may be better measures of relationship strength than observable interactions.

When collecting behavioural data, an important distinction is between events and states (Altmann 1974). Events occur virtually instantaneously, whereas states are continuous. Breaches, lobtails, and upsweep vocalizations are events, feeding and travelling are states. From a social perspective, interactions are events and associations states. It is common to define several states, such as milling, travelling, resting, and socializing (Mann 2000), so that at any instant an individual or group is in one state (or perhaps more than one if they are not mutually exclusive).

Those studying the societies of marine mammals often define associations using spatio-temporal groups: animals are considered associated if they are members of the same group. This makes sense if it can be assumed that interactions generally take place within groups (Whitehead 2008b). Once again, studies of communication can help buttress this assumption.

Observations of interactions, associations, or groups are then used to calculate relationship measures, which quantify the second level of Hinde’s framework, the relationships between dyads. Relationship measures for marine mammals usually take the form of interaction rates or association indices. These can then be synthesized into descriptions and models of social structure, Hinde’s third level, using ordinations, cluster analyses, network analyses, lagged association rates, and other univariate and multivariate techniques.

Social structures are influenced by, and influence, demography, genetic population structure, population biology, culture, patterns of kinship, and fitness. Techniques, such as Mantel tests, allow data and models of social structure to be linked to data on age, sex, genetics, range use, movement, and diet allowing hypotheses about the drivers and effects of social structure to be investigated (Whitehead 2008b). Almost none of this is feasible without knowledge of the identity of the interacting, associating, or grouped animals. Thus, a prerequisite for moving

beyond a most basic analysis of social structure is some method of distinguishing individuals. Available techniques are summarized in Chapter 2.

So to study marine mammal social systems we usually need:

- a method of identifying individuals;
- observations, or other records (such as those from acoustics or telemetry), of interactions, associations, or groups;
- if using associations or groups, a basic understanding of the communication system of the species;
- statistical methods for producing relationship measures between individuals from records of interactions, associations, or groups;
- displays and models of social structure produced from the relationship measures; and
- supplemental data in areas such as sex, age, kinship, ranging, diet, non-social behaviour, and statistical methods for integrating these with the social data and results.

Marine mammalogists have quite frequently used ingenuity to bypass behavioural observations. Indirect but revealing inferences have been made about social behaviour and social structure from genetic data (Amos *et al.* 1993), parasite fauna (Best 1979), anatomy (Brownell and Ralls 1986), scarring (MacLeod 1998), and life history data (Kasuya *et al.* 1988).

### 12.1.3 Styles of studying social structure

The social systems of species of the two principal orders of marine mammals have been studied in contrasting manners. Studies of pinniped social structure have largely been based on understanding mating systems and mother–pup relationships while the animals are hauled out on land or ice (Stirling 1983; Boness 1991; Bowen 1991; Le Boeuf 1991; Insley *et al.* 2003). In contrast, cetacean social structures have usually been approached from the perspective of a fission–fusion society in which groups form and break-up. Animals are identified photographically, associations are recorded either directly or using group memberships, association indices are calculated between pairs of animals and used as relationship measures to construct models of social structure (Whitehead *et al.* 2000). A rarer, but particularly revealing, type of research is the detailed study of relationships using focal animal follow data (Mann and Smuts 1998; Mann 2000). There has been much less study of social structure in sirenians (see P.K. Anderson (2004) for a summary).

## 12.2 Field research

### 12.2.1 Identifying individuals

Studies of social structure generally require many identifications (usually, at least thousands) of many individuals, typically many more than are required in studies of

population size using mark–recapture methods (see Chapter 3). Quantities of data required to produce useful descriptions of social structure are estimated by Whitehead (2008a). For instance, for an association index (which estimates the proportion of time that a pair of animals spend together) to have a coefficient of variation of less than 20%, requires about 15 observations of the pair associated; and, when the population is fairly homogeneous socially (coefficient of variation of true association indices of 20%) for the estimated association indices in a population to have a correlation greater than 0.4 with their true values needs an average of at least five observed associations of each dyad in the population (Whitehead 2008a). In practice this means that among the methods used to identify individuals (see Chapter 2), those that are cheap and simple to employ in the field, and cheap and straightforward to analyse in the laboratory are most suitable. Currently, photo-identification best fulfils these requirements, and has been the most important field method for studying the social structures of marine mammals, especially those of cetaceans. For pinnipeds, visual observations of individual markings at haul-out sites as well as tagging (i.e. flipper, radio, satellite, or other) have served as the primary forms for identifying individuals. However, photo-identification is rapidly becoming more widespread as technology facilitating pelage recognition improves (e.g. Karlsson *et al.* 2005). Acoustic techniques are also becoming increasingly useful as a method for individual recognition (e.g. Van Parijs and Clark 2006).

### 12.2.2 Collecting interaction, association, and group data

Observational field data can be collected using several protocols. The collection of observational data is more difficult at sea than on land, and protocols for doing this more crucial (Mann 1999; Whitehead 2008b). A primary distinction is whether to follow or survey. In a survey, when animals are encountered, their identities, associations, and perhaps behavioural states are recorded, and then attention moves towards finding another individual or group. In a follow, the individual or group is tracked and remains the focus of attention. It is usual in a group follow to collect information, as far as possible, on all members of the group, usually their identities, but perhaps including their behavioural states, fine-scale associations within the group, or interactions. In an individual follow, interactions and perhaps associations between the focal animal and any others are usually recorded. The protocols can be nested within one another. For instance, Gero and Whitehead (2007) conducted focal follows of individual calves within group follows of sperm whale groups.

Once a follow protocol is decided, a second, related choice is the sampling protocol. These are described and discussed in some detail by Altmann (1974), Lehner (1998), and Mann (1999). Options include ‘*ad libitum*’ (all behaviour recorded as far as possible), ‘focal-animal’ (the behaviour of the focal animal and those it interacts with are recorded), ‘all-event’, ‘predominant activity’ (the state of the majority of the members of a group), ‘point’ (the state of an animal

**Table 12.1** *Using interactions or association data: some guidelines. (Adapted from Whitehead 2008b.)*

	Interactions	Associations
Dyadic measure:	Usually counts of interactions	Usually 1:0 (associated : not associated)
Applicable when:	Interactions reliably and frequently observable	Interactions not reliably or frequently observable; coordinated behaviour predominates
Follow protocol:	Usually individual follow is best	Usually survey or group follow is best
Sampling protocol:	All interactions involving focal animal with times and interactant identities is best	Associations are noted at regular times or when they change

or animals at a particular time), or ‘scan’ (the state of an animal or animals when observed).

The major styles of collecting social data on marine mammals can be classified by the follow protocol (survey, individual follow, or group follow), and whether social structure is being studied using interactions, associations, or groups. Combinations of these suggest optimal sampling protocols (Whitehead 2008b) for the study of marine mammals in different circumstances. In general, it is more efficient to use group follows or surveys when collecting association or group data, whereas, except in unusual circumstances, interaction data can only be collected reliably during individual follows. Recommended field methodologies for collecting observational social data on marine mammals are given in Table 12.1 (also see Whitehead 2008b).

*Group follows, recording interactions*—Recording all interactions taking place within a group of animals requires high visibility, small group size, and low interaction rates. However, this is sometimes possible with hauled-out pinnipeds (e.g. Kovacs 1989), in captive situations (e.g. Davies *et al.* 2006), or ideal field situations and with prominent behaviours (see Connor 2001). In such cases, interactions are recorded when observed, together with the identities of the animals, the type of interaction, and the time. Additional information that may be useful includes the locations of the members of the group (so, who could interact with whom) and non-social behaviour, either in state (e.g. resting, scanning) or event (e.g. a movement, echolocation signal) form.

*Individual follows, recording interactions*—This is the methodology which produces the finest scale portrait of the social behaviour of marine mammals at sea (e.g. mother–calf relationships in bottlenose dolphins; Mann and Smuts 1998). Time-referenced interactions involving the focal animal are recorded along with

the identity of the individuals involved. Additional information that should generally be recorded at regular intervals includes geographical positions, the behavioural state of the focal animal, its non-social behaviour (e.g. feeding attempts), and which animals are in a location to interact with the focal animal. This style of study requires excellent observation conditions, so that the focal animal can be followed and interactions observed consistently.

*Group follows, recording associations or groups*—This is the methodology often used with larger odontocetes and sometimes with baleen whales. Usually, group membership is noted at regularly spaced sampling times or whenever it changes, or photographs are taken opportunistically, with times recorded, to document group membership in retrospect. The location and predominant behavioural state of the group is also recorded. Additionally, fine-scale associations such as synchronous movement, or behavioural events such as breaches of vocalizations, are noted, preferably with the identity of the performer.

*Surveys, recording associations or groups*—When animals are encountered, their identities and associations or groups are noted, and then the survey moves on to find more animals. This method is often used with small-boat surveys of cetaceans, with the identities of animals in well-defined groups being determined on encounter, generally using photo-identification. It is usual, and recommended, also to record geographical location and behavioural state, as well as additional social measures, such as distinct subgroups, when feasible.

Most observational studies of marine mammals are made from 3–20-m long motor vessels or auxiliary sailing vessels. Vessels larger than about 20 m are generally too high and unmanoeuvrable to collect good observational and identification data. In all boat-based studies, it is important to minimize the effects of the boat on the animals' behaviour, both for ethical reasons and so that recorded social behaviour is representative. Studies of captive animals or hauled-out pinnipeds do not need boats, and in some cases inshore or freshwater animals can be watched and individually identified from land. Aerial platforms are also theoretically feasible. However, fixed winged aircraft are not stable, and it is hard to observe animals for any time, while helicopters are noisy and expensive. Powered or tethered lighter-than-air balloons or blimps are in many ways ideal, providing stable, quiet platforms which can be manoeuvred into optimal locations (Hain 1991; Nowacek *et al.* 2001a). However, they are currently expensive and often difficult to operate out at sea.

### 12.2.3 Collecting social data without observing animals

Identifying individuals other than visually has usually proved challenging. While marine mammals can be individually identified using genetic profiles (Palsbøll *et al.* 1997), given the number of identifications needed for useful studies of social structure, expense, and the ethical and logistic difficulties of collecting many samples from the same animals usually precludes this method. There have been

successes in acoustic individual identification (e.g. Campbell *et al.* 2002), and as marine mammals use the acoustics so prominently for communication (Tyack 1999), if individual acoustic identification is feasible then studies of vocalizations have the potential to provide the raw material for models of social structure, although they will be more powerful if tied to observational data. For example, Van Parijs and Clark (2006) have been able to study the mating tactics of acoustically identified individual bearded seals, *Erignathus barbatus*, over 16 years.

Tags identify animals, and modern tags have the ability to collect interaction or association data (see Chapter 10). For instance, ‘D-tags’ record sounds and so can identify vocal exchanges which could be assigned to the tag-holders (Johnson and Tyack 2003). Unfortunately, though, such tags are unlikely to be deployed in sufficient numbers at the same time to give a comprehensive model of social structure on their own.

Quite simple tags may be more effective. If the tags exchange information with each other when they come within proximity, either acoustically or by radio, then they effectively record associations (see Chapter 10). With a moderate number of these types of tags deployed, a large body of association data might be collected.

## 12.3 Relationship measures

The second stage of Hinde’s (1976) framework for the study of social structure is the analysis of relationships between animals. So records of interactions or associations need to be transformed into relationship measures.

### 12.3.1 Interaction rates

Perhaps the simplest relationship measure is the interaction rate, the rate at which a pair interacts per unit time, so we might have a touching rate, or a fighting rate. The ‘per unit time’ can refer to continuous time within a study or just periods during which the pair were in circumstances under which they could interact (e.g. both may be hauled out at the same site). For either concept, we need measures of effort: during how much time could we have observed interactions? Some interaction measures are asymmetric, so that if A interacts with B, this does not necessarily imply that B interacts with A. Examples include winners of fights, leadership in dives, or beak-to-genital touching. With asymmetric interactions, a number of additional relationship measures are feasible. These include Van Hooff and Wensing’s (1987) directional consistency index and de Vries’ *et al.*’s (2006) dyadic dominance index which vary between 0, indicating equal interaction rates from A to B and B to A, and 1 when A is always the actor and B the receiver, or vice versa.

### 12.3.2 Association indices

When association data are collected, the usual relationship measure is an association index (Cairns and Schwager 1987) which is an estimate of the proportion of

time that a pair is in association. Thus association indices are naturally symmetric (although in some circumstances it may be possible to identify active and passive participants in an association). To construct association indices, the study needs to be divided into sampling periods, which could be hours, days, surveys, or encountered groups. Then, for each period and dyad, say A and B, we note whether A and B were observed, and if both were observed, whether they were observed in association with one another. Counts are made of the number of sampling periods in which A and B were observed associated,  $x$ , those when both were observed but not associated,  $y_{AB}$ , those when A was observed but not B,  $y_A$ , and those when B was observed but not A,  $y_B$ . The two most popular association indices in marine mammal work are:

$$\text{Simple ratio} : x / (x + y_{AB} + y_A + y_B)$$

$$\text{Half-weight} : x / (x + y_{AB} + (y_A + y_B) / 2)$$

If individuals are equally likely to be identified during any sampling period and all associates are identified, then the simple ratio is an unbiased estimate of the proportion of time individuals spend together (Ginsberg and Young 1992). However, if individuals are more likely to be identified when not associated, or not all associates are identified, then the half-weight is less biased. As associates are often missed in photo-identification studies of marine mammals, and at least one member is more likely to be identified when they are in separate groups, the half-weight is generally preferred. For more information on these and other association indices and their biases, see Cairns and Schwager (1987) and Whitehead (2008b).

### 12.3.3 Temporal measures

One element of Hinde's (1976) definition of relationship that is rarely considered in practice (but see Mann and Smuts 1998) is temporal patterning. There are ways to quantify the temporal patterning of a dyadic relationship (see Whitehead 2008b), for instance using dyadic variants of the lagged association rate (described below).

### 12.3.4 Matrices of relationship measures

Using the methods described above, or others, we can produce one or more relationship measures (usually interaction rates or association indices) between each pair of animals in the population. These can be arranged into square matrices, such as that shown in Table 12.2. If there is interest in particular elements in this matrix (relationships between particular dyads), then standard errors, or other measures of confidence, should be attached to each (see Whitehead 2008a). More usually, however, we consider the general patterns in these tables as indicators of the social structure of the population.



**Table 12.2** Half-weight association indices among nine female sperm whales observed off the Galapagos Islands on 19 days between 12 April 1998 and 12 April 1999. Sampling periods are days, and two whales are associated if they dived within 5 min of one another.

Sperm whale identification number	#3700	1.00								
	#3701	0.32	1.00							
	#3702	0.32	0.46	1.00						
	#3703	0.31	0.22	0.22	1.00					
	#3704	0.34	0.27	0.33	0.32	1.00				
	#3705	0.38	0.30	0.22	0.21	0.19	1.00			
	#3706	0.19	0.08	0.23	0.22	0.20	0.37	1.00		
	#3707	0.32	0.08	0.38	0.07	0.27	0.30	0.46	1.00	
	#3708	0.12	0.07	0.36	0.34	0.31	0.21	0.36	0.29	1.00
	#3700	#3701	#3702	#3703	#3704	#3705	#3706	#3707	#3708	
	Sperm whale identification number									

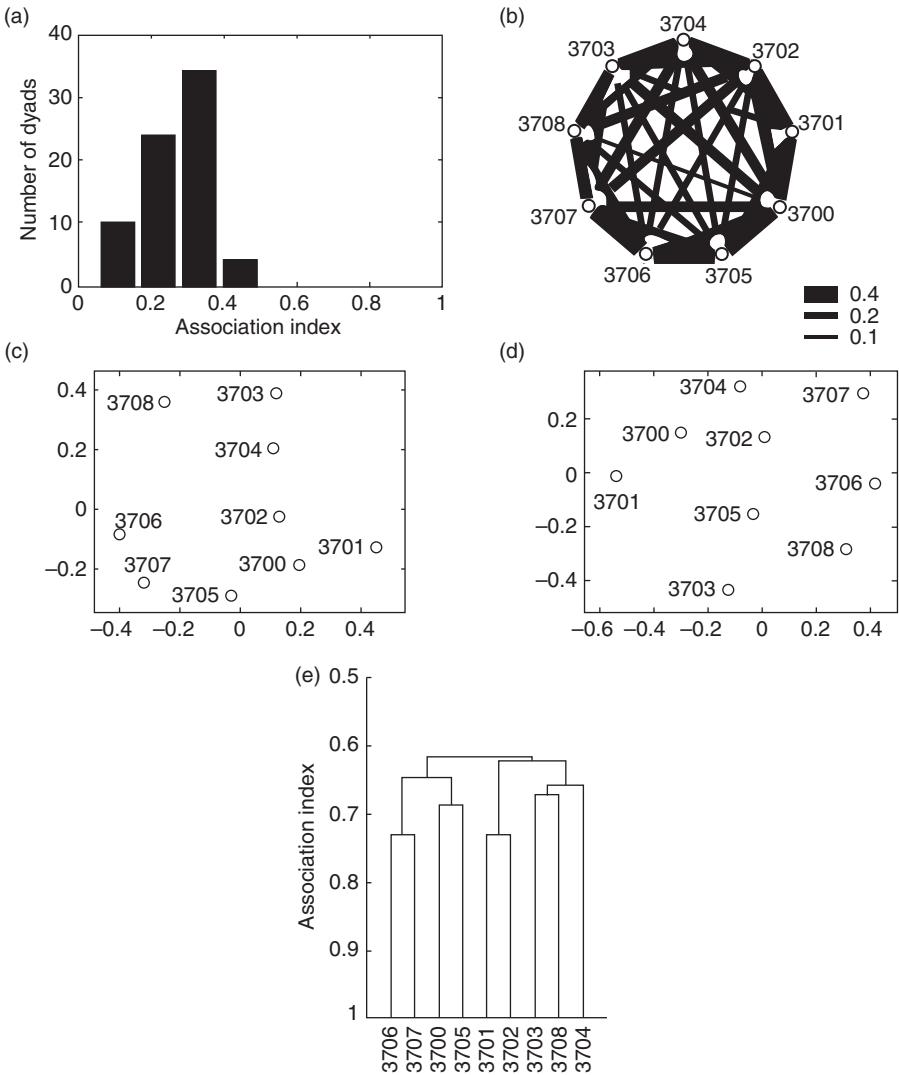
## 12.4 Describing and modelling social structure

Matrices of interaction rates or association indices (e.g. Table 12.2) are not easily assimilated by the human brain, especially when there are more than a handful of individuals, or more than one relationship measure. Thus visual displays, model-fitting techniques, and statistical measures are used to analyse such tables. As marine mammal study populations are generally larger than those of most large terrestrial mammals and the observational data sparser (Whitehead and Dufault 1999), these integrative methods have become disproportionately important. Displays and models of social systems are richer if information is available to allocate individuals into classes, usually age/sex classes, but there are other ways of classifying animals, for instance by mitochondrial haplotype, or using the results of a social clustering method (see below).

### 12.4.1 Visual displays

Of the methods commonly used to display matrices of association indices or interaction rates, four are illustrated for the data in Table 12.2 in Fig. 12.1 (for further information on these and other display techniques, see Whitehead 2008b):

*Histograms* of association indices or interaction rates indicate the variation among relationships. For instance, in Fig. 12.1a, a rather homogeneous social system is indicated by rather little variation in association indices. Note that quite different social systems could produce similar patterns in histograms. For instance, a range-based social structure where individuals interact often with their neighbours and weakly with non-neighbours would show a bimodal pattern of a few strong relationships and many weak ones, as would a social structure



**Fig. 12.1** Visual displays of association data for nine sperm whales shown in Table 12.2: (a) histogram of association indices; (b) sociogram; (c) principal coordinates analysis (first two axes explain 39% of variance); (d) non-metric multidimensional scaling (stress 0.19); and (e) average linkage cluster analysis (cophenetic correlation coefficient 0.58). All indicate a relatively homogeneous social system.

consisting of small permanent social units, with many interactions within units and few between.

*Sociograms* are displays in which individuals are represented by nodes (Fig. 12.1b). These are linked by lines whose widths indicate the strength of the relationship measure. These useful displays become unwieldy when many

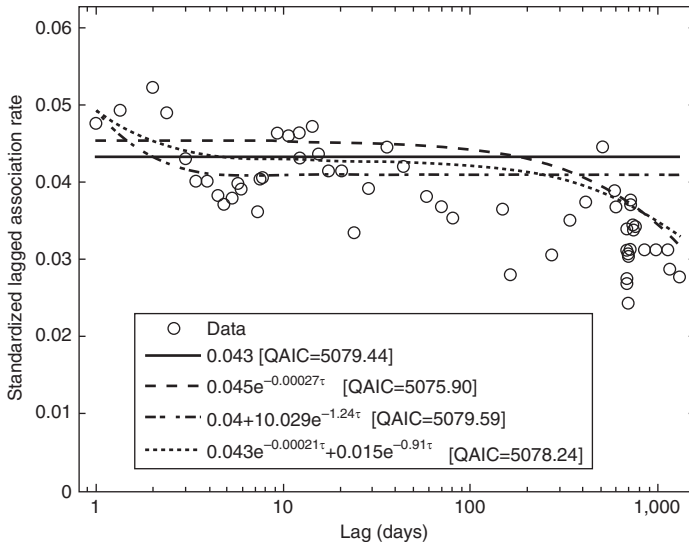
individuals are studied, although the sophisticated network drawing displays of programs like NetDraw can help (see below).

*Principal coordinates analysis* and *non-metric multidimensional scaling* display individuals as points with the distances between the pairs of points, ideally, being inversely related to the dyad's association index or interaction rate (Figs 12.1c and 12.1d). Ideally, in the principal coordinates method the measure of relationship is linearly related to the distance, whereas in non-metric multidimensional scaling it is monotonic. These methods can use any number of dimensions but, given human perceptual abilities, it is normal to display just two. They can indicate general attributes of social systems, such as social units, as well as how particular individuals fit into the social structure. The success of the principal coordinates method for displaying a matrix of relationship measures in a given number of dimensions is indicated by the proportion of variation accounted for (with perhaps >40% indicating a useful display). 'Stress' (varying between 0 and 1) assesses the success of non-metric multidimensional scaling, with values less than about 0.1 indicating satisfactory ordinations. The criteria of non-metric multidimensional scaling are less stringent than those of principal coordinates, so it generally produces a more satisfactory arrangement in a given number of dimensions. However, non-metric multidimensional scaling is an iterative technique and may not work with more than about 50 individuals.

*Hierarchical cluster analysis* produces a dendrogram (tree diagram; Fig. 12.1e) which seems to give a very useful display of the relationship measures. However, it presumes a hierarchically arranged social structure in which the clusters at one level are the elements of higher level clustering. This is true of some social systems, such as those of resident killer whales (Bigg *et al.* 1990), but if it is not the case then cluster analysis can be misleading. The cophenetic correlation coefficient, which measures the fit between the relationship measures of dyads and their level of clustering in the dendrogram, is a good way of assessing the value of a cluster analysis. Values greater than 0.8 are often taken to indicate that a dendrogram is a reasonable display of the matrix of relationship measures. There are several types of hierarchical cluster analysis, of which average linkage is generally recommended for social analysis (Whitehead 2008b). Hierarchical cluster analyses, as well as non-hierarchical cluster analyses, can be used to split populations into social units or communities such that relationships are strong within units or communities and weak between them.

### 12.4.2 Testing for preferred/avoided companions

It is increasingly being realized that hypothesis testing is often a poor way to make inferences, especially when studying wild animals, partially because null hypotheses are unrealistic (Johnson 1999). However, in social analysis, there are circumstances in which realistic null hypotheses exist and should be tested. It is entirely reasonable that animals may see each other as 'equivalent' (Schusterman *et al.* 2000), and not



**Fig. 12.2** Standardized lagged association rates plotted against time lag ( $\tau$  in days) of female sperm whales and immature sperm whales from data collected off the Galapagos Islands between 1985 and 1995. Several models of the exponential family are fitted to the data. That with the lowest QAIC could be considered ‘best’.

distinguish between social partners. Bejder *et al.* (1998), working on Hector’s dolphins (*Cephalorhynchus hectori*), developed a permutation test of the null hypothesis that individuals have no preferred or avoided companions. Extensions of this test control for differences in gregariousness among individuals and demography, as individuals within the study area at the same time are more likely to be observed in association with one another (Whitehead 2008b). These tests are often a prelude to further analysis of the social structure. If the null hypothesis is not rejected, then displays and analyses, such as dendrograms and network analyses, have little validity. For the data that produced the association indices in Table 12.2, the variant of the Bejder *et al.* test that permutes associations within sampling periods, while maintaining the total number of associations of each animal in each sampling period, did not reject the null hypothesis of no preferred or avoided associates at  $P = 0.51$ , confirming the homogeneous nature of this social structure indicated in the ordinations (Fig. 12.2).

### 12.4.3 Network analyses

The social system of a marine mammal population can be viewed as a network, with nodes (individuals) being connected by edges (relationships). The network can be described by a matrix of relationship measures (such as Table 12.2) and is then amenable to the large, and quickly growing, body of quantitative techniques known as network analysis. For introductions to the application of network techniques to

**Table 12.3** Weighted network measures that can be calculated for each individual (node) from matrices of association indices or interaction rates ( $a_{ij}$  is the association between individuals  $I$  and  $J$ ;  $a_{ii} = 0$  for all  $I$ ). (Adapted from Whitehead 2008b.)

Measure:	What it means:	Formula for weighted network
Strength	How connected to other individuals	$s_i = \sum_j a_{ij}$
Eigenvalue centrality	How well connected, in terms of number and strength of connections, and to whom	$e_i = (1^{st} \text{ eigenvector of } a)_i$
Reach	Overall strength of neighbours	$r_i = \sum_j a_{ij} \cdot s_j$
Affinity	Weighted mean strength of neighbours	$f_i = r_i/s_i$
Clustering coefficient	How well connected are neighbours to one another	$c_{ij} = \frac{\sum_k \sum_l a_{ij} \cdot a_{ik} \cdot a_{jk}}{\max(a_{jk}) \cdot \sum_k \sum_l a_{ij} \cdot a_{jk}}$

non-human social systems see Croft *et al.* (2008) and Wey *et al.* (2008). Network analysis has been applied to marine mammal social systems (Lusseau 2003; Lusseau and Newman 2004). A drawback of almost all current applications of network analysis to non-human social systems has been that the network has been considered binary, with relationships either existing (1) or not existing (0). However, especially in rather labile marine mammal social systems, all pairs of animals possess a relationship, but they differ in strength. Thus attention is shifting to weighted networks in which edges are represented by continuous variables, for instance by association indices or interaction rates (Lusseau *et al.* 2008). Although less well developed than the analysis of binary networks, there is a growing body of techniques that can be applied to weighted networks (Newman 2004). Sifting out those that are useful for the study of marine mammal social systems can be a challenge, but here are some recommendations.

For each individual we can calculate a suite of nodal statistics (Table 12.3). The mean and standard deviation of these are then usually presented for the population, as well as for classes of animals (e.g. males and females), and in some cases between classes (for instance, the strength of relationships between males and males, males and females, females and females). Relationships between measures can also be examined. For instance, if individuals with high strength also have high affinity (the mean strength of an individual’s neighbours), then there are preferential links among ‘important’ individuals. This situation is known as assortative mixing, and is often found in social networks (Newman 2003). Lusseau *et al.* (2008) showed how permutation tests, variants on those described earlier, can be used to test a variety

of null hypotheses about weighted social networks, such as that relationships are similar within and between classes or that there is no assortative mixing. Network analysts have also developed a wide array of techniques for subdividing networks, some of which (such as Newman's 2006 eigenvector modularity) are very useful for finding social units and other social entities within study populations.

#### 12.4.4 Lagged association rates

Temporal patterning is a part of Hinde's (1976) definition of social structure that is poorly covered by visual displays, tests for preferred companions, and most network analysis. Lagged association rates explicitly address temporal change in social relationships, and have been used to describe cetacean social systems (e.g. Karczmarski *et al.* 2005). The lagged association rate of lag  $\tau$  is the probability that two individuals associated at time 0 are also associated  $\tau$  time units later. Lagged association rates can be estimated from observations of the associations between identified individuals using formulae provided by Whitehead (2008b). However, these assume that all associates of an identified individual are identified, which is often not the case in studies of marine mammals. Instead, we use the standardized lagged association rate, which is the probability that given that B was associated with A at time 0, an identified associate of A  $\tau$  time units later is B (estimation formulae in Whitehead 2008b).

The estimated lagged association rate, or standardized lagged association rate, is usually plotted against time lag,  $\tau$ , often with time lag logged, as in Fig. 12.2. Lagged association rates usually decline in relation to the time lag because associations weaken or break down, but the pattern of decline tells us much about the temporal dynamics of a social system. For instance, in Fig. 12.2, standardized lagged association rates of sperm whales decline over periods of a few days, indicating disassociation of groups of social units, and a few years, indicating emigration from social units or mortality. A number of ancillary methods help us interpret lagged association rates and standardized lagged association rates (see Whitehead 2008b for details and Fig. 12.2 for an example).

Confidence intervals in lag duration can be estimated using the temporal jackknife technique in which, for instance, month-long periods of data are omitted in turn. Null association rates, and standardized null association rates, give the expected values of the lagged rates if associations were random within the study population, and thus allow us to assess over what time scales individuals show preferences in their associations. Models, often of the exponential family, can be usefully fitted to lagged association rate data by maximizing the sum of logged likelihoods over different lags. The estimated parameters of these models (and their standard errors from the temporal jackknife procedure) quantify social processes, for instance the rate of disassociation per hour or day, or the typical group size. If several models are fitted, their fits can be compared using the quasi-Akaike Information Criterion, QAIC (Whitehead 2007 see Fig. 12.2).

Lagged association rates are particularly useful for studying the social systems of marine mammals because they integrate large amounts of quite sparse data (i.e. with little information on any particular individual or period, but with many individuals studied over a long time).

#### 12.4.5 Describing mating systems

To describe mating systems, we need to know who mated with whom and, especially, which matings produced viable offspring. In marine mammals, the maternal side of the mating process is usually easily inferred, because in most species the mother–infant bond is sufficiently tight that successful mothers can be easily identified (an exception is the sperm whale, in which frequent babysitting and some allo-suckling makes maternal discrimination less straightforward; see Gordon 1987). Paternal input is harder to assess. In land-mating pinnipeds, copulations can be observed (e.g. Le Boeuf 1974), but may not always correlate with paternity (e.g. Worthington *et al.* 1999). For most marine mammals that mate in the water, copulation is rarely observed, and even more rarely can the identities of the individuals be ascertained. Thus most conclusions about marine mammal mating systems are based upon molecular genetic analysis (e.g. Hoffman *et al.* 2007).

To assign paternity to an individual with some certainty, genetic data are needed from the individual, as well as a substantial proportion of the potential fathers. The analysis is much more effective if genetic data are also collected from the mother of the focal individual, thus allowing the paternal genes to be determined by elimination. Currently, microsatellites are the preferred method of determining the paternities of marine mammals (see Selkoe and Toonen 2006), but other markers are being developed. Once paternities are determined, rates of reproductive success can be calculated for different ages and the behavioural strategies of males.

#### 12.4.6 Other methods of social analysis

We have concentrated so far on the methods that have been most used, or we think have most potential, in the study of marine mammal social systems. There are other techniques which are important in particular circumstances, or are just beginning development:

- A well-developed methodology is available for examining dominance hierarchies (see de Vries 1998; Bayly *et al.* 2006). Individuals may be assigned dominance indices or dominance ranks, and the linearity of dominance hierarchies can be assessed using methods such as Landau's (1951) index. The analysis of dominance hierarchies is particularly important for land-breeding pinnipeds (e.g. Le Boeuf and Reiter 1988) and captive populations (e.g. Samuels and Gifford 1997).
- The analyses described to this point have assumed just one relationship measure, usually an interaction rate or association index. However, in many studies we can calculate two or more relationship measures. For instance,

Gero *et al.* (2005) measured association indices between bottlenose dolphin dyads in four different behavioural states: travelling, feeding, socializing, and resting. Whitehead (1997) suggests several techniques for displaying and analysing such multivariate social data.

- Especially among the larger odontocetes, there appear to be permanent, or nearly permanent, social units. However, these social units often group with one another, making their delineation less than straightforward. While cluster analyses may be used to distinguish members of social units, they may produce ambiguous or incorrect clusters. Lagged association rates and other analyses can suggest the development of more appropriate techniques in particular circumstances. For instance, for long-finned pilot whales (*Globicephala melas*), ‘key’ individuals were defined as those identified on at least 4 days at least 30 days apart (Ottensmeyer and Whitehead 2003). Social units were formed from key individuals, and animals identified with key individuals on at least 3 days, separated from one another by at least 30 days.
- Although informative mathematical models can be fitted to lagged association rates and network statistics, they are post hoc statistical models and are therefore descriptive rather than prescriptive. Ideally, one or more biological models of social structure would be translated into statistical terms, and then these fitted to the data. Unfortunately, with current software and hardware, fitting such theoretically initiated models to real social data is demanding.

#### **12.4.7 Useful software**

In the study of marine mammal social systems, computers have become essential tools. A list of some of specialized software that can be useful for analysing data using methods such as lagged association rates and network analyses is given in Table 12.4.

### **12.5 Broader issues**

We have highlighted methods for describing and modelling the social structures of marine mammals. Having produced displays, statistics, and models of social structure, most scientists wish to place their results in a broader perspective to make comparisons among social structures, to investigate the evolutionary forces in social evolution, and to find out how social structure may affect other areas of biology. Here is a summary of a few of these issues (for more details see Whitehead 2008b).

#### **12.5.1 Evolutionary forces behind marine mammal social structures**

Experiments are almost never practical to examine the function and evolution of behaviour in marine mammals. So we are left with comparisons between individuals,



**Table 12.4** Software that may be useful for social analysis. (Adapted from Whitehead 2008b.)

Name	URL	Free?	Notes
MatMan	www.noldus.com/site/doc200401030	No	Manipulates matrices, good for analyses of dominance and reciprocity
SOCPROG	myweb.dal.ca/~hwhitehe/social.htm	Yes*	Wide range of social analyses
UCINET	www.analytictech.com/ucinet_5_description.htm	No <sup>+</sup>	Range of network and other analyses
Pajek	vlado.fmf.uni-lj.si/pub/networks/pajek	Yes	Range of network analyses
NetDraw	www.analytictech.com/netdraw.htm	Yes	Visualizes networks
GraphViz	www.graphviz.org	Yes	Visualizes networks

\* To run SOCPROG in its original form you need to have installed MATLAB plus the Statistics toolbox, which are not free. However, there is a compiled version of SOCPROG available for which MATLAB is unnecessary.

<sup>+</sup>Free evaluation version available.

groups, populations, and species (see Box 12.1). Many of the statistics and measures discussed earlier can be used in such studies, often by relating them to non-social attributes. For instance, the functions of mating strategies can be examined by relating male reproductive success, usually obtained through genetic paternity analysis, with attributes such as age and mass, or the function of grouping by comparing group size with attributes of prey distribution. Kinship is believed to be one of the major forces for sociality, with Hamilton's (1964) rules predicting a relationship between genetic relatedness and affiliative interactions. This is sometimes tested in marine mammals (e.g. Möller *et al.* 2006) by using a Mantel test to compare dyadic association indices with estimates of kinship derived from analyses of microsatellites.

If comparisons are made between species, for instance group size versus brain size across species (Marino 1996), there is a potential problem of independence. Related species may tend to have similar brain sizes because of common descent. The method of independent contrasts (Felsenstein 1985) restores independence to such analyses.

### 12.5.2 How can we study culture in marine mammals?

It is becoming increasingly clear that the standard paradigms of behavioural ecology, including Hamilton's (1964) rules, are insufficient to explain the patterns of diversity of cetacean behaviour. We need to evoke culture, defined as the

### Box 12.1 Comparing and classifying social structures

We may wish to compare social structures between populations or species, between pinnipeds and cetaceans, between marine and terrestrial mammals, or with other animals. Some measures which can be used in such comparisons include:

- Skew in reproductive success, especially among males (e.g. Worthington *et al.* 1999)
- Group size (although it is important that groups are defined in comparable ways)
- Sexual and age segregation. To what extent do animals associate with their own sex, and how does social behaviour change with age?
- Presence and size of social units in females, or coalitions in males
- Rates of disassociation from groups and units
- ‘Social differentiation’: an estimate of the coefficient of variation among association indices between members of a community (Whitehead 2008b).

These, or other, measures can potentially be used to classify social systems, although classification should only be used when clear classes exist.

transmission of information or behaviour through social learning (Rendell and Whitehead 2001). The study of culture in marine mammals, and other wild populations, has generally used an exclusionary protocol, in which patterns of behaviour that cannot be explained by genetic differences, ontological change, or environmental variation are ascribed to culture (e.g. Krützen *et al.* 2005).

This methodology has been criticized on several grounds. For example, it falls back on culture only as a last resort when no other explanations can be found, even though it may not have been possible to exhaustively investigate those alternatives; or that many important aspects of culture, such as foraging techniques, covary with ecology or genetics, and that the boundary line for exclusion is unclear (Laland and Janik 2006). New methods are being developed, including a dyadic multiple regression technique that apportions behavioural variation into genetic, ecological, and cultural sources using extensions of the Mantel test (Whitehead 2008b).

## 12.6 Acknowledgements

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### Glossary (extracts from Appendix in Whitehead 2008b)

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**Aggregation:** Spatio-temporal cluster of individuals that is entirely the result of some non-social forcing factor.

**Association:** Two animals are associated if their circumstances (spatial ranges, behaviour states, etc.) are those in which interactions usually take place.

**Association index:** An estimate of the proportion of time that a pair of animals [is] in association.

**Assortativity:** The extent to which nodes in a network are connected to nodes that are similar to themselves.

**Asymmetric relationship:** A dyadic relationship in which the members interact with one another at significantly different rates.

**Clustering coefficient:** In a network, the extent to which the nodes connected to a focal node are themselves connected.

**Culture:** Information or behaviour shared by a population or subpopulation that is acquired from conspecifics through some form of social learning.

**Dendrogram:** Tree-diagram, in which individuals are represented by nodes and the branching pattern indicates degrees of association, the results of a hierarchical cluster analysis.

**Dominance:** ‘An attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favor of the same dyad member and a default yielding response of its opponent rather than escalation’ (Drews 1993).

**Dominance hierarchy:** An ordering of individuals such that more highly ranked individuals generally win agonistic encounters over, or receive submissive behaviour from, those ranked lower.

**Dominance index:** A measure of an individual’s ability to dominate others in its community.

**Dominance rank:** The ranking of an individual, within its community, in its ability to consistently win repeated agonistic encounters with other members of the community.

**Eigenvector centrality:** In a network analysis, eigenvector centrality is a measure of how well connected an individual is. Mathematically, it is the first eigenvector of the matrix of edges or weights.

**Equivalence:** Things, including social partners, that become mutually interchangeable through common spatiotemporal or functional interactions.

**Fission–fusion:** ‘A society consisting of casual groups of variable size and composition, which form, break-up and reform at frequent intervals’ (Conradt and Roper 2005).

**Follow:** A research strategy in which the researcher’s attention stays with an individual or group (as opposed to a survey).

**Group:** Sets of animals that actively achieve or maintain spatio-temporal proximity over any time scale and within which most interactions occur.

**Interaction:** An action of one animal directed towards another or affecting the behaviour of another.

**Kinship:** Genetic relatedness through common ancestry.

**Lagged association rate:** The probability that a dyad are associated at some time after a recorded association.

**Mantel test:** Permutation test of the significance of the relationship between the corresponding, non-diagonal, elements of two similarity or dissimilarity matrices indexed by the same individuals, with the null hypothesis being that there is no relationship.

**Modularity:** For some arrangement of individuals into clusters, the difference between the proportion of the total association within clusters and the expected proportion for randomly associated individuals.

**Network:** Pattern of connectedness among members of a population.

**Null association rate:** The expected probability that members of a dyad are associated at some time after a recorded association if association had no time dependency.

**Ordination:** Visual display in which points represent individuals and their proximity to one another indicates their degree of association.

**Reach:** A measure of indirect connectedness in a network such that nodes with high reach are connected indirectly to other nodes of high degree or strength (Flack *et al.* 2006).

**Relationship:** A synthesis of the content, quality and patterning of the interactions between two individuals, where patterning is both with respect to each others' behaviour and to time.

**Relationship measures:** Quantitative descriptors of the content, quality or temporal patterning of dyadic relationships.

**Social differentiation:** The degree to which the dyads within a population differ in their probability of association, measured using an estimate of the coefficient of variation of the true association index.

**Social structure:** A synthesis of the nature, quality, and patterning of the relationships among the members of a population.

**Sociogram:** Diagrammatic representation of social structure in which individuals are represented by nodes, and edges between nodes indicate the strength of the dyadic relationship.

**Strength:** In a weighted network analysis, the sum of the weights of the edges connected to a node.

**Survey:** A research strategy in which an individual or group is first encountered, then observed, and then the researcher moves on to another individual or group (as opposed to a follow).

**Typical group size:** The mean group size that an individual, or set of individuals, experiences.