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Analysing animal social structure

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Abstract. This paper presents a framework for analysing the social structure of populations in which interactions between some identified individuals can be observed. Statistics describing the nature, quality and temporal patterning of one or more interaction measures are used to define relationships between pairs of individuals or classes of individual. Multivariate techniques can then be used to display the social structure of the population. These displays indicate the social complexity of the population and can be used to classify relationships and examine patterns of relationship between classes of animal. They can also be used to define and delineate groups. This framework and these techniques should be particularly useful when analysing complex fission–fusion societies, as are found among the primates and cetaceans.

A knowledge of the social structure (here synonymous with social organization) of a population is important for a range of fundamental and applied purposes. Social structure defines an important class of ecological relationships, those between nearby conspecifics. It may include competition, cooperation and dominance in the acquisition of mates or resources, as well as competitive or cooperative care of offspring, and even cannibalism. Thus social structure is often an important element of the population biology of a species, influencing gene flows, spatial pattern and scale, and the effects of predation or exploitation by humans (Wilson 1975). Social structure also sets the scene within which communication and cognition take place, and appears to be an important correlate, and perhaps evolutionary determinant, of communicative and cognitive behaviour (Byrne & Whitten 1988).

For some phylogenetic groups of animals, the range of social structures is sufficiently constrained (by anatomy, environment, physiology or life history) that a fairly simple set of principles can be used to describe and classify them (e.g. Michener 1969 for the social insects). In contrast, the more cognitively advanced mammals often have complex social structures, which vary considerably and nearly continuously between and within species (e.g. Dunbar 1988). Describing and classifying these societies is complex and challenging (Costa & Fitzgerald 1996).

Hinde (1976) proposed a conceptual framework for examining social structure involving three principal levels: interactions between individuals, relationships among individuals described by the content, quality and temporal patterns of interactions, and social structure described by the content, quality and patterning of relationships. Hinde (1976) developed this framework to structure the analyses of primatologists, anthropologists, sociologists and social psychologists, and it has been implicitly or explicitly referred to in a number of subsequent analyses of primate social organization (e.g. Cheney et al. 1987; Dunbar 1988).

To analyse the social structure of a population in the manner proposed by Hinde (1976) requires detailed information on the interactions between individual members of the population collected over a considerable period of time (so that the temporal patterning of interactions can be described). This has been possible for some primate populations (e.g. Goodall 1986). Many animals whose social structures appear complex and interesting, however, live in situations that make it impossible to collect detailed data on interactions between individuals. These include nocturnal animals, migratory animals, animals that live in large groups or spend much of their time below

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ground, in dense vegetation or under water. Among these moderately inaccessible, but apparently socially complex, species are spider monkeys (genus *Ateles*) and many species of Cetacea (Tyack 1986; Robinson & Janson 1987). These are, for many reasons, interesting and important species, and we need to learn all we can about their societies. We should neither renounce the study of social structure in these less accessible species, nor adopt an overly simplistic alternative, such as categorization by mean group size.

In this paper I suggest a general analytical framework (Fig. 1), and more specific statistical techniques, which may be useful for structuring the analysis of social organization for populations. The framework is applicable both to populations that are easily viewed and studied, and those in which it is possible to identify some individuals, but particular animals, and their interactions with each other, cannot always be viewed clearly or on demand. I illustrate this framework using data from one real and four simulated animal populations.

INTERACTIONS

Interactions between pairs of individuals are the basic elements of social structure (Hinde 1976), but they can take a variety of forms of which only a proportion will be apparent to even the best-placed observer. Often, especially when animals are hard to view, it is useful to consider events or situations as 'interactions' even though neither animal was observed to react to the presence or behaviour of the other. In more cryptic species, we might be able to consider only one category of interaction, perhaps based on spatial proximity, but for others it may be possible to distinguish affiliative, agonistic or other types of interaction. In the collection of data, each type of observable interaction will be represented by one or more 'interaction measures'. The measures of interaction between known individuals are recorded during observation periods, indexed by time.

Each measure of interaction needs to be carefully defined and be appropriate for the animals being studied (Michener 1980). The dyadic measures may be categorical (e.g. 'touching or not touching') or continuous (e.g. 'inter-individual distance'); they may be symmetric (e.g. 'distance between X and Y') or asymmetric (e.g. 'grooming bouts by X on Y'); between any pair of individuals in the population, a measure may be missing for one or more observation periods (e.g. 'both individuals invisible'). Association indices (Cairns & Schwager 1987; Ginsberg & Young 1992) may often be suitable interaction measures. I will represent the measure of interaction of type f, between individuals X and Y (X on Y if it is an asymmetric measure), during observation period t by:

$$I_f(\mathrm{X},\mathrm{Y},t)$$

Then $\{I_f(\mathrm{X},\mathrm{Y},t)$, for all $t\}$ represents the information available on interactions of type f between individuals X and Y: a 'first stage abstraction' in the terminology of Hinde (1976).

If individuals can be allocated to classes (often based on age, sex or reproductive status), then we can carry out a second stage abstraction (again following the terminology of Hinde): $\{I_f(\mathrm{X},\mathrm{Y},t)$, for all t, $\mathrm{X}\in C_1$, $\mathrm{Y}\in C_2\}$ is the information on interactions of type f carried out by members of class C_1 on members of class C_2.

RELATIONSHIPS

Statistics of these measures of interaction, and their first and second stage abstractions, can then be used to describe relationships: the content, quality and patterning of interactions.

Content and Quality of Interactions

The content and quality of the interaction between X and Y may be represented by a vector of summary statistics for the interaction measures over observation periods. Useful summary statistics include the mean, median or whether an interaction was ever observed. Such a vector might look like:

$$\mathbf{Q}(\mathrm{X},\mathrm{Y})=\begin{bmatrix}\text{Mean }\{I_1(\mathrm{X},\mathrm{Y},t)\}\\ \text{Median }\{I_2(\mathrm{X},\mathrm{Y},t)\}\\ I_3(\mathrm{X},\mathrm{Y},t)>0\text{ for any }t?\end{bmatrix}$$

The overall content and quality of interactions between classes of animals C_1 and C_2 can be represented by:

$$\mathbf{Q}(C_1,C_2)=\text{Mean }\{\mathbf{Q}(\mathrm{X},\mathrm{Y}),\text{ for all }\mathrm{X}\in C_1,\ \mathrm{Y}\in C_2\}$$

INTERACTIONS (between individuals X, Y) → INTERACTIONS (between classes C_1, C_2)

Interaction measures, I_f, at different observation periods

↓ ↓

RELATIONSHIPS (between individuals X, Y) → RELATIONSHIPS (between classes C_1, C_2)

Content and quality:

Interaction measure >0 for any observation period
Mean of interaction measures over observation periods

Patterning:

Standard deviation, c.v., half-life
Lagged interaction rates over various lags
Autocorrelations over various lags
Interactions on pairs of days > d days apart?

↓ ↓

SURFACE STRUCTURE

Nature, quality and patterning of relationships

Single measure methods

Association matrix of mean interaction rates displayed using spanning trees, cluster analyses, multidimensional scaling
Association matrix of temporal patterning measures displayed using spanning trees, cluster analyses, multidimensional scaling
Plots of autocorrelations, lagged interaction rates, model fitting

Multivariate methods

Plot of continuous interaction measures in multidimensional space
- Simplify using principal components analysis

Multi-way table for categorical measures
Use to:
- Examine complexity of social structure
- Classify relationships between animals
- Summarize relationships between classes of animal
- Examine relationships of individual
- Define and find groups (region(s) in which relationships are transitive)

Figure 1. Framework for analysing the social structure of identified individuals, with some suggested statistical techniques.

Temporal Patterning of Interactions

The third characteristic of a relationship, the patterning of interactions, is less easy to represent. Appropriate descriptors will depend on factors such as the types of relationship present within a population, the population size, the time scales over which observations were made and the mean rate of interaction.

The standard deviation, or coefficient of variation, of an interaction measure over time may give some information on temporal patterning between individuals or classes of individual over short time scales. Both of these statistics are greatly influenced, however, by the degree of measurement or recording error, and by how well the measure of interaction reflects the underlying behaviour.

Over longer time scales, for social systems in which relationships persist for periods of time and then change, it may be useful to consider the 'half-life', τ, of an interaction measure between two individuals or classes of individuals. This could be defined loosely as the time period until the mean rate of interaction (averaged over some suitable time scale) either halved or doubled. An example of a more formal definition for the half-life of a continuous measure might be:

$$\tau_f(X,Y): \underset{t}{\text{Mean}}\ \{\text{Abs}\ [\text{Log}_2\ (I_f(X,Y,t+\tau)/I_f(X,Y,t))]\}=1$$

and for a categorical (1:0) measure:

$$\tau_f(X,Y):\ g_f(X,Y,\tau)=0.5$$

where $g_f(X,Y,\tau)$ is the 'lagged interaction rate', the rate of interaction between X and Y at τ time units after a previous interaction (at which $I_f(X,Y,t)=1$). Whitehead (1995) gave more information on lagged interaction rates, calling them 'lagged association rates'. Lagged interaction rates were also used (but with different terminology) by Underwood (1981) and Myers (1983).

An autocorrelation analysis provides a more complete description of the temporal patterning of the interactions between individuals or classes of individual. For any time lag d, then the autocorrelation in a measure of interaction f between individuals X and Y, $a_f(X,Y,d)$, is the correlation between the values of I_f at times $t=\{1,2,3,\ldots,T-d\}$ and times $t=\{1+d,2+d,3+d,\ldots,T\}$. In the case of a zero-one categorical measure, with equally spaced observation periods, then the autocorrelation reduces to:

$$a_f(X,Y,d)=\{g_f(X,Y,d)-\text{mean}(I_f(X,Y,t))\}/(1-1/n)$$

where n is the number of observation periods considered. Therefore, for zero-one categorical measures the lagged interaction rate, g, is a suitable substitute for the autocorrelation, a.

Autocorrelations, and lagged interaction rates, are high over a lag of d if this type of interaction persists (or is re-established) over these time scales and low if it does not. The set of autocorrelations for any type of interaction (indexed by time lag) form an autocorrelation function. In some cases it may be possible to abstract a few parameters which describe the autocorrelation function, or a lagged interaction function, perhaps by fitting models of exponential decay with time to these functions (Whitehead 1995).

For moderately inaccessible animals, lagged interaction rates or autocorrelations between dyads may be based on too few data to be useful. Thus abstractions to relationships between different classes of animals may be necessary. These are obtained by lumping the data for interactions between animals of different classes. The lagged interaction rate between classes C_1 and C_2 is:

$$g_f(C_1,C_2,d)=\Sigma I_f(X,Y,d+t)/\Sigma I_f(X,Y,t)$$

where the summations are made over all individuals $X\in C_1$, all individuals $Y\in C_2$, and all observation periods t, such that $I_f(X,Y,t)=1$ and $I_f(X,Y,d+t)$ exists (Whitehead 1995). The autocorrelation between classes C_1 and C_2 is:

$$a_f(C_1,C_2,d)=\frac{\text{covariance}\{I_f(X,Y,d+t),I_f(X,Y,t)\}}{\sqrt{[\text{var}(I_f(X,Y,d+t))\times\text{var}(I_f(X,Y,t))]}}$$

where the summations in calculating covariances, variances and means are made over all individuals $X\in C_1$, all individuals $Y\in C_2$, and all observation periods t, such that $I_f(X,Y,t)$ and $I_f(X,Y,d+t)$ exist.

In particular cases, alternative or additional descriptors of relationships, either between individuals or classes of individual, may be useful. For instance, when trying to distinguish between repeated temporary association and permanent companionship, it may be useful to calculate 'intermediate interaction rates' during the period between the first and last observed interaction of a pair (Whitehead 1995).

With sparse data, very simple measures of temporal patterning may be appropriate, such as a categorical measure equal to one if two animals were ever seen interacting on two occasions over *d* days apart, and equal to zero if they were not.

The Relationship Described

In this framework, we leave the conceptual level of the relationship with a set of statistics for each relationship between two individuals, or abstraction to two classes of individual. The content and quality of the interactions can be represented by a vector of mean (or median) values of interaction measures, and the temporal patterning by a vector of standard deviations, coefficients of variation, or half-lives, and/or a matrix describing the lagged interaction rates or autocorrelations of the interaction measures at different time lags. These statistics can now be used to describe the surface structure of the population.

SURFACE STRUCTURE

The surface structure of a society is described in terms of the nature, quality and patterning of relationships (Hinde 1976). From the analysis of relationships outlined above, each dyadic relationship will be described by several statistics calculated from one or more measures of interaction, which I will call the measures of relationship. There are a number of ways in which these can be summarized and presented to reveal social structure. The most appropriate will depend on the form of the society that is being studied and the nature of the data collected. I will first outline the current methods of displaying social structure from information on relationships before describing a more powerful, integrated multivariate approach.

Strength of Relationship: Association Matrices and their Display

If only one measure of interaction is being considered, and temporal patterning is ignored, then the relationship between a pair of animals is reduced to one measure, the mean (or median) measure of interaction. The surface structure of a population of animals is then represented by an association matrix of these interaction rates indexed (for both rows and columns) by the identities of the members of the population. If the interaction measure is symmetric, then only a triangular matrix is needed.

Techniques that can be used to display such an association matrix include spanning trees, cluster analyses (e.g. Morgan et al. 1976; Slooten et al. 1993; Lazo 1994), multidimensional scaling (e.g. Morgan et al. 1976; Connor et al. 1992; Smolker et al. 1992), correspondence analysis (e.g. Lependu et al. 1995) and 'sociograms' (e.g. Smolker et al. 1992). Such techniques allow a visualization of the surface structure of a society.

The visualization may be useful and a good representation of important elements in the social structure of a population, suggesting groups of animals and the relative rates of interaction within and between groups. This approach suffers from several restrictions, however. It is univariate, so that if several interaction measures are collected, then they must be analysed separately; with more than 100 or so animals the association matrices become unwieldy, and some of the display techniques cannot be used with standard software. (On my 486 computer, the statistical package Systat (Wilkinson 1990) is restricted to cluster analyses of about 125 individuals, and non-metric multidimensional scaling analyses of about 75 individuals.) The major drawback of the use of association matrices to describe social structure, however, is that the temporal patterning of interactions, a key element of the relationship, is ignored.

Temporal Methods

The statistics representing the temporal patterning of relationships can be examined in a number of ways. One univariate measure of the temporal patterning of interactions between individuals (e.g. half-life) forms an association matrix, which may be displayed using the methods just mentioned.

Autocorrelations or lagged interaction rates can be plotted against lag for different classes of animal (e.g. Underwood 1981; Whitehead 1995). Inferences about the temporal patterning of relationships between classes of animal, and thus about some aspects of the surface structure of the population, can be drawn from an examination of these plots. For instance, Whitehead (1995) suggested fitting models based on exponential decay in the probability that individuals continue interacting.

These temporal methods of examining patterns of relationships only allow either the examination of one univariate measure of the temporal patterning of relationships between pairs of individuals, or a combined analysis for all relationships between two classes of animal. Therefore I sought more general methods of studying social structure, which can be used on as many statistics as are available for describing the interactions between animals (or classes of animal) and their temporal patterning.

Multivariate Representation of Relationships

If an analysis of interactions produces *m* relationship measures; then each pair-wise relationship can be represented by a point in *m*-dimensional space: the multivariate relationship space (e.g. Fig. 2; Kappeler 1993). The positions and patterning of these points in multivariate relationship space represent the surface social structure of the animal population. If the interaction measures are categorical, then the relationship space becomes a multi-way table. This is possible only for relationships for which there are no missing relationship measures. If relationship measures are missing, then the population of individuals and relationships considered will be a subset of the true population. In the following, by ‘population’ I refer to the animals and relationships for which full data sets are available.

In some cases, the dimensionality of the representation in multivariate relationship space may be reduced by principal components analysis or some related technique (Manly 1992). This reduction in dimensionality will work especially well if the relationship measures are correlated, for instance if two or more original measures of interaction describe similar underlying types of interaction (if, for instance, a vocalization and physical display are both indicative of submission), or if measures of temporal patterning are related. The axes of the new representation of reduced dimensionality may be related to the measures of relationship. On occasion, rotation of the reduced dimensionality display (e.g. varimax) may aid interpretation of the axes.

To illustrate the technique, I have simulated four animal societies of varying complexity (Appendix) and produced plots of relationship measures for each (Fig. 2).

A multivariate display of relationships can be examined from a number of perspectives. These include the following.

Complexity of social structure

If the points representing the relationships fall into only a few small, tight clusters (such that the diameter of the cluster is of the order of the precision in the recorded measures for a particular dyad), then the social structure is simple (Fig. 2a, b). With more complex social structures, then the multivariate display should itself have more structural complexity (Fig. 2c, d).

Classification of relationships

If the points representing relationships appear to fall into a number of clusters, representing categories of relationship, (Fig. 2b, c) then these can be formally delineated using cluster analysis (*K*-means).

Patterns of relationships between classes of animals

Relationships between classes of animal can be examined in two ways using plots in multivariate relationship space. If points are coded by different symbols or colours depending on the classes of the two animals represented by the relationship (e.g. Kappeler 1993), then differences between the relationships among the classes may be apparent. Alternatively, or additionally, analyses can be carried out on the mean measures of relationship between classes of animal. In resulting multivariate displays, each point represents the relationships between one class of animals and another.

Relationships of an individual animal

The relationships of any particular animal with the other members of the population can be displayed on a plot in multivariate relationship space. Plots like this can illustrate individual variability in the pattern of relationships.

Groups

These displays in multivariate relationship space do not assume that the population is structured into groups. They do allow levels of grouping to be defined and delineated. Suppose a region within multivariate relationship space can be defined such that relationships within it are transitive (i.e. if the relationship between X and Y is within the region, and the relationship

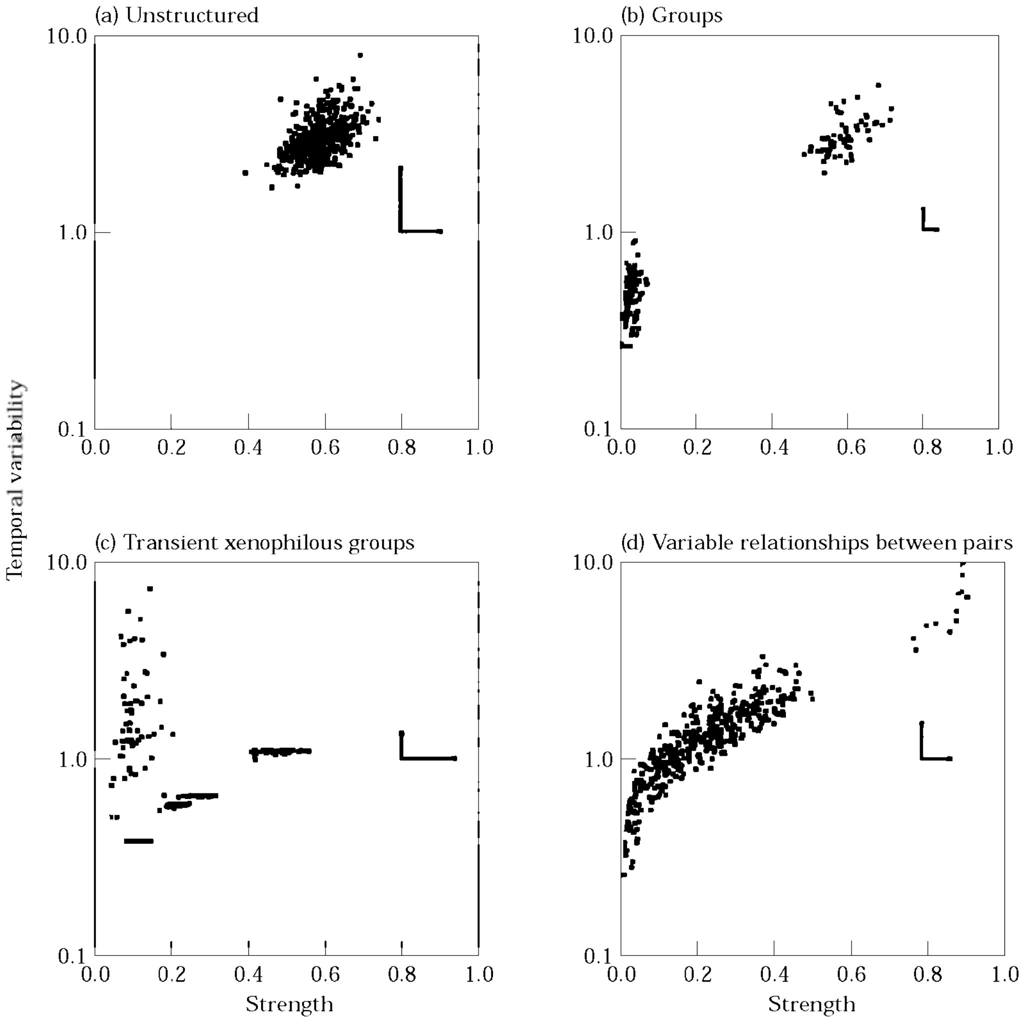


Figure 2. Representation of the relationships between 30 individuals in four simulated social organizations. Each point represents one relationship between two individuals. The temporal variability of the relationship (*Y*-axis) is plotted against its strength (*X*-axis). Also shown are measures of the precision of the plots for each relationship on each axis (1.96 × SE). See Appendix.

between X and Z is within the region, then the relationship between Y and Z is within the region). Then the population can be divided into closed groups defined by the relationships found within the region. Figure 3 is the same plot as Fig. 2b, except that trios of relationships (X and Y, Y and Z, X and Z) are linked to form a triangle when at least two of them are in the region with strength greater than 0.4. Because all such triangles are contained within this region, relationships in this region are transitive and define closed groups. The upper left-hand dispersed cluster in Fig. 2c also delineates a region in which relationships are transitive. If some measures of interaction represent dominance asymmetries, then regions within which relationships are transitive may exist which represent dominance hierarchies. In some cases it may be useful to relax the condition of transitivity (e.g. if it is true for 80% of the pairs of relationships within the region) to define semi-closed groups, or to account for imperfect data recording.

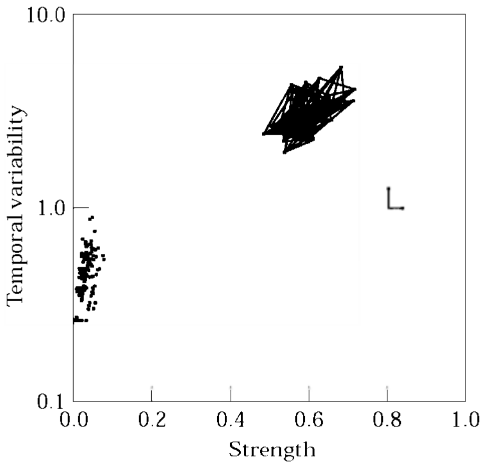


Figure 3. Representation of the relationships between 30 individuals in a simulated social organization as in Fig. 1b, but with triangles joining trios of relationships between three animals in which at least two of the relationships have strength greater than 0.4. The relationships in this region are transitive and can be used to delineate closed groups.

Hierarchical levels of grouping

More than one region in multivariate relationship space may be found that satisfies the condition of transitivity, so that different types of grouping are present. Frequently these regions will enclose one another so that the levels of grouping are hierarchical (e.g. Dunbar 1988; Connor et al. 1992; Whitehead et al. 1992; Lazo 1994), but this need not necessarily be the case.

AN EXAMPLE: SPERM WHALES OFF ECUADOR

The Data

To illustrate some of these techniques, I have used data on sperm whales, *Physeter macrocephalus*, collected off the Galápagos Islands and mainland Ecuador between 1985 and 1992 (Whitehead et al. 1991). This data set is large (many recorded interactions), but because the population is also large (~3500 individuals; Whitehead et al. 1992) and the animals are mobile and hard to view, it necessarily contains only little information on most pair-wise relationships.

Although the results presented in this paper are generally valid representations of what we know of sperm whale sociality, here the data and the results drawn from them are used illustratively and are not discussed in their full biological context.

Observation periods were days from 0600 to 1800 hours during which individual whales were photographically identified when available (Arnbom 1987). To simplify these presentations, I consider only the 202 whales identified on 3 or more days (except in Fig. 4, where individuals sighted on 2 or more days are used).

Interactions

Three interaction measures were calculated for each pair of whales on each day. Each measure was zero if only one of the whales was identified on the day, and missing if neither were. The interaction measures follow.

$I_1=1$ if whales photographed diving together during the day;
$I_1=0$ otherwise.

$I_2=1$ if whales photographed within 2 h of one another during day;
$I_2=0$ otherwise.

$$I_1=I_3(X,Y)=[\Sigma_{i=1}^{N(X)} 5/(5+t(i))]/N(X)$$

where whale X was identified N(X) times during the day, and $t(i)$ was the shortest interval between the ith identification of X and an identification of Y (taken to be infinity if greater than 4 h) (Whitehead & Arnbom 1987). Thus, if two whales were always sighted together, $I_3=1.0$; if usually sighted 15 min apart, $I_3=\sim 0.25$; if never sighted within 4 h, $I_3=0.0$.

Two classes of individual were considered: mature males (5 individuals) distinguished from their much greater sizes, and females and immatures (197 individuals), hereafter termed ‘females’.

Relationships

There are 20 301 (symmetric) relationships between the 202 animals. Discussing even a few of them individually is not productive. Shown in Table I are the means of each interaction measure, both overall and within and between classes.

Female–female and male–female relationships as expressed by I_1, I_2 and I_3 appeared to be similar

Table I. Mean values of interaction measures for Ecuador sperm whales

	Interaction measure		
	I_1	I_2	I_3
Overall	0.004	0.024	0.006
Female–female	0.004	0.024	0.006
Female–male	0.005	0.021	0.005
Male–male	0.000	0.020	0.001

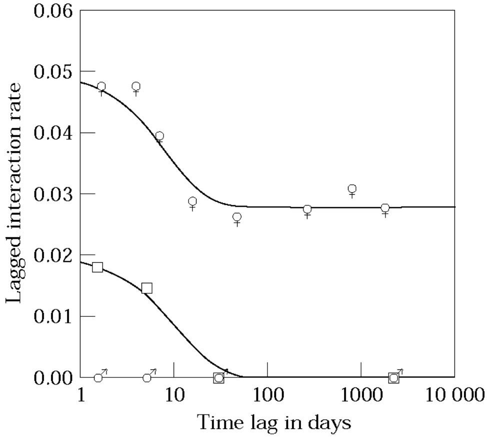


Figure 4. Lagged interaction rates over time periods from 1 day to several years for pairs of male sperm whales (♂), female sperm whales (♀) and male–female pairs (□) (modified from Figure 3 of Whitehead 1995). For the male–female and female–female data, curves are fitted based on exponential decay in the probability that individuals continue interacting.

in nature and quality (Table I), but males rarely interacted closely with one another (measures I_1 and high values of measure I_3 represent closer interactions than measure I_2). When lagged interaction rates are used to examine the temporal patterning in measure I_2, however (Fig. 4), the three inter- and intra-class patterns look very different: the males have no relationships with each other over intervals of a day or more and interact with particular females for periods of days but no longer; in contrast, pairs of females can, and often do, have relationships lasting years.

For each pair of individuals and each interaction measure, I defined a simple measure of temporal stability: the mean cross-product of the interaction measure between all pairs of days (on which an individual was identified) at least 10 days apart. This is zero if the whales were never associated on 2 days at least 10 days apart, and 1 if, on each pair of days (separated by at least 10 days) either animal was observed, the interaction measure equalled 1 on both days. The 10-day cutoff is suggested by the pattern in Fig. 4.

Social Structure

Association matrix and representations

A 202 × 202 association matrix is unwieldy, as are representations of it. The computer packages available to me cannot implement either cluster analyses or non-metric multidimensional scaling representations on such large matrices. Restricting to the first 60 whales identified (including no males) gave the representations in Figs 5 and 6.

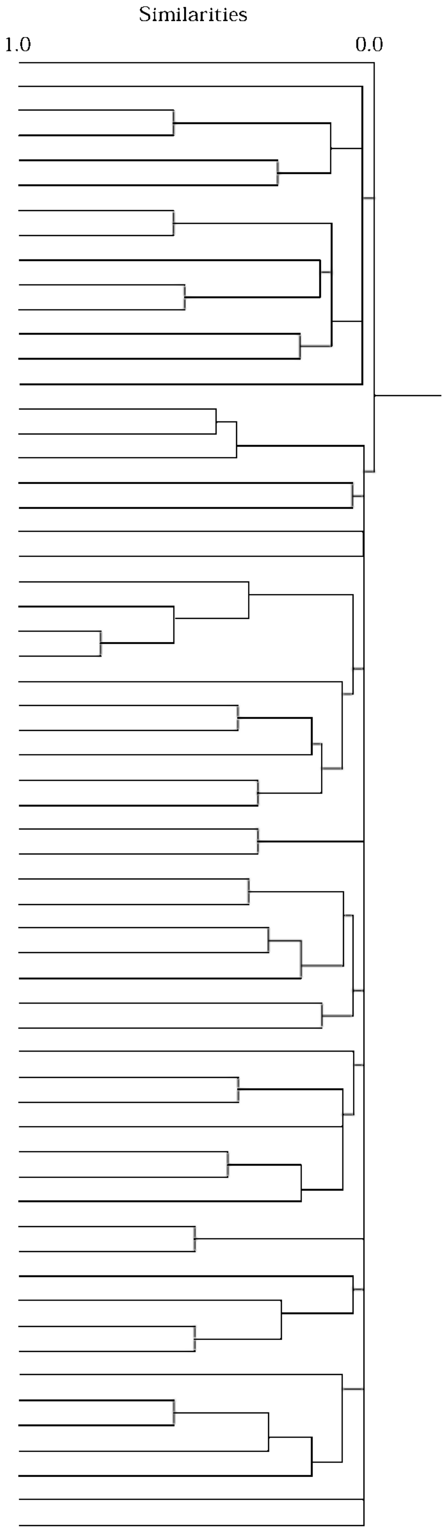
The average linkage cluster analysis using measure I_3 (Fig. 5) suggests some fairly closely associated pairs, some apparently solitary whales and a number of clusters of 5–10 animals. Interpretation is difficult, however, because it is not obvious which clusters are meaningful, although Whitehead & Arnbom (1987) suggested a procedure for delineating closed groups. The non-metric multidimensional scaling two-dimensional representation of the same association matrix (Fig. 6) is similarly ambiguous: there appear to be closely linked pairs, a somewhat distinct cluster (at the bottom of the diagram), but otherwise individuals possess a wide, and almost continuous, range of relationships.

Models of temporal change

Fitting models of exponential decay to the lagged interaction rates (for I_2) in Fig. 4 gives a more useful view of social structure. The methodology of choosing and fitting these models is described by Whitehead (1995). For female–female relationships, the probability of two individuals that are associated at any time, also interacting d days later is estimated to be:

$$0.051\ (0.51 + 0.49\ e^{-0.094d})$$

Thus about half the interactions remain at a similar level over periods of at least years. The other half decay to zero over periods of about 10 days. This result suggests that at any time



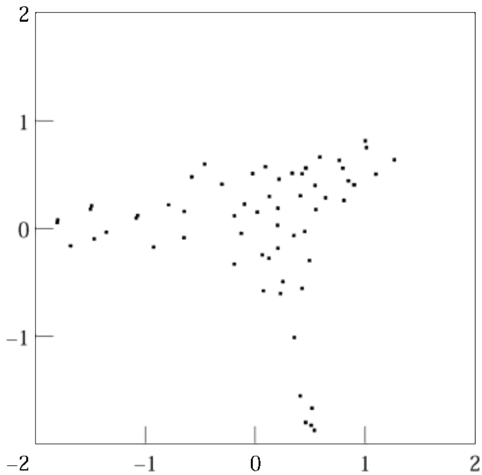


Figure 6. Two-dimensional non-metric multidimensional scaling plot of 60 female/immature sperm whales using interaction measure I_3. Each whale is represented by a point; those plotted closer together generally have closer relationships than those plotted further apart.

half an animal's associations (I_2 is a general measure of association) are with long-term companions, and half with temporary associates who will remain together for a few days (Whitehead et al. 1991). For male–female relationships, the probability of two individuals, associated at any time, also associating d days later is:

$$0.021\ e^{-0.085d}$$

This result suggests that mature males associate with females over periods of a few days, but rarely for longer.

Although these models of temporal change in interaction measures can give important insight into the social structure of a population, they do so measure by measure.

Multivariate representations

Principal components analysis was used to combine the three interaction measures (I_1 and I_3

Figure 5. Dendrogram showing average linkage cluster analysis of 60 female/immature sperm whales using interaction measure I_3. Each whale is represented by a horizontal line at the left-hand side of the diagram. Pairs of whales, or clusters of whales, are joined by vertical lines. Joins on the left of the diagram represent closer relationships than those on the right.

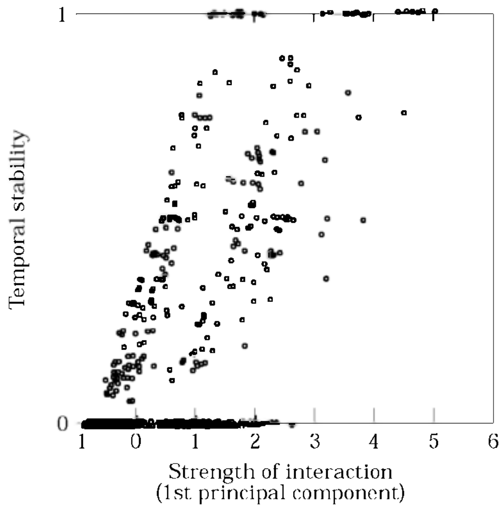


Figure 7. Relationships between Ecuador sperm whales. Each point represents one relationship, and the temporal stability (a measure of how frequently the two whales were identified within 2 h of one another over intervals of 10 days or more) is plotted against the mean strength of the interaction (the first principal component summarizing three measures of interaction).

were given arcsine square-root transformations to remove skew) into one composite ‘strength of interaction’, which represented 81% of the original variation in the interaction measures. Of the three measures of temporal stability (cross-products of interaction measures over more than 10 days), the first (derived from I_1) was zero for almost all (98.6%) relationships, and the other two, I_2 and I_3, were highly correlated (r_S=0.87), so only the measure of temporal stability from I_2 was retained. Then temporal stability (from I_2) was plotted against strength of interaction (the first principal component of the three interaction measures) in Fig. 7, where each point represents a relationship between two whales.

Figure 7 suggests three general categories of relationship between pairs of whales: (1) those plotted along the X-axis, with no temporal stability over more than 10 days and relatively weak interactions (all relationships including at least one male were of this type); (2) a few with strong and fully persistent (temporal stability equals one) interactions; and (3) an intermediate type with some temporal stability, in which temporal stability generally increases with the strength of the interaction.

Some features of Fig. 7 (e.g. the apparent discontinuity between relationships with perfect and partial temporal stability) may be artefacts of the methods used in manipulating the data. These issues can be explored theoretically or using simulation, but because the purpose of this analysis is to illustrate general methods, they will not be discussed further here.

A simpler and more tractable representation of the relationships is obtained by defining two categorical variables for each relationship, G the strength of interaction, and H the temporal stability:

- G=3 if whales ever observed diving together (I_1>0)
- G=2 if whales ever identified within 2 h of one another (I_2>0)
- G=1 if whales ever identified within 4 h of one another (I_3>0)
- G=0 otherwise (I_3=0)
- H=1 if whales identified within 4 h of one another on 2 days at least 10 days apart (cross-product of I_3 over $\geq$10 days >0)
- H=0 otherwise (cross-product of I_3=0)
- H=missing if neither whale identified over at least 10 days

A summary table for G and H for those relationships with G>0 and H not missing is given in Table II. The lack of long-term relationships for males is clear, as is the association between the strength (G) and temporal stability (H) of a relationship. The relationships of one individual (#234 identified on 11 days) are also summarized: it has temporally stable relationships with 19 individuals, and more temporary ones with 6 individuals.

The presentations of the patterns of relationships between pairs of female sperm whales in Fig. 7 and Table II suggest that closed, or nearly closed, groups may exist. In Table III, the transitivity of relationships is summarized using relationship measures G and H. In 79% of the cases in which an animal X has temporally stable relationships (H=1) with two other individuals, Y and Z, then Y and Z also have temporally stable relationships (H=1). When the X–Y and X–Z relationships are both temporally stable and strong (H=1, G=2–3), then 79% of the Y–Z relationships are also stable and strong. These results suggest closed, or nearly closed, temporally

Table II. Categorical summary of relationships for Ecuador sperm whales, for three levels of interaction strength (G), and two levels of temporal stability (H), between different classes of individuals and for relationships of female #234

Strength G	Stability H	Number of pair-wise relationships			
		♀–♀	♀–♂	♂–♂	♀#234–?
1 (2–4 h)	0 (unstable)	252	21	0	1
2 (0.1–2 h)	0 (unstable)	619	45	1	5
3 (together)	0 (unstable)	145	20	0	0
1 (2–4 h)	1 (stable)	10	0	0	0
2 (0.1–2 h)	1 (stable)	205	0	0	12
3 (together)	1 (stable)	148	0	0	7

Table III. Transitivity of relationships

Y–Z relationship		X–Y and X–Z relationships Stability: H(X,Y)=H(X,Z)=1 Strength: min(G(X,Y), G(X,Z))= Number of triads		
Strength: G(Y,Z)	Stability: H(Y,Z)	0–1	2	3
0–1	0	143	130	7
2	0	346	304	34
3	0	98	93	18
0–1	1	51*	45*	1*
2	1	1125*	1052*†	127*†
3	1	828*	808*†	279*†‡

Tabulated are the numbers of different types of Y–Z relationships in cases when relationships X–Y and X–Z are temporally stable (H(X,Y)=H(X,Z)=1; pairs observed together over 10 days apart), for 3 minimum levels of strength in the X–Y and X–Z relationships: min(G(X,Y),G(X,Z))=0–1 (not seen within 2 h), 2 (seen within 2 h), 3 (seen together).
*H=1 (stable relationships), 79% transitive.
†H=1, G=2–3 (stable and strong relationships), 78% transitive.
‡H=1, G=3 (stable and very strong relationships), 60% transitive.

stable groups. The typical group size, i.e. the average number of animals in the group of a randomly chosen animal (Jarman 1974), can be examined by plotting the number of temporally stable relationships an animal has against the number of pairs of days it was identified at least 10 days apart (Fig. 8). Fitting a binomial model to these data suggests that the whales have a mean of 17.4 temporally stable relationships. Thus the typical group size (number of constant companions plus one) is estimated to be about 18.

Summary: the social structure of Ecuador sperm whales

The analyses described above give an overall view of the surface structure of Ecuador sperm whales, as indicated by the nature, quality and temporal patterning of pair-wise relationships: females seem to live in temporally stable groups of typical size about 18; they interact with other females over periods of a few days or less, but show generally stronger interactions with their long-term companions. Males interact with the groups of females for periods of a few days, but rarely with each other. These results are consistent with earlier analyses of some of the same data by these and other techniques (Whitehead et al. 1991; Whitehead 1993).

In this section I have deliberately used a variety of analytic techniques. Some, such as the temporal analysis (Fig. 4) and examination of transitivity (Table III), were successful at uncovering aspects of the social structure of the sperm whales.

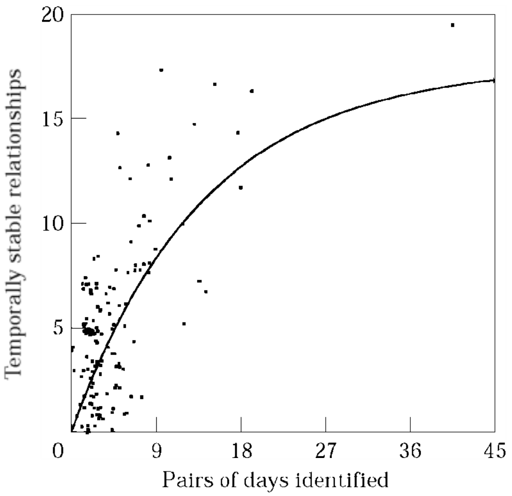


Figure 8. Number of temporally stable relationships (over more than 10 days) possessed by individual Ecuador sperm whales plotted against the number of pairs of days each individual was identified more than 10 days apart. Points are 'jittered' so as not to be superimposed. A fitted binomial model is indicated.

Others, such as the cluster analysis (Fig. 5), added little useful information. In situations with smaller population sizes and simpler structures, however, the reverse may be true. All the techniques illustrated here, as well as others, may be potentially useful in uncovering the surface structure of a population of identified individuals.

DISCUSSION

Hinde (1976) introduced a useful and generally accepted conceptual framework for considering social structure in animal populations. There has been no corresponding analytical framework, however. This has been a particular problem for species that have complex and fluid social organizations that cannot easily be classified hierarchically using dichotomous features. In some cases, involving populations in the laboratory or in especially favourable conditions in the wild (Goodall 1986), it is possible to describe a social organization in detail in the manner envisaged by Hinde (1976). Much more frequently, however, practical constraints on observing social interactions between identified individuals, and the lack of any standard analytical framework, have inhibited analysis of social structure. As a result, it is common practice to present little more than the mean size and composition of groups as a representation of social structure.

The central thesis of this paper is that if interactions between some identified individuals can be observed, then it is possible to analyse and describe the social structure of a population in an objective and rigorous manner that includes several measures of interaction and the vital dimension of time. This will not only give a more complete and realistic description of the social environment of individual animals, but also permit useful comparisons between populations and species. These, in turn, should assist us in classifying social organizations and defining social complexity.

In these analyses, it is often important to distinguish real features from methodological artefacts and random noise. For instance, a paucity of data points may induce apparent discontinuities in displays (e.g. Fig. 7), and cluster analyses of random interaction data (in which all pairs of animals have the same probability of interacting) will often appear to have structure. Monte Carlo analysis, in which simulated data sets with the same properties as the real data (number of animals, observation periods, sampling intensity) are run through identical statistical routines, can indicate methodological artefacts: do displays of simulated data also have the observed discontinuity? They can also be used to explore the patterns of display produced by 'null' models of social structure (e.g. random associations within the population).

More formal statistical hypothesis tests may give insight in several ways during an analysis of social organization. Often we may wish to know whether different segments of the population have different patterns of interactions. For instance: do the relationships of males with females differ from those between males and juveniles, or, do three communities within a population have different patterns of relationship? The Mantel test (Mantel 1967) is often an appropriate technique for looking at such questions, because it accounts for the lack of independence of relationships within a population, is non-parametric and versatile (Schnell et al. 1985). It can also be used to examine correlations between social structure and spatial patterns, ecological factors, or genetic structure.

Figure 1 shows the proposed analytical framework for analysing social organizations. The statistical methods used and referred to in this paper (summarized in Fig. 1) should be considered a list of the most commonly used current techniques augmented by procedures suggested to me by the implications of Hinde's (1976) framework, and by my analyses of social structure in cetaceans. There are surely other useful methods, some suited for particular types of data or social structure, and others of general relevance.

We will learn much more about the social structures of animal populations if we analyse them using clear conceptual and analytical frameworks, and develop better statistical techniques to work within these frameworks.

APPENDIX: DISPLAYS OF SIMULATED DATA

The displays in Fig. 2 illustrate how simple data on pair-wise interactions can be used to describe, and distinguish between, social structures.

I simulated four social structures, each containing 30 identified animals, which were observed on 15 consecutive days. On each day, 120 standard focal animal watches were made, with animals in the study area being selected randomly and independently for each watch. The absence/presence of an interaction between the focal animal and all other members of the population in the study area was noted for each watch. During a watch, interactions occurred with a probability p(X,Y) for focal animal X and other animal Y. On each day, an interaction measure between X and Y was calculated as the mean of: the proportion of watches of focal animal X during which an interaction with Y was observed, and the proportion of watches of focal animal Y during which an interaction with X was observed.

Two relationship measures were derived from these interaction measures. (1) The strength of the relationship: the mean of the interaction measure between X and Y over the days during which at least one of X and Y was watched. (2) The temporal variability (inverse of temporal stability) of the relationship: the coefficient of variation of the interaction measure between X and Y over the days during which at least one of X and Y was watched.

In Fig. 2, these relationship measures are plotted against one another to illustrate the surface structure of four simulated social organizations:

(1) Unstructured system in which p(X,Y)=0.6 for all X and Y.

(2) Groups in which the population consists of six groups of five members each:
 p(X,Y)=0.6 if X and Y are in the same group
 p(X,Y)=0.02 if X and Y are not in the same group.

(3) Transient xenophilous groups in which the population consists of six groups of five members each; all groups, except one which is resident, spend only 3 days (randomly chosen and consecutive) in the study area (so are transient); and individuals preferentially interact with members of different groups (so are xenophilous):
 p(X,Y)=0.1 if X and Y are in the same group;
 p(X,Y)=0.8 if X and Y are not in the same group, but both are in the study area;
 p(X,Y)=0.0 if X is in the study area, but *Y* is not;
 p(X,Y)=missing if *X* is not in the study area.

(4) Variable relationships between pairs in which the population consists of 15 pairs of animals:
 p(X,Y)=0.9 if X and Y are in the same pair;
 p(X,Y)=u; where u is a uniform random variable in the range 0–0.45 chosen separately for each relationship between pairs (and p(Y,X)=p(X,Y)) if X and Y are not in the same pair.

The temporal variability (logged) of each relationship is plotted against its strength in Fig. 2 for each of these social organizations. Also shown in each plot is an indicator of the precision (1.96 × SE) of each relationship measure.

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