

Investigating structure and temporal scale in social organizations using identified individuals

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Studies of individually identified animals can produce substantial data sets containing information on the structure and temporal scale of social organizations. However, methods of analyzing such data are not well established. Important features of a social organization are revealed by plotting the rate of persistence of the associations between pairs of individuals over a range of time lags (lagged association rate). The consistency of long-term relationships can be characterized using the rate of association of pairs of individuals between their first and last observed associations (intermediate association rate). A hierarchical series of models featuring exponentially decaying lagged association rates may be fitted to these data. This technique retrieved the essential parameters of five simulated social organizations and, when used on real data, portrayed the essential features of the patterns of temporal change in relationships between animals. The method should be especially useful for analyzing fission–fusion societies containing 10–10,000 individually identifiable animals. *Key words*: association, individual identification, social organization, temporal scale. [*Behav Ecol* 6:199–208 (1995)]

An accurate model of social organization is vital if we are to gain understanding of the ecological pressures affecting sociality (Myers, 1983). However, our current quantitative methods of describing social organization are relatively crude, and rarely incorporate the significant dimension of temporal scale.

Many studies of captive or wild populations generate large quantities of data on associations between known identified individuals. A standard and frequently employed procedure is to calculate indices of association between each pair of individuals (Cairns and Schwager, 1987). Maximum spanning trees, cluster analyses, and multidimensional scaling are often used to assist interpretation of these resulting association matrices (Morgan et al., 1976; Penzhorn, 1984). A simple way of incorporating temporal changes in relationships into such descriptions is to produce different association matrices, and displays of them, for different time periods (e.g., Lott and Minta, 1983; Morgan et al., 1976).

This approach suffers from several drawbacks. The time intervals must be long enough for sufficient data to be collected within each to provide a reasonably accurate association matrix. Thus changes in social organization over small time intervals are not examined. Second, the common techniques used to uncover social organization from association matrices become unwieldy with data sets containing hundreds or thousands of individuals. Nonmetric multidimensional scaling and some of the preferred clustering techniques, such as average linkage clustering, are often hard to implement on large data sets, and the resulting plots or dendrograms usually contain too much information to be assimilated easily. However large data sets from many animals, especially when collected over long time periods, potentially contain very detailed information about social organization. Finally, and perhaps most importantly, this approach does not quantify how the relationships between animals change over time.

There is no standard way in which the variability of social relationships over different time periods can be described.

Here, I develop a technique which uses data on associations between identified individuals to investigate how relationships between animals change over time. The methods of displaying information on social organization used by Underwood (1981) and Myers (1983) inspired the development of this technique, a form of which has been used by Whitehead et al. (1991) to examine social organization in female sperm whales (*Physeter macrocephalus*). The technique produces a simple portrayal of the principal temporal elements of the social organization of a population.

In many cases, it is possible to fit quantitative hierarchical models to the data based on exponential decay in the probability of an association persisting between two individuals. The models allow several different mechanisms of association and disassociation to operate at the same time between pairs of individuals within a population (e.g., constant companionships, temporary feeding associations, passing “tourist” relationships, death). These models will be appropriate in the many cases when the probability of disassociation is independent of the duration of an association. Included are most instances when disassociation might be triggered by the behavior of a third animal, or an unpredictable environmental event, or when the animals’ behavior towards one another does not change systematically during the length of the association. Excluded are situations where association and disassociation are related to external cycles, where animals tend to associate for a fixed time (e.g., an estrous or breeding period), or change their behavior toward one another as the association progresses (e.g., a courting pair). However, these models would appear to be appropriate approximations for many cognitively advanced animals which are flexible in their behavior and live in fission–fusion societies.

The method models the temporal duration of associations between individuals, and does not give a full description of the society. This has the advantage that many forms of social organization are included. However, once a particular set of parameters has been selected by the method described here, further tests may be required to elucidate details (e.g., distin-

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guishing between casual acquaintances within a society and migratory individuals passing through).

I will describe the method and show how it works on simulated data from five different social organizations, demonstrate its use on real data, and then discuss its advantages and limitations. For those interested in using the method, Appendix A steps through a simple example and Appendix B shows how the method can be modified to be used on data in which not all associates of an identified individual were necessarily recorded.

Analyzing the temporal scales of a social organization

The data

I assume that a population is observed during several short periods of time. These need not be regularly spaced but should be at integer multiples of some time unit. During each observation period a number of "key individuals" are observed (not all key individuals in the population need be observed each period), and the identities of the associates of the key individuals are recorded. Key individuals can be recorded as associates of other key individuals and often all individuals in a population may be considered key. However, there are circumstances in which it is useful to restrict the animals that will be considered key (see below). I will initially assume that all current associates of key individual are recorded, but the method can be modified to permit the incomplete recording of all associates (see Appendix B). The method of determining associates could be spatial (e.g., "seen within x meters of key individual"), temporal (e.g., "seen within x min of key individual"), or behavioral (e.g., "groomed key individual during observation period").

Thus the data set consists, for each observation period, of the identities of the key individuals seen during the period and, for each key individual, the identities of its associates.

Selection of key individuals

Sometimes it may be illustrative to consider one class of individuals (e.g., males) as key individuals, and another as associates (e.g., females). In this way it is possible to examine how relationships between individual males and individual females change with time.

Another reason to restrict the selection of key individuals may be to reduce bias caused by oversampling animals in large groups. Suppose two animals are considered to be associated if they are members of the same group, and that group size varies. Associations between members of large groups will often be less persistent than those between members of small groups. If, during any sampling period, groups are encountered with probabilities proportional to their size, then associations between members of large groups will be preferentially sampled. Then the mean persistence of randomly chosen associations between members of the population will be underestimated. In this case restricting the number of key individuals chosen from any group to the minimum group size will remove bias.

We may be more interested in the persistence of the average association of a randomly chosen member of the population than the persistence of a randomly chosen association between members of the population. If groups are sampled with the same probability regardless of size and all members of each sampled group are considered key, then we examine the persistence of randomly chosen associations. To examine the persistence of the average association of a randomly chosen member of the population, the number of key individuals chosen from any group should be restricted to the minimum size of a group in the population.

Lagged association rates

For any discrete length of time, d , and for each key individual, A , the pairs of sampling periods that A was identified d time units apart, are listed (indexed by j): $(t_{A,1,d}, t_{A,1,d} + d)$; $(t_{A,2,d}, t_{A,2,d} + d)$; ...; $(t_{A,j,d}, t_{A,j,d} + d)$; ... If the number of associates that were seen with key individual A at both time $t_{A,j,d}$ and time $t_{A,j,d} + d$ is $c(A, j, d)$, then the total number of repeat associations in the data set after time lags of d is:

$$C(d) = \sum_A \sum_j c(A, j, d). \quad (1)$$

This will include some repeat associations twice, if, for instance, both A and B were observed as key individuals and associating with each other at times t and $t + d$.

Let $g(d)$ be the probability that if B is an associate of A at time t , then it is an associate d units later. I assume that $g(d)$ is independent of t , so that the process is stationary in the statistical sense. If the number of associates of key individual A at time t is $N(A, t)$, then the expected number of repeat associates observed with key individual A at both times $t_{A,j,d}$ and $t_{A,j,d} + d$ is $N(A, t_{A,j,d}) \cdot g(d)$. Thus, the expected number of repeat associations after lags of d is:

$$Ex[C(d)] = \sum_A \sum_j N(A, t_{A,j,d}) \cdot g(d). \quad (2)$$

Then, combining Equations (1) and (2), the probability of association with a lag of d , $\hat{g}(d)$, can be estimated from:

$$\hat{g}(d) = \frac{\sum_A \sum_j c(A, j, d)}{\sum_A \sum_j N(A, t_{A,j,d})}. \quad (3)$$

$\hat{g}(d)$ is the association rate between individuals after a time lag d from a previous association. I call $\hat{g}(d)$ the "lagged association rate." The lagged association rate is, in many contexts, the same as Underwood's (1981) "proportion of companions remaining," and the "reassociation rate" of Whitehead et al. (1991). (I have been shown that "reassociation rate" is a confusing term in this context, and so I suggest its replacement with "lagged association rate.")

Plots of $\hat{g}(d)$ against d , such as in figure 3 of Underwood (1981) and on the time axis of figure 2 of Myers (1983) and in Figures 1–4 of this article can reveal much about the social organization of a population. If $\hat{g}(d)$ is roughly constant over a certain range of d , then this suggests that there is little change in the rate of association over this time scale. On the other hand, if $\hat{g}(d)$ falls dramatically, then there is significant disassociation over this time scale.

Distinguishing between reassociations and permanent companions

Plots of lagged association rates against time lag showing a similar shape, with a fairly constant, but nonzero, $\hat{g}(d)$ for large d , can be produced by very different models of social organization. For instance Figure 1c,d both show falls in the lagged association rate, $\hat{g}(d)$ over periods of 1–50 days, followed by constant, nonzero $\hat{g}(d)$. But (as explained below) Figure 1c represents data from a simulated population in which pairs of individuals with casual relationships repeatedly reassociated by chance in a small population, whereas Figure 1d represents a population in which there were permanent companions who associated constantly with one another. How can these situations be distinguished?

If a population estimate of the number of potential associates of a key individual, P , is available (e.g., from mark-recapture methods on the identification data), then an estimate of the lagged association rate for all lags d in the case of completely random association is:

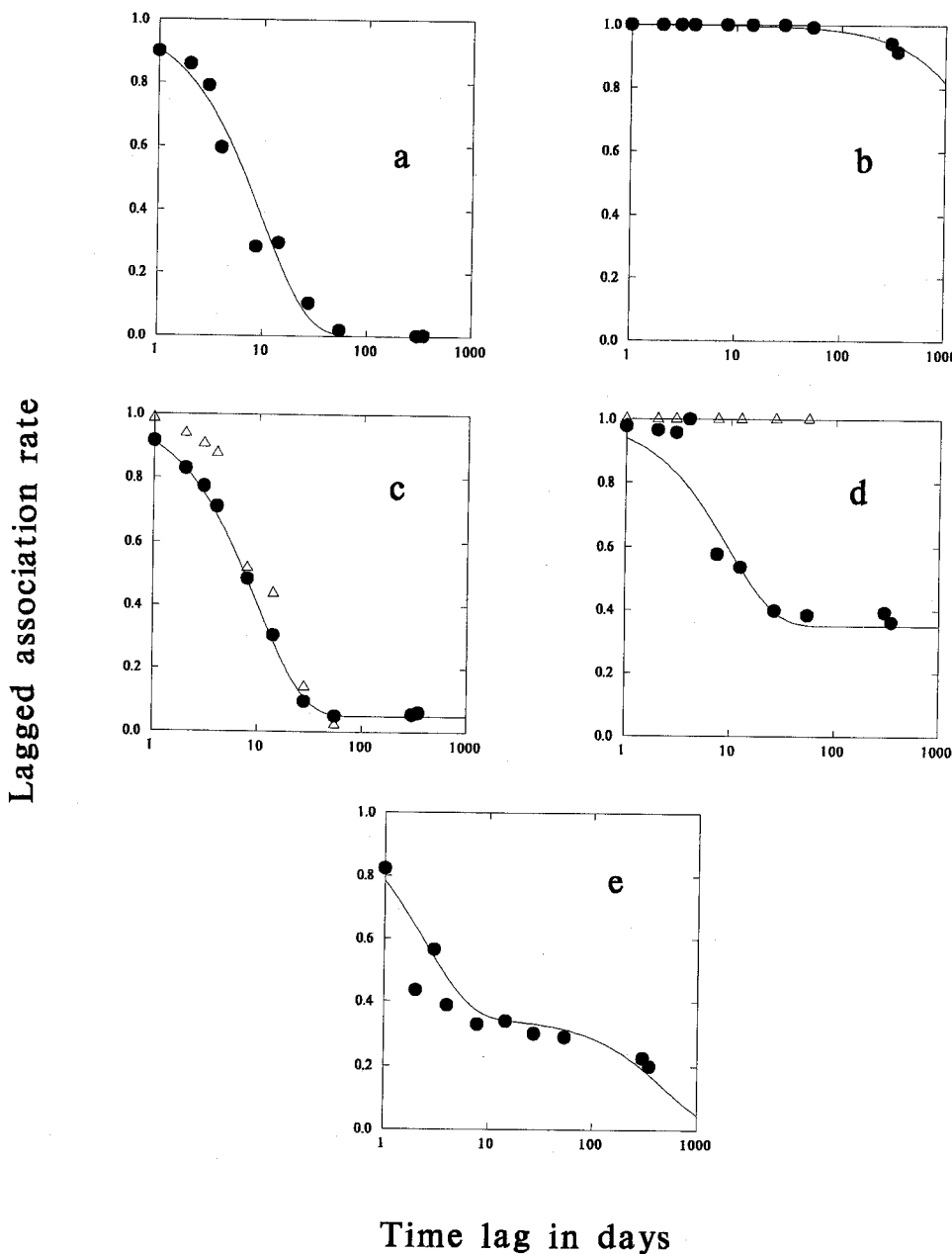


Figure 1
 Lagged association rates (●) over different time lags calculated from simulated observations of members of five social organizations. In each case the theoretical lagged association rate is shown by the curve. For simulations (c) and (d), intermediate association rates are shown by Δ.

$$\hat{g}(d) = M/P \tag{4}$$

where M is the mean number of associates of a key individual in any observation period. This “null” association rate can be compared with the lagged association rates calculated from the data as described above. In many cases P , the number of potential associates of a key individual, will simply be the population size minus one.

Additionally, or alternatively when the number of potential associates is not known, the association rates of pairs of individuals during observation periods between their first and last recorded associations can be examined (Whitehead et al., 1991). An “intermediate association rate” is calculated in a similar way to the lagged association rate, except that only time periods between the first and last recorded association of each diad are considered. An intermediate association of lag d between key individual A and individual B is recorded if B was observed associated with A d time units after their first association (and $\geq d$ time units before their last associa-

tion) or d time units before their last association (and $\geq d$ time units after their first association). Let $L(d)$ be the number of such intermediate associations of lag d . The number of potential intermediate associations of lag d , $Q(d)$, is calculated by summing for each key individual A , and each associate B , the number of occasions that A was observed d time units after the first association of B with A or d time units before the last association of B with A (which ever interval is smaller). The intermediate association rate is then:

$$\hat{h}(d) = L(d)/Q(d). \tag{5}$$

The intermediate association rate is an estimate of the probability that associates remain associated between their first and last identifications together. It will approximate 1.0 if associations with long lags are between members of permanent groupings which do not disassociate between observed associations (e.g., simulation d below; Figure 1d). Alternatively, if long-term reassociations often follow periods of separation

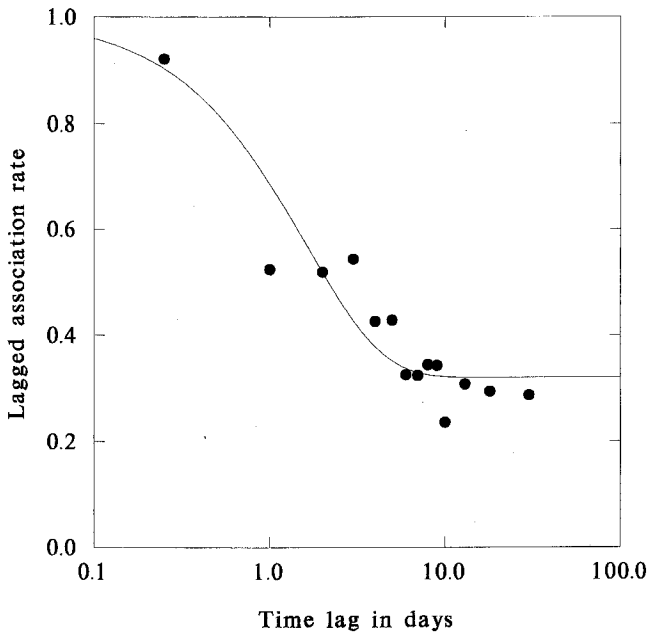


Figure 2
Lagged association rates (●) for Underwood's (1981) data on eland, together with fitted curve from model 3.

then the intermediate association rate's relationship with time lag will show a similar form to the lagged association rate (e.g., simulation c below; Figure 1c).

Modeling social organization

It is possible, in many cases, to proceed beyond displays of $\hat{g}(d)$ against d to quantify the major elements of the social organization.

A general model of a stationary (general features unchanged with time) social organization, can be built as follows. At any time, each individual, A , possesses K classes of associates. Each class contains a proportion p_k of the total number of associates (so that $\sum p_k = 1$) and members of class k stay associated with A for a random length of time distributed according to the negative exponential distribution with parameter μ_k . Then:

$$g(d) = \sum_{k=1}^K p_k \cdot e^{-\mu_k \cdot d}. \tag{6}$$

For one class we can have $\mu = 0$ so that pairs of animals in this class do not change their probabilities of association over the period of the study. Theoretically, complex societies might be modeled by considering many classes of associate (large K). However, it seems unlikely that it will often be profitable to consider more than three classes of associate when fitting models of the type represented by Equation (6) to actual data, as with $K > 3$ the model will have too many parameters for them to be estimated with any precision. This general model, then, includes the following specific models:

1. $g(d) = 1.0$. This corresponds to individuals forming permanent units, members of which never associate with members of other units. $K = 1, \mu_1 = 0$.
2. $g(d) = e^{-\mu \cdot d}$. This corresponds to a society of casual acquaintances in which associations last about $1/\mu$ time units, but are never permanent. $K = 1, \mu_1 = \mu$.
3. $g(d) = p_1 + (1 - p_1) \cdot e^{-\mu \cdot d}$. This can represent a society in which each individual has a number of permanent com-

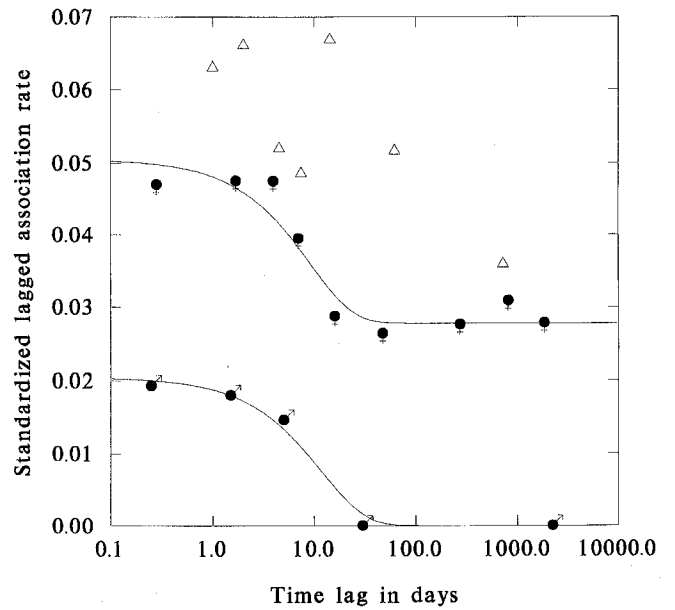


Figure 3
Standardized lagged association rates (●), and standardized intermediate association rates (Δ), for female and immature sperm whales off the Galápagos Islands. Also given are the lagged association rates when key individuals were mature males and associates were females or immatures (◐). Curves are fitted to both sets of data using model 3 when females and immatures were key individuals, and model 2 when mature males were key individuals.

panions, and also a number of casual acquaintances (e.g., Whitehead et al., 1991). $K = 2, \mu_1 = 0, \mu_2 = \mu$.

4. $g(d) = p_1 \cdot e^{-\mu_1 \cdot d} + (1 - p_1) \cdot e^{-\mu_2 \cdot d}$. This could correspond to a society in which each individual has some casual acquaintances with limited association periods, and more permanent

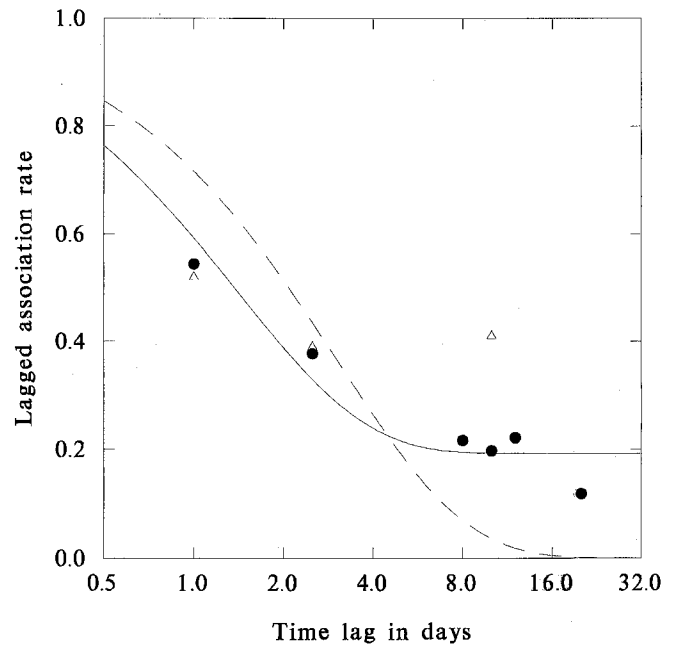


Figure 4
Lagged association rates (●) and intermediate association rates (Δ) for the data set in Table 2, from the calculations in Tables 5 and 7. The fit of model 2 to the lagged association rates is shown by a dashed line, and model 3 by a solid line.

companions, who, however, do eventually disperse or die. $K = 2$.

5. $g(d) = p_1 + p_2 \cdot e^{-\mu_2 d} + (1 - p_1 - p_2) \cdot e^{-\mu_3 d}$. In this society each individual has some permanent companions, and two other classes of acquaintances, one more casual than the other. $K = 3$.

From Equation (6), a relationship between the estimates of $g(d)$, the lagged association rates, obtained from pairwise association data, and the parameters of the model can be derived:

$$\hat{g}(d) = \sum_{k=1}^K p_k \cdot e^{-\mu_k d} + \text{Error}. \quad (7)$$

There are as many relationships (7) as there are lags d . These can be used to estimate the parameters (μ 's and p 's) of the model using nonlinear estimation procedures such as those in the NONLIN module of SYSTAT (Wilkinson, 1990). In my experience with analyzing simulated data, it appears that the exact form assumed for the error term has little effect, and it is usually easiest to assume normally-distributed error terms with mean 0 and constant variance so that least-squares estimation procedures can be used.

The parameter estimates resulting from such a procedure might be considered representative of the true social organization. However, the $\hat{g}(d)$'s are not always independent (as observations on particular days are used in calculating $\hat{g}(d)$'s for different d 's) and the fit of the model to reality is at this time unknown. Therefore, the estimated standard errors resulting from the nonlinear estimation procedure should be treated carefully. Jackknife methods of assessing standard errors are almost certainly better. To do this, parameter estimates are calculated with different sets of observation periods being omitted from the analysis in turn. If the sets of observation periods are reasonably separated in time, they can be considered independent. Jackknife estimates of the parameters and their standard errors are then calculated as usual (e.g., Sokal and Rohlf, 1981).

Suggested procedure for analyzing a data set

I suggest the following procedure when analyzing a data set:

(A) Decide on procedure for selecting "key" individuals, either when sampling in the field or from a comprehensive data set collected previously. Care should be taken not to bias the selection of key individuals (e.g., oversampling those in large groups—see above).

(B) Decide on criteria for association.

(C) Calculate $C(d)$'s, number of repeat associations, and $\Sigma \Sigma N(A, t_{A,j,d})$, the potential number of repeat associations, for each time lag d .

(D) Group time lags so that $\Sigma \Sigma N(A, t_{A,j,d})$ is reasonably large for each d .

(E) Calculate estimates of lagged association rates, $\hat{g}(d)$, for each d , and plot $\hat{g}(d)$ against d . Usually it will make sense to plot d on a logarithmic scale. Plotting the lagged association rates on a logarithmic scale may help interpretation in some cases but is impossible in situations where $\hat{g}(d) = 0$ (e.g., Figure 3), and will overemphasize the importance of variation in the lagged association rate when it is small.

(F) Examine the plot and choose one or more of the models given above, or others, to fit to the data (e.g., if $\hat{g}(d) \approx 1.0$ for all d then try model 1; if $\hat{g}(d)$ is declining at high d then try models 2 and/or 4; if $\hat{g}(d)$ falls and then rises with increasing d then consider models of cyclical association).

(G) Estimate the parameters of each model tested and their standard errors, preferably using the jackknife procedure.

(H) From the fit of the model to the data decide on the most appropriate model.

(I) Examine null association rates and/or intermediate association rates to learn more about longer term associations. An example of this procedure is given in Appendix A.

Examples

Examples using simulated data sets

Five simulated data sets were used to verify this technique:

(a) *Casual acquaintances with no permanent companions.* A closed population of 2000 individuals was randomly assigned to 200 social groups. At any time, pairs of individuals were considered associated if they were members of the same group at that time. Individuals left groups at a rate of 0.05 per day. On leaving they randomly joined any of the 200 groups (which could include their previous group; groups could temporarily have zero members). The population was observed on the following days: 1, 2, 3, 4, 5, 11, 12, 13, 14, 15, 31, 32, 33, 34, 35, 61, 62, 63, 64, 65, 361, 362, 363, 364, 365. On each observation day, 12 individuals were randomly chosen from the population, and their associates (animals within their group) were noted. All animals observed (the original 12 on each day as well as their associates) were considered key animals for the analysis. This procedure corresponds to a random search for 12 groups in the field on each day with the probability of detecting a group being proportional to its size. For the model that generated this data set the probability that two individuals were associated after a lag d from a recorded association, which I will call the theoretical lagged association rate, $g(d)$ was nearly $e^{-2 \times 0.05d} = e^{-0.1d}$, as each member changed groups at a rate of 0.05 per day.

(b) *Nearly stable groups with some mortality/emigration.* This data set was generated with the same parameters and observational protocol as the preceding one except that the rate of leaving a group was 0.0001 per day, giving a mortality/emigration rate of about 3.6% per year. The theoretical lagged association rate was $e^{-0.0002d}$.

(c) *Casual acquaintances within a small population.* The social structure was as in simulation (a) except that the population size was 200 individuals, and it contained 20 groups. In this case the probability of a pair of individuals being grouped together at any time, once their common grouping had been severed by one leaving, was the inverse of the number of groups, $1/20 = 0.05$. Then the theoretical lagged association rate was $e^{-0.1d} + (1 - e^{-0.1d}) \times 0.05 = 0.05 + 0.95 \cdot e^{-0.1d}$.

(d) *Constant companions and casual acquaintances.* Each individual from a population of 2000 was randomly assigned to one of 200 permanent units (so that some units might have no assigned members), between which there was no migration. Each unit was randomly assigned to one of 100 groups (which could have no members temporarily). Units left their group with a probability of 0.05 per day. On leaving they randomly joined any of the 100 groups. The observation schedule was as in (a) above, except that the groups of eight randomly selected individuals were used on each observation day, and five members of each group were randomly chosen to be key individuals. The restriction to five key individuals per group eliminated virtually all of the bias caused by preferentially sampling large groups (see "Selection of key individuals," above). The probability that a randomly chosen association of a randomly chosen individual was between members of the same permanent unit, p_1 (the lagged association rate over long time periods), is then given by the ratio of the number of associations at any time that are between members of the same unit to the number which are between members of the same group. This is:

Table 1
Comparison between theoretical parameters and mean and SD (in parentheses) of estimated parameters for ten runs of each of five simulated social organizations

Simulation	Model tested	Theoretical parameters			Estimated parameters		
		p_1	μ_1	μ_2	\hat{p}_1	$\hat{\mu}_1$	$\hat{\mu}_2$
a	2	—	0.1	—	—	0.097 (0.010)	—
b	2	—	0.0002	—	—	0.00017 (0.00004)	—
c	3	.05	0.1	—	.050 (.005)	0.094 (0.010)	—
d	3	.349	0.1	—	.343 (.035)	0.094 (0.029)	—
e	4	.349	0.4	0.002	.350 (.023)	0.530 (0.116)	0.0018 (0.0003)

$$\hat{p}_1 = \frac{\sum_{w=1}^W u(w) \cdot [u(w) - 1]}{\sum_{i=1}^I v(i) \cdot [v(i) - 1]}$$

where there are W units with $u(1), u(2), \dots, u(W)$ members each and I groups with $v(1), v(2), \dots, v(I)$ members each. In this simulation, using the initial unit and group sizes, \hat{p}_1 was 0.349. The theoretical lagged association rate for this social organization was then $0.349 + 0.651 \cdot e^{-0.1d}$.

(e) *Nearly constant companions and casual acquaintances.* This simulation was similar to simulation (d) except that units left groups with a probability of 0.2 per day, individuals died and were immediately replaced by new individuals in the same unit and group at a rate of 0.001 per day, and a total of 10 key individuals were randomly chosen from each group observed. In this case the theoretical lagged association rate was $0.349 \cdot e^{-0.002d} + 0.651 \cdot e^{-0.402d}$.

For these five simulated data sets, plots of lagged association rates against time lag (on a logarithmic axis) for the first simulation run are shown in Figure 1, together with the theoretical lagged association rate derived above. In Table 1, the means and standard deviations of the parameters of the fitted models for 10 runs of each simulation are compared with the parameters of the theoretical lagged association rates of the models used to simulate the data. The characteristics used to generate the simulated social organizations seem to have been retrieved by the method.

Intermediate association rates are plotted against d for simulations (c) and (d) in Figure 1. There are clear differences between the intermediate associations in the two cases. In simulation (c), the intermediate association rate closely follows the lagged association rate, suggesting that individuals are no more likely to be associated a reasonable period after an observed association whether they were known to reassociate much later or not, so individuals frequently disassociated between known associations. For simulation (d), in contrast, the intermediate association rate was virtually 1.0 for all measured d suggesting that individuals never disassociated between observed associations. Thus, in many cases, intermediate association rates can shed further light on the structure of the social organization.

Examples using real data

Eland. Underwood (1981) presents lagged association rates for an eland (*Taurotragus*) herd numbering about 70–80, in Loskop Dam Nature Reserve, South Africa. His lagged association rates are transcribed in Figure 2, and the fit of model

3 is indicated. The estimated parameters were $p = 0.321$ and $\mu = 0.618/\text{day}$. The groupings of eland are not very stable. The mean "number of companions found with the average eland" was about 10 (figure 4b in Underwood, 1981), which, together with a population size of 75, from Equation (4) gives a "null" association rate of about 0.13/day in the case of random associations. This is about half the estimate for p , suggesting that there are some long-term preferred companionships among the eland.

Sperm whales. Whitehead et al. (1991) used an earlier version of the method described in this article to analyze the social organization of female sperm whales and their offspring around the Galápagos Islands using identification data collected between 1985 and 1989. Roughly 4000 individuals use the study area, of which about 1500 have been identified from photographs of their natural markings (Whitehead et al., 1992). In this case "association" was defined as "potentially able to be photographed within 2 hr," and, as not all associates of a key individual were photographed on each occasion, standardized lagged association rates were used (see Appendix B). The plots in Figure 3 essentially represent the data and analysis of Whitehead et al. (1991) with a few modifications. A small data set collected in 1991 was added, extending the range of time lags available. The analysis only used the first 10 individuals photographed each day as key individuals, to avoid the bias of counting proportionally more associations per individual in larger groups (see "Selection of key individuals," above). Standardized intermediate association rates for females and immatures are shown in Figure 3. Figure 3 also presents the standardized lagged association rates when large mature males were considered as key individuals and females and immatures as potential associates.

As in the Whitehead et al. (1991) presentation, the plot of standardized lagged association rate suggests two levels of relationship among females and immatures: reasonably long-term associations and more casual acquaintances that disassociate over periods of about 10 days. The standardized intermediate association rates are similar to, but rather higher than, the standardized lagged association rate over short time-lags, implying that most long-term repeat associations are between permanent companions. However the intermediate association rate appears to decrease with increasing time lag (Figure 3), suggesting that some of the associations over long lags may not have been permanent. The low value of the intermediate association rate found over lags of about 2 years is based on few data and so this conclusion must be viewed cautiously.

Fitting model 3 to these standardized lagged association

rates, and using a jackknife procedure (with sets of observation periods in the same calendar year as units), gave estimates of $p = 0.511$ (SE 0.108), $\mu = 0.094/\text{day}$ (SE 0.195), and the mean number of associates $M = 19.7$ animals (SE 2.8). The small differences between these estimates and those of Whitehead et al. (1991) are largely due to the removal of bias by considering only 10 key individuals per day in the current analysis, and the use of the jackknife procedure. Thus, the female and immature sperm whales off the Galápagos seem to live in permanent units containing about 11 individuals ($19.7 \times 0.511 + 1$). These form temporary groups with an average of about one other unit which last about 10 days.

The large males, which were very rare and never reassociated with one another, had associations with the females and immatures lasting about 10 days, but never, in our data set, any longer (Figure 3). Fitting model 2 to these data gave estimates of $\mu = 0.085/\text{day}$ and $M = 49.0$. There were too few data for jackknife estimates of standard errors of these parameters to have much meaning, so they should be treated most cautiously. The males seemed to stay associated with particular females and immatures for just a few days.

Discussion

The method described in this article allows major features of a social organization to be extracted from information on associations between identified individuals. It is not a substitute for the detailed portrayals of individual association patterns which can be realized by cluster analyses, maximum spanning trees, or multidimensional scaling. But these techniques implicitly portray social organization as static, and they can become very unwieldy with more than 100 or so animals. In contrast, the technique described in this article explicitly displays, and then models, how relationships between animals change over different time scales from an animal-centered viewpoint, as advocated by Jarman (1982). It thus appears particularly appropriate for use on "fission-fusion" societies, and especially when data are collected over long time-periods for hundreds or thousands of animals. The use of this approach on the Galápagos sperm whales gave us a much more powerful model of their social organization than previous studies of the same data using cluster analysis (Whitehead and Waters, 1990; Whitehead et al., 1991). The model of social organization generated by the method described herein was then used as an important part of a mark-recapture analysis of population size (Whitehead et al., 1992).

The method can use a wide range of definitions of an association between individuals, can examine associations between and within different classes of individual (e.g., male and female sperm whales in the example), and is not dependent on a knowledge of the population size (although this is useful when interpreting results). It also allows the persistence of relationships between animals to be portrayed simultaneously over a wide range of time periods. It seems likely that if two definitions of association (e.g., ones based on spatial proximity and coordination in behavior) reflect the same underlying social organization of a population, then parameters of the fitted models will be similar. Thus the fitted model of social organization may be reasonably robust with respect to the definition of association employed. If this is borne out by tests, then the methods described in this article may be useful in comparing the social organizations of different populations or species for which data have been collected in different ways.

The ability to model aspects of social organization may be of use in comparative studies, or in searches for the ecological correlates of social organization. For instance, the time scales of disassociation of units of female sperm whales from each

other, and mature males from females, which are both about 10 days, may be related to some feature of their environment, dispersion, or physiology which also varies on this temporal scale.

The method is not suitable for studies of all social organizations. It will add little to straightforward description when the population size is smaller than about 10 animals, and it will require very large data sets and become computationally unwieldy with more than about 10,000 animals, as a substantial portion of the population must have been identified on several occasions. Substantial data sets are needed to obtain good estimates of the lagged association rate, and especially the intermediate association rate, over long time-lags. In situations where animals form clearly closed groups, it will confirm the obvious. However, many animals live in populations of between 10–10,000 and are organized into societies where pairwise associations show some change with time. There has been no standard analytical technique suitable for analyzing these social organizations, particularly over the temporal scale.

The method is not theoretically applicable in situations where the nature of the social organization shows changes with time (i.e., is not "stationary"), as when there are seasonal changes. This problem can be partially overcome by just considering data from time periods short enough for the change in the nature of the social organization to be small, or data from the same season in different years. A comparison of analyses on such subsets of the data could be used to examine the assumption of stationarity.

Although the models considered in this article based on exponential decays in lagged association rates incorporate many likely forms of real social organization, some possibilities are excluded. For instance, if individuals reassociate on a cyclical schedule, this might lead to a rise in association rate with increasing time lag. However, the hierarchy of models should approximate most natural systems. They contrast with Cohen's (1971) models of group size in that they do not assume particular processes for the formation and break up of groups, and so are more generally applicable.

APPENDIX A

Analyzing the temporal scale of a social organization, a worked example

To demonstrate this method of analyzing the temporal scale of a social organization, I have made up a data set which is small enough to be viewed easily and analyzed by hand, but which contains some potentially interesting features.

Suppose a small population of individually identified birds uses a number of roosts. Five of these roosts are surveyed during 4 days at the start of each 10-day period over a total of 24 days. The surveys are carried out at the same time each day and it is noted who is roosting at each of these five roosts. The complete data set is given in Table 2.

These data can be analyzed as follows (following the steps outlined in the "Procedure" section):

- (A) All individuals sighted are considered "key."
- (B) Individuals are considered associated on a particular day if they are observed in the same roost.
- (C) In Tables 3 and 4, the individuals observed with lags of 3 days and 23 days are listed with the numbers of repeat associations and potential repeat associations. Similar calculations to this were done for other lags.
- (D) These numbers of repeat associations and potential repeat associations for each time lag are listed in Table 5. The lags are then grouped so that the number of potential repeat associations is greater than 120 for each set of lags.

Table 2
Hypothetical observations of the roosting associations of 18 individually identified birds (a, b, . . . , r) observed on twelve different days

Day	Roosting companionships					
1	ab	c	defg	hi	j	
2	abde	kl	chi	fgm	n	
3	ade	fgmo	klj	hi	n	
4	ad	mo	cihp	q	kjn	
11	cdej	fh	hi	l	mo	
12	abq	cder	fh	mo	j	
13	abn	cdmno	lq	e	fhi	
14	elq	fgh	abd	cmno	j	
21	jk	hir	ceg	p	do	
22	af	dmo	bjkp	e	n	
23	af	dmno	er	jp	cg	
24	bceg	dmn	jp	o	afn	

(E) The lagged association rates, $\hat{g}(d)$, are calculated for each of the grouped time lags (Table 5), and are plotted in Figure 4.

(F) The data set is small so that only simple models can be fitted with any utility. The lagged association rate decreases with time lag (Figure 4) so that models 2 [$\hat{g}(d) = e^{-\mu \cdot d}$] and 3 [$\hat{g}(d) = p + (1 - p) \cdot e^{-\mu \cdot d}$] are indicated.

(G) The fit of the models 2, dashed line, and 3, solid line, is shown in Figure 4. These models were fitted to the lagged association rates [the $\hat{g}(d)$'s shown in the last column of Table 5], using the NONLIN module of SYSTAT (Wilkinson, 1990).

(H) It is clear in Figure 4 that model 3 (solid line) is a much better fit to the data than model 2 (dashed line). The fitted parameters of model 3 are $p = 0.192$ (SE 0.077) and $\mu = 0.714$ (SE 0.259). The standard errors of these estimates

Table 3
Number of repeat associations and potential number of repeat associations for lags $d = 3$ in the data of Table 2

Key individual <i>A</i>	Times seen <i>j</i>	Observed with lag 3 on days		Repeat associations $c(A, j, 3)$	Potential repeat associations $N(A, t_{A,j,3})$
		$t_{A,j,3}$	$t_{A,j,3} + 3$		
a	1	1	4	0	1 (b)
c	1	1	4	0	0
c	2	11	14	0	3 (dej)
c	3	21	24	2 (eg)	2 (eg)
d	1	1	4	0	3 (efg)
d	2	11	14	0	3 (cej)
d	3	21	24	0	1 (o)
e	1	11	14	0	3 (cdj)
e	2	21	24	2 (cg)	2 (cg)
f	1	11	14	0	1 (h)
g	1	21	24	2 (ce)	2 (ce)
h	1	1	4	1 (i)	1 (i)
h	2	11	14	0	1 (i)
i	1	1	4	1 (h)	1 (h)
j	1	1	4	0	0
j	2	11	14	0	3 (cde)
j	3	21	24	0	1 (k)
l	1	11	14	0	0
m	1	11	14	1 (o)	1 (o)
o	1	11	14	1 (m)	1 (m)
o	2	21	24	0	1 (d)
p	1	21	24	0	0
Total				10	31

Table 4
Number of repeat associations and potential number of repeat associations for lag $d = 23$ in the data of Table 2

Individual <i>A</i>	Times seen <i>j</i>	Observed with lag 23 on days		Repeat associations $c(A, j, 23)$	Potential repeat associations $N(A, t_{A,j,23})$
		$t_{A,j,23}$	$t_{A,j,23} + 23$		
a	1	1	24	0	1 (b)
b	1	1	24	0	1 (a)
c	1	1	24	0	0
d	1	1	24	0	3 (efg)
e	1	1	24	1 (g)	3 (dfg)
f	1	1	24	0	3 (deg)
g	1	1	24	1 (e)	3 (def)
j	1	1	24	0	0
Total				2	14

were calculated by estimating p and μ for three data sets as in Table 2 but with days 1–4, days 11–14, and days 21–24 missed out respectively, and then using the jackknife procedure (Sokal and Rohlf, 1981: 796).

(I) The population size is 18 so the potential number of associates $P = 18 - 1 = 17$. From the data in Table 2, the mean number of associates of any individual $M = 1.89$. This gives a null association rate of $M/P = 0.11$, which is less than the estimate of p but greater than its lower 95% confidence limit. This suggests (although not significantly) that some of the longer-term associations indicated in Figure 4 are preferred companionships, not simply the results of random reassociation within a small population. Intermediate association rates for lags of 3 days and 9 days are calculated in Table 6. Similar calculations were made for other lags, and the results are shown in Table 7. The lags are grouped so that the number of potential intermediate associations for each group of lags is greater than 20. The intermediate association rates are plotted in Figure 4. They are clearly less than 1.0 so that pairs do disassociate and then reassociate. However, the intermediate association rate at lags of about one week is greater than

Table 5
Calculating lagged association rates from data in Tables 3 and 4

Lag in days <i>d</i>	Number of repeat associations $\sum \sum c(A, j, d)$	Potential repeat associations $\sum \sum N(A, t_{A,j,d})$	Lagged associations rate $\hat{g}(d)$
1	86	158	86/158 = 0.544
2	36	91	
3	10	31	
7	4	28	44/204 = 0.216
8	14	70	
9	26	106	
10	28	142	28/142 = 0.197
11	24	111	
12	16	67	
13	6	30	46/208 = 0.221
17	4	18	
18	8	29	
19	8	48	30/252 = 0.119
20	6	62	
21	0	48	
22	2	33	}
23	2	14	

Table 6
Intermediate associations of lags 3 days and 9 days from data in Table 2

Key individual	Companion individual	Seen together on days:		Key individual seen on day:	Companion an associate? 1 = Yes
		First	Last		
Time lag of 3 days					
a	b	1	14	4	0
c	e	11	24	14	0
c	e	11	24	21	1
d	a	2	14	11	0
d	b	2	14	11	0
d	e	1	12	4	0
d	m	13	24	21	0
e	b	2	24	21	0
e	c	11	24	14	0
e	c	11	24	21	1
e	g	1	24	21	1
f	g	1	14	11	0
g	e	1	24	21	1
h	i	1	21	4	1
i	h	1	21	4	1
Total: 6/15					
Time lag of 9 days					
e	b	2	24	11	0
h	i	1	21	12	0
j	k	3	22	12	0
m	o	3	23	12	1
m	o	3	23	14	1
o	m	3	23	12	1
o	m	3	23	14	1
Total: 4/7					

For each pair of key and companion individuals, listed are the occasions on which the key individual was sighted 3 days after the first sighting of the two animals together (and at least 3 days before their last sighting), or 3 days before the last sighting (and at least 3 days after the first sighting). The final column indicates whether the companion individual was an associate on each occasion. Similarly for lags of 9 days.

the lagged association rate, suggesting some consistent preference for roosting companions over about this time scale.

This analysis indicates that pairs of these (imaginary) birds remain roosting companions for periods of about 1.4 days ($1/\mu$). Over periods of 1–3 weeks there seem to be some preferred associations between pairs, although these are not constant.

APPENDIX B

Procedure when not all associates are recorded

The procedure described in this article can be amended to be used in situations when not all associates of a key individual are necessarily recorded. In this case $N(A, t)$ is the observed number of associates of key individual A at time t . Of these $N(A, t) \cdot g(d)$ will be expected to be real associates at time $t + d$. At time $t + d$ a proportion $N(A, t + d)/M$ of the real associates will be observed, where M is the mean number of real associates of a key individual. Then the expected number of observed associates of key individual A at time t that are also observed associates at time $t + d$ is approximately $N(A, t) \cdot g(d) \cdot N(A, t + d)/M$, and the expected total number of repeat observed associations over lag d is:

$$E\{C(d)\} = \sum_A \sum_j N(A, t_{A,j,d}) \cdot g(d) \cdot N(A, t_{A,j,d} + d)/M.$$

Table 7
Calculation of intermediate association rates from the data in Table 6

Lag in days d	Number of intermediate associations $L(d)$	Potential intermediate associations $Q(d)$	Intermediate association rate $\hat{h}(d)$
1	28	54	28/54 = 0.52
2	14	36	
3	6	15	
7	0	1	20/51 = 0.39
8	4	6	
9	4	7	
10	4	11	
11	0	4	
Total: 12/29 = 0.41			

Then, $g(d)/M$, which I will call the “standardized lagged association rate” (“standardized reassociation rate” in Whitehead et al., 1991) can be estimated from:

$$\hat{g}(d)/M = \frac{\sum_A \sum_j c(A, j, d)}{\sum_A \sum_j N(A, t_{A,j,d}) \cdot N(A, t_{A,j,d} + d)}.$$

These standardized lagged association rates can be plotted against time lag d (e.g., Figure 3), and M becomes another parameter to estimate in the generalized model given by Equation (7):

$$\hat{g}(d)/M = \sum_{k=1}^K p_k e^{-\mu_k d}/M + \text{Error}.$$

M can usually be estimated successfully by this technique if there is little disassociation over the shortest time lags considered. In this case $\hat{g}(d)/M \approx 1/M$. If the shortest time lags considered are greater than the $1/\mu_k$'s then M will not be estimable by this method.

A “standardized intermediate association rate” can be calculated from a modification to Equation (5):

$$\hat{h}(d)/M = L(d)/Q(d).$$

This can be compared with the standardized lagged association rate. If, for a particular range of d , the standardized intermediate association rate, $\hat{h}(d)/M$, is similar to the standardized lagged association rate for short time lags then little temporary disassociation is indicated. If, on the other hand, $\hat{h}(d)/M$ falls with d as $\hat{g}(d)/M$, then individuals separate between observed association events.

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