Techniques for Analyzing Vertebrate Social Structure Using Identified Individuals: Review and Recommendations

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I. INTRODUCTION

Social structure is an important level of biological organization, influencing processes at both lower and higher levels. For instance, social structure seems to be closely related through evolution to the cognitive and communicative ability of animals (Byrne and Whiten, 1988) and is often an important element of population dynamics (Wilson, 1975). Thus both behavioral and population biologists have concerned themselves with the description and classification of social structure (here synonymous with social organization).

There is a fairly standard system for describing and classifying the social structures of insects based on aggregative behavior, the reproductive division of labor, and cooperation in the care of offspring (Michener, 1969). This system, an axis ranging from "solitary" to "eusocial," is sometimes applied to vertebrate social structures (e.g., Jarvis, O' Riain, Bennett, and Sherman, 1994). However, it does not encompass much of the richness and flexibility found in some vertebrate societies, and its utility has even been questioned for insects (Costa and Fitzgerald, 1996).

The description and classification of vertebrate social systems have generally developed in a piecemeal way with few sets of guiding principles. An exception is the framework suggested by Hinde (1976), which he hoped would be useful in structuring the analyses of primatologists, anthropologists, sociologists, and social psychologists. In this framework, the basic elements are interactions between individuals (Fig. 1). The content, quality, and temporal patterning of the interactions between a pair of individuals describe their relationship, and the content, quality, and patterning of the relationships between members of a population define the social structure
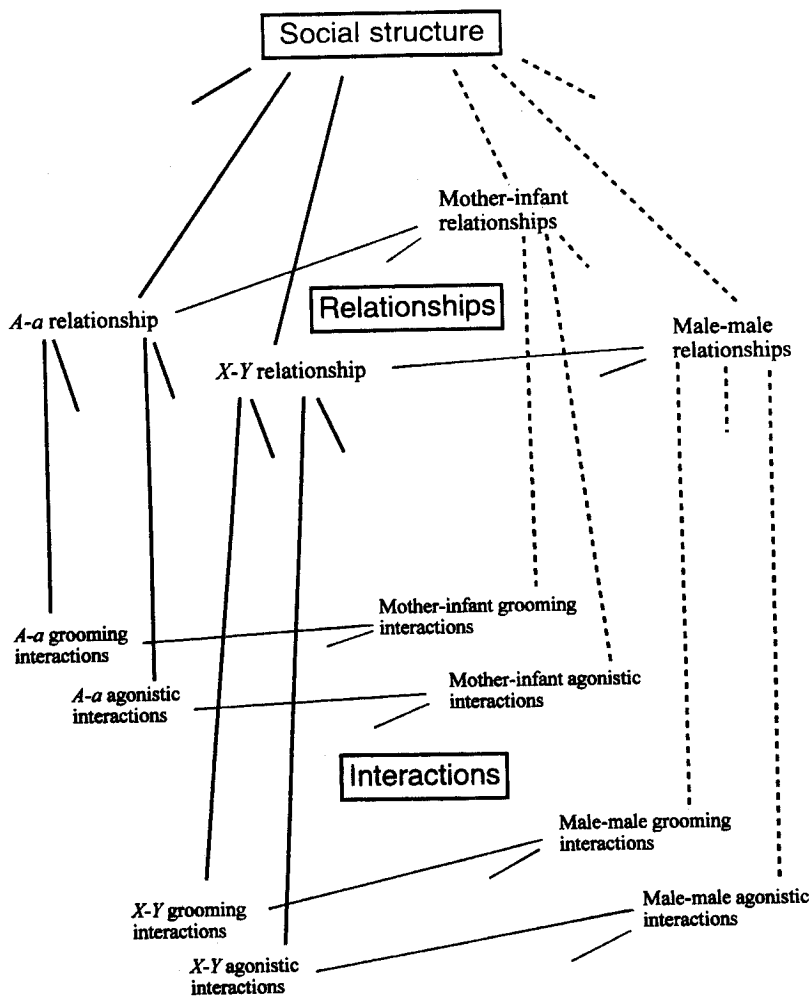
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FIG. 1. Diagrammatic representation of the relations between interactions, relationships, and social structure (simplified from Hinde's, 1976, Fig. 1). "*A–a*" is a mother–infant dyad and "*X*" and "*Y*" are males. Interactions and relationships between pairs of individuals are shown on the left, abstractions to classes of individuals on the right.

(Hinde, 1976; Fig. 1). At the levels of interactions and relationships, abstractions can be made from dyads to classes of individual (Fig. 1). Hinde's framework has been explicitly referred to in a number of influential books on social organization, especially in primates (e.g., Goodall, 1986; Cheney, Seyfarth, Smuts, and Wrangham, 1987; Dunbar, 1988).

Hinde (1976) implicitly assumes the ability to collect detailed data on interactions between all members of a social community, a situation which is rarely achieved in the wild habitat of most species. Although it is possible to adapt Hinde's framework for use with less-accessible species (Whitehead, 1997), there is no standard procedure for describing or classifying vertebrate social structures, and an array of techniques has been developed by scientists working more or less independently.

In this chapter we review the analytical methods used in fairly recent attempts to describe nonhuman vertebrate social structures using identified individual animals. If animals are not identified individually then any description of social structure is constrained to be simplistic in many respects. We first describe the methods used in selecting studies and summarize the characteristics of the study populations. We then roughly follow Hinde's framework in summarizing and discussing the techniques used to examine interactions (including how associations may be used in place of interactions), relationships, and social structure. We end with a series of recommendations aimed at scientists involved in this kind of research and a brief discussion of its value. Our intentions are to help those conducting new studies to choose appropriate methods and, perhaps, to structure the search for better techniques.

II. METHODS

The following CD-ROM data bases (those available to us) were searched for the terms "social organization," "social structure" and "association pattern": Silver Platter Aquatic Sciences and Fisheries Abstracts (1978–1995); Silver Platter Psychlit (1985–1995); Silver Platter Life Sciences (1986–1995); and Science Citation Index (January, 1994 to March, 1996). Additionally, the Science Citation Index (January, 1994 to March, 1996) was searched for papers in which Hinde (1976) was cited. This search yielded 1635 references, of which 421 papers appeared to describe studies of nonhuman vertebrates (based on their titles and abstracts).

From a quick inspection of the materials and methods sections of these 421 papers, we restricted attention to those in which individual animals had been identified by any means (whether radiocollared, tagged, banded, or through natural markings). At this time, additional references were added by manually searching through the tables of contents of journals too recent to be on the CD-ROM system and through the reference lists of some of the more informative papers found in the CD-ROM search. The result was 239 articles which looked at the social organization of a population of nonhuman vertebrates by means of identification of individual animals.

From a more detailed reading of these 239 papers, we selected those which endeavored to measure pairwise interactions or associations between individual animals and attempted a synthetic description of social structure. Where more than one study looked at the same population of animals we used the most comprehensive or, if they were equally comprehensive, the most recent. This left 84 papers which described a total of 88 studies. These are listed and summarized in Appendix A.

In each of these studies, we noted whether the population was captive or wild; the size of the study population (when given); the number of identified individuals; and whether animals were classified by sex, age, or age class. Studies were classified by how interactions or associations between individuals were defined and how relationships between pairs of animals were measured. We also noted methods of displaying an overview of the social structure of the population, any consideration of the temporal patterning of interactions or associations, and whether the paper contained a reference to Hinde's framework.

III. STUDY POPULATIONS

A. CHARACTERISTICS OF STUDY POPULATIONS

Characteristics of the 88 study populations are summarized in Table I: 75 (85%) were of nonhuman mammals, 11 (13%) of birds, and 2 (2%) of fish (Table I). Among the mammals, studies of ungulates, primates, and cetaceans were most common but 10 mammalian orders (including the 2 orders of ungulates, which we combined) were represented. The majority (86%) of studies were of wild animals, although our list included six studies of captive ungulates, five of primates and one of bats (Table I). Population sizes (usually the size of the study population), when given, ranged from 4 captive crowned lemurs (*Eulemur coronatus*) (Kappeler, 1993) to ~3500 sperm whales (*Physeter macrocephalus*) (Whitehead, Waters, and Lyrholm, 1991) and 3500 Hector's dolphins (*Cephalorhynchus hectori*) (Slooten, Dawson, and Whitehead, 1993). Population sizes were generally higher for nonterritorial species, including all cetaceans and many ungulates, than for territorial animals, such as some primates (Table I).

The number of identified individuals in each study varied from 4 (the crowned lemurs) to just over 1000 for a few ungulate and cetacean studies. In most cases (60%) between 20 and 200 animals were identified (Fig. 2).

Both the age (or age class) and sex of individuals were reported in the majority (77%) of studies, and sex alone was available in an additional 14%.

TABLE I

SUMMARY OF THE NUMBER OF STUDIES FOUND FOR EACH VERTEBRATE TAXON, THE CODE FOR THAT ANIMAL, AND THE NUMBER OF STUDIES OF CAPTIVE ANIMALS

Taxon	Animal code	Number of papers	Number captive	Population size	Number identified
Ungulate	Un	25	6	8–2500	8–1084
Primate	Pr	18	5	4–160	4–160
Cetacean	Ce	12	0	155–3500	32–1295
Carnivore	Ca	7	0	6–3000	6–216
Rodent	Ro	6	0	74–1250	18–60
Chiropteran	Ch	4	1	27–≥524	27–524
Marsupial	Ma	1	0	98	98
Proboscidea	Pb	1	0	615	615
Insectivore	In	1	0	≥ 26	26
Bird	Bi	11	0	13–≥786	12–786
Fish	Fi	2	0	≥33–≥66	33–66
Total		88	12	4–3500	4–1295

B. BIASES OF THIS REVIEW

Our method of selecting studies of social organization for this review, those whose methodology approximated that proposed by Hinde (1976), biased our search toward certain types of social organization, principally
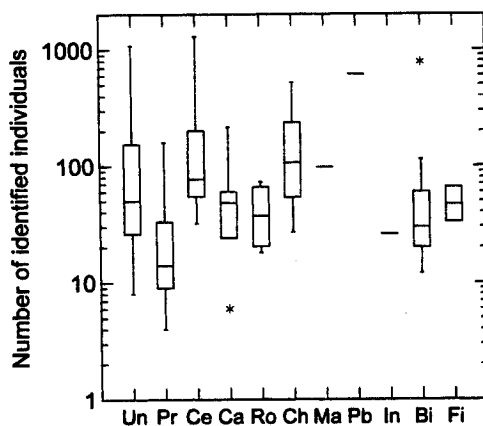

FIG. 2. Boxplot of numbers of identified animals in studies of different taxa. See Table I for abbreviations for the x-axis.

those described as "fission–fusion." These are societies in which most animals associate with a number of other animals at different times, but associations form and are broken over a range of time scales. Although the most common taxa in our survey, the ungulates, primates, and cetaceans, often have fission–fusion societies, they are not unique in this respect: many birds form temporary flocks and fish schools rarely, if ever, have unchanging membership. However, bird flocks and fish schools often contain too many individuals for individual identification to be practical, and studies of the social organization of populations in which animals cannot be individually identified were excluded from our sample, as Hinde's (1976) framework is not really applicable.

Some vertebrate taxa which have received considerable attention from behavioral ecologists are conspicuously absent from our sample, such as amphibians and pinnipeds. Although many frogs and seals are social, they principally aggregate to breed, and breeding aggregations are generally studied using a different set of techniques from those suggested by Hinde (1976).

Thus our sample is strongly biased toward populations with continuous fission–fusion social organizations where interactions or associations between identified individuals can easily be viewed. It is biased against very large populations or populations in which large groups are often formed, against solitary species, and against those that aggregate principally for breeding.

C.   Taxonomic Styles in Studies of Social Organization

Within our sample, there are some general differences in style between studies of the different taxa. For instance, studies of primates generally considered a few tens of animals (Fig. 2) of known age class and sex and often used several different measures of interactions or associations. In contrast, cetacean populations were usually larger, ranging into the thousands, and studies frequently lacked information on age class and sex and only considered one measure of interaction or association, often based on presence in the same group (Appendix A; see below). However, cetacean studies were generally more sophisticated in their treatment of the temporal patterning of interactions or associations (see below). Studies of ungulates ranged over both primate and cetacean styles with wide variation in population size, available information about age class and sex, the number of measures of interaction or association considered, and analysis of temporal patterning (Fig. 2; Appendix A).

IV. INTERACTIONS, ASSOCIATIONS, AND GROUPS

A. INTERACTIONS

In Hinde's (1976) framework for the examination of social structure, the fundamental elements are behavioral interactions between dyads (or possibly larger numbers) of animals (Fig. 1). These interactions define relationships, which in turn determine social structure (Fig. 1). Therefore, to follow Hinde's framework literally, we must observe and measure interactions. This can be done quite well with captive animals (e.g., Kappeler, 1993), but it poses severe problems for field researchers working with less-accessible animals. For instance, many cetologists rarely view anything that might reasonably be called an interaction between identified members of their study population. Therefore, consciously or unconsciously, they adopt an alternative.

B. ASSOCIATIONS

If we know the circumstances in which interactions between animals usually take place (spatial ranges, behavioral types, etc.), then we can use records of the presence of dyads in such circumstances—often termed "associations"—as substitutes for records of actual interactions in analyses of relationships and social structure (Whitehead, 1997). Costa and Fitzgerald (1996) emphasize the utility of using communication, which forms the basis for most interactions, in studying social organization. With detailed information relating rates and types of interaction to types of association—for instance, "at what spatial ranges do animals interact?"—then the observation of associations is a legitimate and useful procedure which shortcuts the need for extensive records of interactions.

However, it is important to recognize that, even when such justifications are available, observations of associations contain less information on social structure than observations of interactions: what animals do to one another is more important than whether they are near one another. For instance, different types of interaction, such as mating or grooming, may take place in very different circumstances and so cannot both be well correlated with one measure of association. Potentially, although rarely in practice, more than one definition of association could be used to lessen the simplification.

Thus it is preferable, where possible, to record interactions instead of, or in addition to, associations. However, in many circumstances and especially with animals that are hard to observe, the systematic observation of interactions is not logistically possible and so records of associations are the best viable route to a model of social structure.

C. THE "GAMBIT OF THE GROUP"

Unfortunately, for many animals (including nocturnal and aquatic animals), information on the circumstances under which interactions take place is also unavailable, and for many it is unlikely to be obtained in the near future. So, consciously or unconsciously, many ethologists studying social organization make what might be called "the gambit of the group": they assume that animals which are clustered (usually spatially, but temporal clustering is sometimes also important) are interacting with one another and then use membership of the same cluster, sometimes called the "group," to define association. This allows measures of association to be calculated and social structure to be analyzed.

In the papers we read, the term "group" often had this connotation but the term was used inconsistently both within and between studies of different taxa. Definitions varied from "all study animals" (frequently the case in primate studies) to long-term associates (some cetaceans, rodents) to short-term spatial aggregations. In this chapter we use "group" for a spatial aggregation over time scales sufficiently short that there are few changes in group membership (giving it a similar meaning to the primatologists "party"). With defined groups, associations may be delineated if we make the gambit of the group.

But, is the gambit of the group justified? Can group membership be used as a substitute for records of interactions? It is clearly reasonable if (1) all, or almost all, interactions take place within groups, and (2) interactions are similar and take place at a uniform rate between all pairs within a group.

Sometimes, the first of these conditions can be defended if, for instance, groups are generally separated by distances greater than the maximum range of communication by the animals. The second condition is harder to verify and less likely to be true. However, in most cases a failure of condition 2) (for instance, if interactions generally take place between the closest animals within a group) will not be disastrous: the proportion of time that two individuals are in the same group will not be a perfect predictor of their rate of interaction but these variables should be well correlated. In other situations, for instance, where a group consists of parent–infant pairs together with other animals, interactions may take place very heterogeneously among dyads in the group.

The greatest concern is that membership in observed groups may have little or nothing to do with rates of interaction. This could happen if the clustering of individuals is not social but related to external factors, such as the presence of prey or in refuges from predators, and no individual would behave differently if other group members were removed.

In summary, in many situations where animals are hard to observe, it is necessary to make the gambit of the group if we are to proceed toward a

model of social structure. However, there are circumstances where this step is not justified. Therefore, it is important to consider all evidence which bears on the validity of the assumption that the rate at which a dyad interacts is well correlated with the proportion of time they are found in the same group.

D. Interaction and Association Measures

Thus, observations of interactions, associations, or group membership can potentially be used to quantify relationships and so to study social structure. These observations are represented by "interaction measures" or "association measures." Examples of interaction and association measures are counts of grooming bouts (interactions), nearest-neighbor records (associations), or "presence in the same group." Interaction and association measures between pairs of individuals are collected during sampling periods indexed by time (Whitehead, 1997). They can be counts (e.g., "number of vocalizations"), continuous (e.g., "time spent grooming"), or one-zero measures (grouped or not).

In most of the studies in our sample only one interaction or association measure was recorded (Table II). However, in some instances two or more types of interaction or association were measured (e.g., Ficken, Witkin, and Weise, 1981; Nakagawa, 1992; Newberry and Wood-Gush, 1986; Somers, Rasa, and Penzhorn, 1995), such as spatial proximity (an association measure) and grooming frequency (an interaction measure). When one measure was collected, this was generally a one-zero record of association (Table II).

Association between individuals was usually determined spatially (Table II). Sometimes animals were considered associated if they were "within x meters of one another" [x varied from 1 m (Koenig and Rothe, 1991) to 500 m (Leuthold, 1979)] "within y body lengths" (e.g., Weinrich, 1991) or

TABLE II
Interaction and Association Measures

Number of studies with
≥ 2 interactions or association measures: 28
One interaction or association measure:
Observations of behavioral interactions: 4
Spatial measure of association: 21
Temporal measure of association: 2
Association based on group membership: 31
Spatial + behavioral measure of association: 2

"nearest neighbors" (e.g., Kappeler, 1993). In special circumstances, other methods were used to define associations. For instance, for rodents association was often inferred from overlap of home ranges (e.g., Behrends, Daly, and Wilson 1986; Karlsson, 1988; Marinelli and Messier, 1993), and in studies of deep-diving sperm whales, time intervals between identifications at the start of dives were used to define association (Whitehead *et al.*, 1991).

Frequently, taking the gambit of the group, animals were assigned to spatially distinct groups and considered associated if they were members of the same group (Table II). Methods of assigning animals to groups were sometimes formal, such as the chain rule (within x meters of another member of the group) (e.g., Smolker, Richards, Connor, and Pepper, 1992), sometimes informal (e.g., "recognizable cluster within school" (Norris, Würsig, Wells, and Würsig, 1994) or "roosting together" in chiropteran studies (Wilkinson, 1985; Williams, 1986; McWilliam, 1988; Kozhurina, 1993), and in other cases not described. On a number of occasions observable behavior, such as coordination, was used as part of the definition of group (e.g., Braeger, Würsig, Acevedo, and Henningsen, 1994).

It is entirely appropriate that studies of different animals measure interactions and associations in different ways: different species have disparate ways of interacting and some animals can be observed much more easily than others. However, the method of measuring an interaction (whether by counting events, noting associations, or making the gambit of the group) should correspond as closely as possible to what is a significant interaction for the animals being studied. Studies of communication, and especially the circumstances in which communication takes place, are very important in making this justification.

V. MEASURES OF RELATIONSHIP (INCLUDING ASSOCIATION INDICES)

The content and quality of the interactions between a pair of animals can be summarized by computing one or more summary statistics for each interaction or association measure (such as the mean, median, or whether a particular type of interaction or association was ever observed). These can be used as measures of a pair's relationship, following the terminology of Hinde (1976; Fig. 1) and so can be termed "measures of relationship" (Whitehead, 1997).

A. ASSOCIATION INDICES

In most of the studies which we read, only one type of measure was considered: the presence or absence of association. The common procedure

was then to use these association data to compute an "association index" for each pair of animals. This was usually (implicitly or explicitly) an estimate of the proportion of time a pair of individuals spent in association. An obvious estimate of the association index of A with B is the proportion of observations of A. or proportion of time observing A, in which it was associated with B.

Such indices have two principal potential problems. If A is more or less likely to be observed when with B than when not with B then they are biased (Cairns and Schwager, 1987) and, generally, when calculated this way, the association index of A with B will be different from that of B with A, whereas the true proportion of time spent associating is the same whichever way the animals are listed (Ginsberg and Young, 1992). For a number of reasons it is desirable to have a symmetric ($i_{AB} = i_{BA}$) association index, and a number of formulae have been used for this purpose (Cairns and Schwager, 1987; Ginsberg and Young, 1992; Appendix B).

The studies in our sample used a range of approaches to the issue of measuring relationships (Table III). Sometimes no attempt was made to calculate an index, with the authors simply reporting counts of joint occurrences (8/88 studies), occurrences within the same group (3/88 studies), or other summary statistics (Table III). In three studies, asymmetric indices of association, the proportion of joint occurrences, or the proportion of time together were presented. However, more usually, a symmetric association index was calculated. The most popular in the studies we read were the "half-weight" (the number of samples in which A and B were observed associated divided by the average of the number of samples in which A and B were observed; 21/88 studies), "twice-weight" (the number of samples in which A and B were grouped divided by the total number of groups observed which contained A or B or both; 11/88 studies), and "simple ratio" (the number of samples in which A and B were associated divided by the number of samples in which A or B or both was observed; 13/88 studies) (Table III). For nine of these simple ratio studies (five of captive animals), all animals were observed in each sampling period, making the simple ratio index equivalent to the proportion of joint occurrences.

An index of association is usually intended to be an estimate of the proportion of time that a pair spend associating. Except in cases (usually involving captive animals) in which the associations of all individuals in the population are observed during each sampling period, choosing an appropriate index of association is not mathematically straightforward (Cairns and Schwager, 1987; Ginsberg and Young, 1992). A number of methods for calculating association indices are in use, some originating in the ecological literature and not necessarily suitable for measuring associa-

TABLE III
ASSOCIATION INDICES AND OTHER MEASURES OF RELATIONSHIP (MORE THAN ONE MEASURE OF RELATIONSHIP OR ASSOCIATION INDEX WAS USED IN SOME STUDIES)

	Un	Pr	Ce	Ca	Ro	Ch	Ma	Pb	In	Bi	Fi	Tot
Indices of association												
Proportion of joint occurrences	1	2				1				1		5
Proportion of time together											1	1
Half-weight[a]	6	4	5	1		1	1			3		21
Twice-weight[a]	2	3	2							4		11
Simple ratio[a]	5		2	2				1	1	1	1	13
Square root[a]	2	1										3
Cole's index of association[b]	1		1									2
Dimensionless information index[b]						1						1
Social affinity index[b]	1											1
Mother–offspring relative affinity[b]	1											1
Distance coefficient[b]	1											1
Other relationship measures												
Counts of joint occurrences	2	2	1	2		1						8
Occurrence within same group	1			1	1							3
Distance between individuals	1			1								2
Distance travelled together				1								1
Coefficient of sociality[b]				1								1
Reciprocal value of proximity frequency		1										1
Occurrence of home range overlap	1			1							1	3
Proportion of home range overlap	1	1		1	4					1	2	10
Proportion of space use overlap					1							1
Counts of nearest neighbor occurrences	1	1										2
Proportion of nearest neighbor occurrences		5										5
Preferred partner for affiliative interactions	1											1
Counts of affiliative interactions	1	7		1	1							10
Proportion of affiliative interactions	1	3										4
Counts of coincident behaviors	1											1
Number of breeding attempts										1		1
Counts of agonistic interactions	1	6			1							8
Counts of outcomes of agonistic interactions	1			1						1		3
Rates of different types of interactions	1										1	2
Proportion of different types of interactions						1						1

[a] Terminology of Cairns and Schwager (1987); see also Appendix B.

[b] See Appendix B.

tion between animals (Cairns and Schwager, 1987; Ginsberg and Young, 1992).

Cairns and Schwager (1987) reviewed the problem of estimating association and concluded that it was very important to consider the procedure by which associations were recorded, preferably by using maximum likelihood techniques to derive association indices. Ginsberg and Young (1992) noted the difficulties of obtaining maximum likelihood estimators and suggest the adoption of the statistically unbiased simple ratio technique.

None of the studies that we read used association indices derived using maximum likelihood techniques. Thirteen of the studies we examined employed simple-ratio indices, but in nine of these cases all animals were observed each sampling period so the simple ratio is identical to the proportion of time observed together. Some authors (e.g., White and Burgman, 1990) were conscientious about using recording and analytical techniques, such as focal animal sampling (Altmann, 1974), to reduce bias in association indices, but this was not always the case. Although most of the studies in our sample (60%) followed the publication of Cairns and Schwager's paper, their important advice has not been generally heeded. The quite heavy use of simple measures, such as counts of joint occurrences, or asymmetric indices, may be partially a reaction to the problems with association indices identified by Cairns and Schwager (1987) as well as by Ginsberg and Young (1992).

B.   OTHER MEASURES OF RELATIONSHIP

Other measures of relationship considered mean distances between individuals or the overlap of ranges (particularly used for small mammals). Primate and ungulate studies sometimes calculated mean rates of observation of affiliative, agonistic, or other kinds of behavior (Table III).

In some cases relationships between sets of animals were assessed. For instance, Bigg, Olesiuk, Ellis, Ford, and Balcomb (1990) measured associations between stable groups of killer whales (*Orcinus orca*), and Lawrence (1990) considered the relationship between a single sheep (*Ovis aries*) and all other group members.

VI.   DISPLAYS OF MEASURES OF RELATIONSHIP

A.   ASSOCIATION MATRICES

In theory it is possible to evaluate any measure of relationship for all pairs of individuals in the population, although, in practice, some values

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may be missing for a variety of reasons (Whitehead, 1997). These values constitute a square, and often symmetric, association matrix, indexed by the individuals in the population (e.g., Table IV). Such an association matrix is a representation of the social structure of the population (Whitehead, 1997). Many of the studies in our sample presented such association matrices or matrices of one or more other measures of relationship. Other displays of measures of relationship included histograms or tables of the magnitudes of associations and mean associations between and within different age and sex classes.

Multivariate analyses, and other methods, were often used to simplify and display association matrices (Table V). Some studies used two of these display methods (e.g., Smolker *et al.*, 1992). The most popular methods were cluster analyses (19/88), sociograms (16/88), and multidimensional scaling (3/88), which are illustrated in Fig. 3.

B. CLUSTER ANALYSIS

All cluster analyses in our sample of studies were hierarchical so that the results could be usefully displayed as a dendrogram or tree diagram (e.g., Fig. 3). They are most appropriately used in cases where a hierarchically organized social structure (not to be confused with a "dominance hierarchy") seems to be present; for instance, when animals form long-term stable

TABLE IV

ASSOCIATION MATRIX (HALF-WEIGHT) FOR JAPANESE MACAQUES (*Macaca Fuscata Fuscata*, 1984, Nonbreeding Season from Corradino, 1990)

Alfa													
.126	Fran												
.055	.367	Fell											
.055	.063	.037	Panc										
.027	.096	.062	.027	Isa									
.004	.003	.022	.211	.060	Gild								
.039	.039	.074	.033	.090	.030	Beti							
.018	.010	.019	.005	.026	.021	.017	Olga						
.073	.024	.068	.008	.021	.014	.026	.339	Orse					
.012	.023	.032	.002	.008	.051	.100	.038	.016	Ross				
.046	.001	.011	.028	.014	.020	.010	.001	.000	.008	Divo			
.003	.003	.026	.001	.017	.003	.035	.009	.003	.024	.035	Cist		
.008	.003	.007	.001	.006	.008	.005	.017	.016	.006	.042	.028	Elet	
.039	.004	.046	.000	.003	.004	.016	.016	.062	.009	.006	.026	.436	Eva

a Each individual is represented by the first four letters of its name, and the association index between a pair is found in the intersection of the row and column containing the two names.

TABLE V
DISPLAYS OF MEASURES OF RELATIONSHIP AND ASSOCIATION MATRICES

Display	Un	Pr	Ce	Ca	Ro	Ch	Ma	Pb	In	Bi	Fi	Tot
Cluster analysis, average linkage	2	3	3							2		10
Cluster analysis, single linkage	2	1										3
Cluster analysis, Ward's error sum of squares	1											1
Cluster analysis, unidentified	1	3								1		5
Sociogram	3	9	1	1				1	1			16
Multidimensional scaling		1	1			1						3
Principal components analysis	1											1
Principal coordinates analysis	1	1										2
Correspondence factorial analysis	1											1
Maximum spanning tree	2											2

groupings which associate preferentially with other groupings (e.g., Bigg *et al.*, 1990). Of the available hierarchical clustering techniques, single linkage produces "stringy" clusters, in which single individuals are progressively added to the largest cluster (Aldenderfer and Blashfield, 1984). In simulation studies single linkage has repeatedly been shown to perform poorly and to be highly sensitive to small error levels in the data (Milligan and Cooper, 1987). Thus it is generally not the best technique for displaying social structure. Instead, average linkage or Ward's technique (which generally produce rather similar dendrograms) are more likely to mimic real structures underlying association data (Milligan and Cooper, 1987).

C. SOCIOGRAMS

In comparison with cluster analysis, sociograms and multidimensional scaling are better at portraying a system in which each individual has a network of associations of varying strengths. Sociograms are diagrams in which individuals are represented by points, and links between points represent the strengths of different relationships. Sociograms give almost complete information, but can become cluttered with many individuals (see Fig. 3, where a sociogram of only 14 individuals is already quite complicated).

D. MULTIDIMENSIONAL SCALING AND PRINCIPAL COORDINATES ANALYSIS

In nonmetric multidimensional scaling and principal coordinates analysis (sometimes called metric scaling and related to principal components analy-
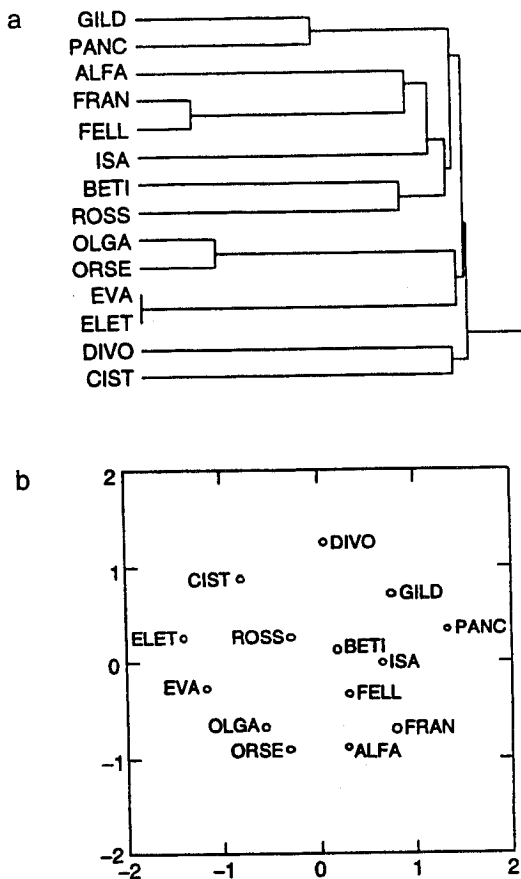
FIG. 3. Displays of the association matrix for Japanese macaques (*Macaca fuscata fuscata*) [Corradino, 1990; Table IV (1984) non breeding season] using (a) average linkage cluster analysis (in which each monkey is listed on the left starting in its own cluster and vertical lines indicate the level of association, decreasing from left to right, at which clusters are merged), (b) multidimensional scaling (in which each monkey is represented by a circle and the distance between circles generally increases as the level of association decreases); and (c) a sociogram (in which the width of the line joining the circles representing two monkeys indicates their strength of association).

sis), animals are also represented by points in space, but in these displays the distance between points is inversely related to the strength of the relationship. In principal coordinates analysis, ideally distances between points are inversely proportional to the strength of the relationship measure (perhaps transformed in some way). In nonmetric multidimensional scaling the correspondence is ordinal only: more closely related animals should be closer.
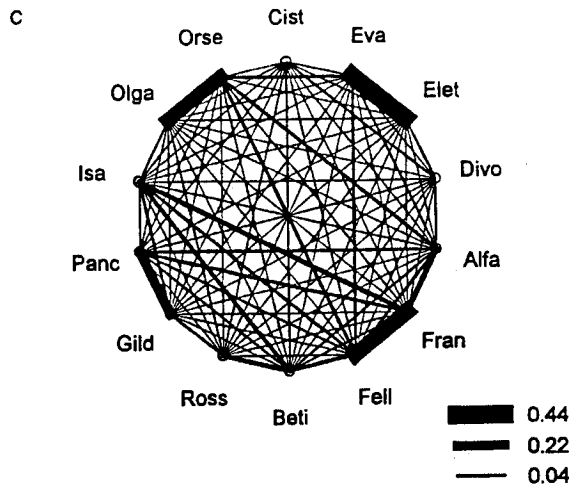
FIG. 3. (Continued)

Multidimensional scaling is most useful when the association matrix can be scaled in one or two dimensions with little "stress" (which indicates the degree of mismatch between the ordering of the distances between the points on the display and the values in the association matrix; see Kruskal and Wish, 1978). In such cases the arrangement of animals in the plot mimics the ordering of their associations, so that closely plotted animals have high association indices. However, reducing associations to ranks can remove some important features of an association matrix.

The plots produced by principal coordinates analysis are usually similar to those from multidimensional scaling. Principal coordinates has the advantage of not reducing the data to ranks, but the disadvantage that generally more dimensions are necessary to represent a given association matrix satisfactorily (see Digby and Kempton, 1987). Multidimensional scaling plots are derived iteratively, whereas principal coordinates analysis results from an eigen-vector analysis of the association matrix. This gives principal coordinates analyses the advantages of being computationally faster, possible with more individuals, and producing a unique display.

E. CHOOSING A DISPLAY TECHNIQUE

Each of the techniques described above has merits and drawbacks, and they can give rather different pictures of the same social structure (e.g., Fig. 3). Sometimes (e.g., White and Burgman, 1990) two of these techniques can give complimentary information. In general we would recommend:

1. For a hierarchically organized social structure in which permanent or nearly permanent groupings interact with other such groupings, use average linkage (or Ward's) cluster analysis.

2. For a social structure consisting of a network of associations of varying strengths, use sociograms (with less than ~20 animals), principal coordinates analysis (with about 10–200 animals, if a satisfactory representation can be obtained in one to three dimensions), or nonmetric multidimensional scaling (with about 10–100 animals, if a satisfactory representation can be obtained in one to three dimensions).

With more than about 200 animals none of these techniques produces a very satisfactory display. It may be possible to display social structures of fairly discrete subsections of the population separately. Alternatively, or additionally, in these large populations, summaries such as histograms of association matrices may be the most suitable method of displaying the data.

F. MULTIPLE RELATIONSHIP MEASURES

The display techniques described above only consider one measure of relationship at a time, and if there are several measures, then several cluster analyses or sociograms may be presented (e.g., Digby, 1995). However, it is possible to link measures of relationship.

Schnell, Watt, and Douglas (1985) show how the patterns in two association matrices may be compared. A matrix correlation is computed between the two association matrices, and a null hypothesis that there is no correlation between dyads' relationships on the two measures can be tested using the Mantel test.

Whitehead (1997) suggests a multivariate technique in which, instead of animals, relationships (defined by several measures of relationship, perhaps including some concerned with temporal patterning) are represented by points in multidimensional space. This representation can be simplified or visualized by techniques like principal components analysis.

VII. TESTS AGAINST "NULL MODELS"

For some animals, such as the killer whales studied by Bigg et al. (1990), a population is so clearly structured that tests against null hypotheses are redundant. However, in many cases hypothesis tests are appropriate and useful. Totally random data will show apparent structure when displayed using techniques such as cluster analyses and multidimensional scaling. In addition, real structure in relationship measures can be produced by nonso-

cial components of the lives of the animals. For instance, animals may interact at random with all other animals within a study area but may spend differing parts of the duration of the study in the study area. If this is the case, then a standard display of association indices will cluster individuals who happened to be in the study area together, suggesting a social structure when none exists. In such situations the biological significance of apparent structures in the results can be indicated by statistically testing interaction, association, or relationship measures against null hypotheses. Furthermore, it may be that within or between certain segments of a population (defined by age, sex, or other attributes) interactions or associations are essentially random, although the society may be structured in other ways.

In our sample, 17 studies tested their data against one or more null hypotheses. Usually the null hypothesis was that individuals associated randomly according to a particular model including elements from the natural history of the animals. For instance, Smolker *et al.* (1992) included the observed distribution of bottlenose dolphin (*Tursiops* spp.) group sizes, and Poole's (1995) null model considered home range overlap of lynx (*Lynx canadensis*).

There are many possible test statistics and procedures. Each of the 17 studies in our sample that tested hypotheses used a different method. Tests usually assumed binomial, multinomial, or Poisson distributions of sample statistics (such as number of times observed together), although a few papers used Monte Carlo permutation or randomization techniques to produce null distributions (e.g., Smolker *et al.*, 1992; Slooten *et al.*, 1993). A straightforward technique is to compare the true distribution of a measure of relationship (e.g., association index) with that expected from a system in which associations occur at the same rate but companions are chosen randomly from all members of the population.

However, to make such tests valid, the assumptions of the test must be met. An important problem occurs when the elements used to calculate a test statistic are not independent. This is the case with entries of a matrix of relationship measures (such as association indices). Each individual animal contributes to all elements in one row and one column of the matrix. A particularly asocial individual might have relatively low values all along its row and column. Therefore, it is not valid, for instance, to test whether relationships between the sexes are stronger than those among members of the same sex by using a *t* test or Mann–Whitney *U* test to compare the mean or median values of the appropriate elements of the matrix. Instead, the Mantel test (Mantel, 1967) and its variants (Hemelrijk, 1990b) and extensions (Smouse, Long, and Sokal, 1986; Hemelrijk, 1990a), which permute individuals to obtain null distributions of a test statistic, are often valid and useful (Schnell *et al.*, 1985; Hemelrijk, 1990b).

Independence may also be a problem in other circumstances. For instance, for some tests, sampling periods are assumed to be independent. If this is not the case, as when the interval between sampling periods is less than the mean duration of an association, then tests are invalid. Such situations can be indicated by measures such as the lagged association or interaction rate (see below): when the lagged association or interaction rate is greater than the "null association rate" (the expected lagged association or interaction rate in a situation when there are no preferred companions; Whitehead, 1995).

It is also important to consider constraints on association. Two animals cannot associate if one has died or migrated out of the study area or if their home ranges do not overlap.

Assumptions can usually be reduced, and validity increased, by using Monte Carlo-type methods, in which the original data are permuted or resampled (usually at least several hundred times) to give null distributions of the sample statistic. Bejder, Fletcher and Bräger (1998) present a very useful routine for carrying out such permutations.

VIII. TEMPORAL PATTERNING

An important element of Hinde's (1976) definition of relationships is the temporal patterning of interactions. Clearly the relationship between two animals which spend a few minutes together every day or two is very different from that between two animals which are solitary except for a brief mating season in which they are together continuously. However, these two relationships might have the same association index.

In 23% (20/88) of the studies in our sample temporal variability in pairwise associations was not considered; in 27% (24/88) it was mentioned but not examined quantitatively; in 40% (35/88) analyses were carried out separately for different portions of the study, or for different age classes of animal, and then compared (the "snapshots" approach); and in 10% (9/88), most involving ungulates or cetaceans, the temporal stability of associations was examined quantitatively over a range of time periods (Table VI).

There are several ways that the temporal stability of a relationship can be quantified. Some studies have looked at changes in group membership with time (e.g., Ginsberg, 1989). Another revealing approach is to plot the changes in association rate with time lag, the lagged interaction (or association) rate (see Whitehead, 1995; Fig. 4). The lagged interaction (or association) rate, for any time lag t, is an estimate of the probability that two individuals interacting (or associated) at a particular time are interacting (or associated) t time units later. It is equivalent to Underwood's (1981)

TABLE VI
CONSIDERATION OF TEMPORAL PATTERNING IN PAIRWISE RELATIONSHIPS

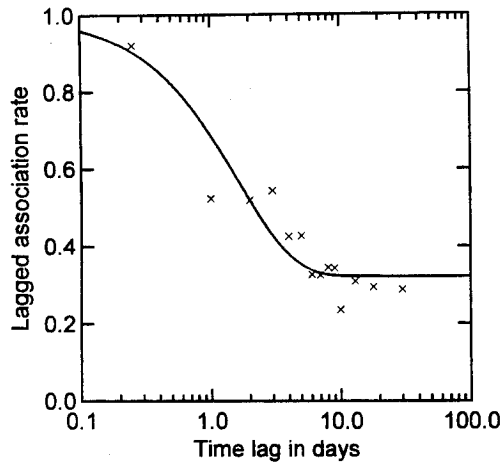| Taxon	No. studies in which temporal patterning was			
	Not considered	Talked about	Snapshots	Quantitative
Un	0	9	11	5
Pr	6	7	5	0
Ce	1	5	4	2
Ca	2	0	5	0
Ro	2	0	4	0
Ch	3	0	1	0
Ma	0	0	1	0
Pb	0	1	0	0
In	0	0	1	0
Bi	5	2	3	1
Fi	0	2	0	0
Total	20	24	35	9

FIG. 4. Lagged association rates for Underwood's (1981) data on eland (*Taurotragus oryx oryx*) plotted against time interval. This indicates the probability two animals associated at a certain time are also associated after a certain time lag (on the *x*-axis). Also shown is a fitted curve of a model in which each animal has permanent companions as well as casual acquaintances (original figure and details in Whitehead, 1995).

"proportion of companions remaining." Usually, as in Fig. 4, the lagged interaction (or association) rate is plotted against lag. Lagged interaction (or association) rates of about 1.0 show little or no disassociation, and a falling rate over a range of lags indicates that companionships are breaking up over these time scales. Thus the data presented in Fig. 4 indicate that two associated eland are likely to stay associated over periods of hours, have a 50% chance of being associated a few days later, and a 30% chance after one to several weeks.

Models of the temporal permanence of relationships can be fitted to the data (such as models of the exponential decay of associations with time; Fig. 4) and can be tested against one another (Whitehead, 1995). This can provide a quantitative model of some aspects of social structure, such as estimates of the mean rate of decay of companionships and the number of companions an individual possesses.

Although the majority of studies in our sample did consider the temporal patterning of interactions or associations to be sufficiently important to receive mention, in only a very few cases was it analyzed in a quantitative manner with time interval as a variable. The snapshot approach, in which separate analyses are conducted for different time periods or age classes, has a number of drawbacks, including the nonquantitative nature of the comparisons between time periods and restriction to large temporal scales (within which sufficient data can be collected to perform meaningful analysis; Whitehead, 1995). We believe that quantitative techniques of examining the temporal patterning of relationships, such as lagged association rates, are both revealing and underused.

In summary although there are no "standard" quantitative techniques for analyzing the temporal patterning of social interactions and associations, there are some quite simple methods available (Whitehead, 1997), such as the lagged association or interaction rate, which can be calculated without too much difficulty (Whitehead, 1995).

IX. DISCUSSION AND RECOMMENDATIONS

A. GENERAL PROCEDURE

Only 2 of the 84 papers made explicit reference to Hinde's (1976) framework (Goodall, 1986; Le Pendu, Briedermann, Gerard, and Maublanc, 1995). However, as it is mentioned in important texts (e.g., Cheney *et al.,* 1987; Dunbar, 1988), the influence may be largely second hand.

Hinde wrote principally from the perspective of very detailed observations of a small colony of captive monkeys. Most of the studies we reviewed

seem quite superficial from his standpoint. For instance, the "quality" of interactions is rarely considered. This does not mean there has been little or no research which provides detailed characterizations of relationships between animals. On the contrary, certain types of relationship, perhaps especially those between parent and offspring, have received a great deal of focused attention (e.g. Bateson, 1994). However, because only a particular subset of relationships in the population were the subjects of these in-depth studies, it is impossible to make Hinde's second step (shown in the upper part of Fig. 1) going from the content, quality, and patterning of relationships to a model of social structure. In contrast, in the studies we reviewed, all, or almost all, classes of relationships were examined but, by Hinde's standards, in a rather simple manner. However, the studies proceeded in the general manner Hinde outlined:

1. Animals were watched during a number of sampling periods using a variety of observation protocols (see Altmann, 1974).

2. Interactions and associations between pairs of identified individuals were measured by: recording specific behavioral events (e.g., grooming, agonism); spatial or temporal proximity; or presence in the same short-term group (with group implicitly or explicitly defined using spatial, temporal, and/or behavioral measures). Association measures during a sampling period were often one/zero: associated/not associated.

3. For each pair of animals, values of interaction or association measures were combined over sampling periods to give measures of relationship. There was usually only one interaction or association measure and only one measure of relationship, frequently a symmetric "index of association."

4. The values of each measure of relationship were usually expressed as a square, and often symmetric, matrix. Occasionally, only the matrix or a table or histogram of the association coefficients was presented. More frequently they were displayed using techniques such as cluster analyses, sociograms, or multidimensional scaling.

5. The temporal patterning of interactions was usually only considered in a rather superficial manner through written comment or by comparing separate analyses for different time periods or age classes.

B. RECOMMENDATIONS

Our reading of the sampled papers suggests several areas which might be considered profitably by those planning studies of the social structure of fission–fusion societies as well as those trying to devise better techniques:

1. The structure of fission–fusion societies, in which interactions between identified individuals are measurable, can be studied using the basic framework of Hinde (1976) in which the content, quality, and temporal patterning of interaction or association measures are used to describe relationships between pairs of animals and the content, quality, and patterning of relationships indicate social structure.

2. These analyses are much richer if the sexes and ages of identified animals are known.

3. The data can either be records of observed behavioral interactions or, less optimally, associations. Association can be based on spatial proximity, common behavior, and/or membership of the same group.

4. If associations are used, it is important to demonstrate as convincingly as possible that association is defined so that important interactions principally take place among associated animals. Likewise, when group membership is used as a measure of association then the assumptions that interactions principally take place within groups, and at equal rates among members of a group, should be justified. Studies of communication systems will often be important in this.

5. The more interaction or association measures that are considered, the richer the description of social structure.

6. Interaction or association measures between a pair of animals during a number of sampling periods can be combined to give measures of relationship. Especially in the case of a symmetric index of association, potential biases should be carefully considered (Cairns and Schwager, 1987).

7. Matrices of measures of relationship indicate social structure. These can be displayed using hierarchical cluster analysis techniques (such as average linkage, but single linkage is not recommended) when the social organization has a hierarchical structure, sociograms (for less than about 20 individuals), and multidimensional scaling or principal components analysis when the social structure consists of a network of associations.

8. When there are several measures of relationship, a combined multivariate representation of relationships may be especially useful (Whitehead, 1997).

9. It may be revealing to compare the distribution of measures of relationship, or some other statistic, with that expected from a "null" model of social structure, perhaps lacking pairwise preferences in interactions. Permutation and resampling methods are often useful in such tests.

10. The temporal patterning of interactions and associations is an important element of a relationship and thus of social structure. Temporal patterning should be considered in analyses of social structure, using measures such as lagged association rates which chart how relationships change with time (Whitehead, 1995).

C. COMPUTER PROGRAMS

There are computer programs available for carrying out many of the analyses discussed in this review. For instance, the "Noldus Observer" (http://www.noldus.com/products/observer/observer.htm) helps collect field data on behavioral interactions and makes preliminary analyses and "Noldus MatMan" analyzes association matrices carrying out Mantel and other tests (de Vries, Netto, and Hanegraaf, 1993). Most statistical packages (including SAS, SPSS, and SYSTAT) will do average linkage cluster analyses, multidimensional scaling, and principal coordinates analysis. One of us (HW) has written a series of programs in the language MATLAB, which carry out the majority of the techniques discussed in this chapter. They are available free of charge. Information, a manual, and downloading instructions are available on the World Wide Web (http://is.dal.ca/~hwhitehe/social.htm).

D. THE VALUE OF DISPLAYS AND MODELS OF SOCIAL STRUCTURE

The methods described in this chapter are almost all firmly embedded in the empiricist tradition: they attempt to describe and model parts of the natural world, in this case the social structures of nonhuman vertebrates, using what we can see (or otherwise sense) of them. The validity of these methods comes from the following:

1. They describe the natural world, a process which can be seen as an end in itself.

2. The models or displays that result often suggest hypotheses about the social structure of the population being examined which are worthy of testing (e.g., "do the sexes associate differently?", "are there permanent preferred companionships within the population?"). Such patterns may in turn indicate functional aspects of the social structure (e.g., "animals primarily aggregate to protect vulnerable offspring") or may be important from the perspective of population biology or management (e.g., "Can we consider adult animals to have independent rates of reproduction, mortality, and migration?").

3. As comparable models and displays of social organization become available for a number of vertebrate species, they will help structure the search for methods of classifying and measuring vertebrate social structure. There is no taxonomy of vertebrate social systems comparable to those that are used for mating systems (Clutton-Brock, 1989) or invertebrate social systems (Michener, 1969).

4. With appropriate measures or classifications of social structures, we can examine how social structure varies intra- and interspecifically with other attributes, such as brain size (Dunbar, 1992).

X. CONCLUSIONS AND SUMMARY

The objective of this chapter has been to help ethologists choose appropriate methods for the analysis of vertebrate social structures. We examined 88 studies of nonhuman vertebrate social structure in which animals were individually identified and interactions or associations between pairs of animals were recorded. Most studies were of fission–fusion societies and concerned mammals, especially ungulates, primates, and cetaceans. In these studies the fundamental data consisted of observations of behavioral "interactions" or "associations" defined by spatial or temporal proximity and/ or presence in the same group. Data from different sampling periods were then combined into one or more measures of relationship for each pair of animals. Most frequently, just one measure of relationship was calculated, an association index. There are difficulties in choosing a suitable association index. To represent the social structure of the population, matrices of association indices or other measures of relationship were displayed using cluster analyses, sociograms, multidimensional scaling, and other techniques. The temporal patterning of pairwise interactions or associations, an important element of relationships and thus of social structure, generally received only superficial treatment. Among our recommendations for future studies are: records of interactions are preferable to those of associations; when used, associations should be defined on the basis of the likelihood of interaction; association can be determined by presence in the same group but groups should be defined so that most interactions take place within them; the temporal patterning of interactions or associations should be an important part of such analyses; a multivariate representation of several measures of relationship may be useful; and it is often instructive to compare the distribution of measures of relationship, or some other statistic, with that expected from null models of social structure.

SUMMARY OF THE METHODS USED IN 88 STUDIES OF VERTEBRATE SOCIAL ORGANIZATION

Reference	Type of animal	Code	Population size	No. ind. ID'ed	Age or sex	Animals considered associated if	Index of association	Displays of association matrix	Treatment of temporal variability
Andelt (1985)	Coyote	Ca	Not given	48	a + s	<100 m apart	Average distance apart and travelled together; simple ratio	Table: assoc. coeff. by age/ sex class; line graph: by age/sex class & season (simple ratio)	Compare six reproductive stages
Arcese et al. (1995)	Oribi	Un	Not given	236	a + s	In the same group (= within 100 m of another group member)	No. of dyadic associations	Line graph: % dyads intact over 5 years	Compare dyads intact in each study year
Arnold et al. (1981)	Dorset Horn sheep	Un	13 (captive)	13	a + s	In the same grid square (400 m² when grazing, 50 m² when camped)	Simple ratio	Single linkage cluster analysis	Compare age classes of individuals
Arnold et al. (1981)	Southdown sheep	Un	35 (captive)	35	a + s	In the same grid square (400 m² when grazing, 50 m² when camped)	Simple ratio	Principal coordinates analysis	Compare age classes of individuals
Ballance (1990)	Bottlenose dolphin	Ce	~155	155	m/c prs. excl.	In the same group (= sighted together repeatedly); surfacing together	Twice-weight	Average linkage cluster analysis	Discuss fluidity of surfacing associations
Behrends et al. (1986)	Merriam's kangaroo rats	Ro	Not given	60	s	Home ranges overlap	% range overlap	Table: mean assoc. coeff. by sex class	Compare three study periods
Bell and Ford (1986)	Striated thornbill	Bi	≥44	44	s	Seen together	% of joint occurrences	Cluster analysis	Discuss variation of group size with season
Bigg et al. (1990)	Killer whale	Ce	261 (in 1987)	All	a + s	Photographed together	Cole's index	Average single-link cluster analysis	Compare mother–offspring bonds in 4-year groups
Braeger et al. (1994)	Bottlenose dolphin	Ce	Not given	1000	No	Members of the same group (= observed in apparent association)	Half-weight	Histogram of classes of association coefficients	Compare association coefficient for 2 years
Byrne et al. (1989)	Drakensberg mountain baboon	Pr	Not given	26 (this study)	a + s	Participants in grooming or approach/retreat interactions; nearest neighbors	Counts of grooming, nearest neighbor and approach/ retreat interactions	Average link cluster analysis; sociogram: matrix only (approach/ retreat)	Discuss variation with season

SUMMARY OF THE METHODS USED IN 88 STUDIES OF VERTEBRATE SOCIAL ORGANIZATION (*continued*)

Reference	Type of animal	Code	Population size	No. ind. ID'ed	Age or sex	Animals considered associated if	Index of association	Displays of association matrix	Treatment of temporal variability
Cantoni and Vogel (1989)	Greater white-toothed shrew	In	Not given	26	s	Within 1 m of one another; in the same nest; home ranges overlap	Simple ratio; proportion of home range overlap	Sociogram; map of home ranges	Compare winter with breeding season
Chapman (1990)	Spider monkey	Pr	42 (within study area)	35	a + s	In the same subgroup (= coordinated activities, close spatial contact)	Twice-weight	Cluster analysis	Discuss sociability in re: to food availability
Chepko-Sade et al. (1989)	Rhesus monkey	Pr	Not given	126	a + s	Participants in grooming interaction	Counts of being groomed & grooming; prop. of total group grooming	Cluster analysis; sociogram	Not considered
Clarke and Fitz-Gerald (1994)	Bell miner	Bi	9 to 58 (on study site)	all	a + s	Ranges overlap	Proportion of foraging range overlap	Map of range overlap	Not considered
Corradino (1990)	Japanese macaque	Pr	14 (captive)	14	a + s	Within 1.5 m of each other	Half-weight	Nonmetric multidimensional scaling	Compare breeding and nonbreeding seasons
Deng and Zhao (1987)	Stump-tailed macaque	Pr	Not given	29	a + s	Within 5 m; participants in affiliative or agonistic interaction	Half-weight; counts of agonistic interactions	Single-link cluster analysis; matrix only (agonistic interactions)	Compare sociability of different age classes
Digby (1995)	Common marmoset	Pr	Not given	33 (this study)	a + s	Participants in dominant/subordinate or grooming interaction; nearest neighbor (<2 m)	Proportion of nearest neighbor & grooming interactions; counts of dominant/subordinate interactions	Sociogram; matrix only (dominant/subordinant interactions)	Discuss changes in sociability prior to emigration
Eckman (1979)	Willow tit	Bi	21 (on study site)	20	a + s	In the same group (= foraging close together)	Twice-weight	Histogram of obs. and exp. prop. of joint occurrences	Not considered
Eckman (1979)	Crested tit	Bi	13 (on study site)	12	a + s	In the same group (= foraging close together)	Twice-weight	Histogram of obs. and exp. prop. of joint occurrences	Not considered
Festa-Bianchet (1991)	Bighorn sheep	Un	Not given	360	a + s	In the same group (group not defined)	Counts of joint occurrences	Table: ratio of obs. to exp. joint occurrences by age/ sex class	Compare ewe-offspring association by age of offspring

Study	Species			Most	s	Nearest associate		Matrices only	
Ficken et al. (1981)	Black capped chickadee	Bi	Not given	Most	s	Nearest associate (<3 m); arrive within 1 min of each other;) feeder area within the same hour; participants in agressive encounter	Half-weight; counts of outcomes of agonistic interactions	Matrices only	Compare early and late prebreeding seasons
Frank (1986ab)	Spotted hyaena	Ca	~3000	60–80 (this study)	a + s	Present within the clan (= all study animals); participants in agonistic interaction	Occurrence within the clan; counts of outcomes of agonistic interactions	Sighting history diagram: matrix only (agonistic interactions)	Compare clan membership for 4 years
Ginsberg (1989)	Grevy's zebra	Un	Not given	1084	s	In the same group (group not defined)	Rate of group turnover	Line graph of ♀ group remaining by study day	Graph ♀ group remaining by day
Goodall (1986)	Chimpanzee	Pr	~160	all	a + s	In the same party (= travel, feed and sleep together)	Twice-weight	Sociogram	Present raw data matrices for different years
Greenberg-Cohen et al. (1994)	Nubian ibex	Un	~300	45	a + s	Participants in agonistic interaction	Counts of outcomes of agonistic interactions	Matrix only	Compare hourly rate of interaction through day
Herrera and Macdonald (1987)	Capybara	Ro	Not given	Not given	a + s	In the same group (= frequently present & generally tolerated)	Occurrence within group	Sighting history diagram	Compare group membership in two years
Hillman (1987)	Common eland	Un	Not given	~180	a + s	In the same group (= within 50 m & moving in same direction or behaving similarly)	Cole's index	Table: frequency of classes of assoc. coeff. by age/sex class; sighting history diagram	Compare duration of association by age class
Hirotani (1990)	Reindeer	Un	~130	All	a + s	In the same group (= apart from other aggregations; coordinating activities)	Twice-weight	Bar chart: mean assoc. coeff. between moms and diff. aged daughters by season	Compare nonruting I & II and calving seasons
Johnson (1989)	Red-necked wallaby	Ma	98 adults (within study area)	98	a + s	In the same group (= a gathering in one place; within 30 m of one another)	Half-weight	Line graph: mean assoc. coeff. by age/sex class vs companion rank	Compare ♀ sociability in different reproductive stages
Kappeler (1993)	Ringtailed lemur	Pr	10 (captive)	10	a + s	Nearest neighbor; participants in affiliative or agonistic interaction	Proportion of nearest neighbor occurrences; counts of affiliative and agonistic interactions	Table: obs. & exp. nearest neighbor scores by sex class; matrices only (affinitive & agonistic interactions)	Not considered

SUMMARY OF THE METHODS USED IN 88 STUDIES OF VERTEBRATE SOCIAL ORGANIZATION (*continued*)

Reference	Type of animal	Code	Population size	No. ind. ID'ed	Age or sex	Animals considered associated if	Index of association	Displays of association matrix	Treatment of temporal variability
Kappeler (1993)	Redfronted lemur	Pr	8 (captive)	8	a + s	Nearest neighbor; participants in affiliative or agonistic interaction	Proportion of nearest neighbor occurrences; counts of affiliative and agonistic interactions	Table: obs. & exp. nearest neighbor scores by sex class; matrices only (affinitive & agonistic interactions)	Not considered
Kappeler (1993)	Crowned lemur	Pr	4 (captive)	4	a + s	Nearest neighbor; participants in affiliative or agonistic interaction	Proportion of nearest neighbor occurrences; counts of affiliative and agonistic interactions	Table: obs. & exp. nearest neighbor scores by sex class; matrices only (affinitive & agonistic interactions)	Not considered
Karlsson (1988)	Bank vole	Ro	Not given	23	s	Home ranges overlap	Proportion of home range overlap	Table: obs. & exp. assoc. coeff.; map of home ranges	Compare home ranges in different months
Knight (1970)	Elk	Un	2000–3000	209	a + s	Observed together	Half-weight	Table: frequency of classes of assoc. coeff.	Compare mean coefficients in different seasons
Koenig and Rothe (1991)	Common marmoset	Pr	8 (captive)	8	a + s	In proximity (<1 m)	Counts of intervals in proximity	Sociogram	Compare before & after birth of infants
Kozhurina (1993)	Noctule bat	Ch	27 (captive)	27	a + s	At the same roost site	Dimensionless information index	Nonmetric multidimensional scaling	Not considered
Lawrence and Wood-Gush (1988)	Scottish blackface sheep	Un	Not given	62	a + s	Used the same grid areas	Euclidian distance	Ward's error sum of squares cluster analysis	Compare four seasons
Lawrence (1990)	Scottish hill sheep	Un	Not given	12 ewe– daughter pairs (this study)	a + s	In the same group (= within 30 m of another member)	Proportion of joint occurrences	Cluster analysis; line graph: median ewe–lamb assoc. coefficient by season	Compare associations by seasons
Lazo (1994)	Feral cattle	Un	≤140 (>1 year old) at any one time	All	a + s	In the same group (= cohesive behavior & spatial distribution)	Social affinity index; proportion of home range overlap	Average linkage cluster analysis	Compare home range overlap for four seasons
Le Pendu et al. (1995)	Mouflon	Un	~127	62	a + s	In the same group (= within 80 m of nearest neighbor)	Square-root; relative mother–offspring affinities	Correspondence factorial analysis	Calculate proportion of associates remaining by day

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Reference	Species		Population	Sample	a + s	Definition of association	Index	Analysis	Purpose
Leuthold (1979)	Giraffe	Un	Not given	Not given	a + s	In the same group (= within 500 m & not moving in different directions)	Half-weight: occurrence of home range overlap	Histogram: assoc. coeff. by age/sex class; map of home ranges	Compare association coefficients by age class
Lott and Minta (1983)	American bison	Un	400	16 cows & 8 calves (this study)	a + s	In the same group (= within 90 m of another group member)	Square-root; distance coefficient	Average linkage cluster analysis	Compare pre- and post-cow–calf separation
Marinelli and Messier (1993)	Muskrat	Ro	Not given	18 radio-tagged	s	Home ranges overlap	% home range overlap	Map of home ranges	Calculate % overlap for 5 months
Matthysen et al. (1992)	Red-breasted nuthatch	Bi	~33 (on study site)	21	s	Within 50 m of each other; home ranges overlap	Twice-weight; proportion of home range overlap	Matrix only: map of home ranges	Not considered
McWilliam (1988)	Free-tailed bat	Ch	~107	107	a + s	Caught at the same roost	Occurrences at same roost	Sighting history diagram	Compare roost composition in two years
Mitani (1986)	Japanese macaque	Pr	28 (study pop. = 1 troop)	12 (this study)	a + s	In proximity (<20 m); participants in vocal exchange or grooming interaction	Reciprocal value of proximity frequency; counts of vocal exchange and allogrooming	Average linkage cluster analysis; sociogram	Not considered
Mobley and Herman (1985)	Humpback whale	Ce	Not given	32 (this study)	calf noted	In the same group (= within a few body lengths & engaged in synchronous activity or interacting closely)	Rate of membership change per pod per hour	Line graph of biweekly rate of change over study period	Discuss affiliations and disaffiliations observed during study
Morland (1991)	Ruffed lemur	Pr	26 (study pop. = 2 communities)	11	a + s	Participants in affiliative interaction	Proportion of affiliative interactions	Sociogram	Compare warm and cool seasons
Moss and Poole (1983)	African elephant	Pb	615	615	a + s	Sighted together	Simple ratio	Sociogram	Discuss changes in relation to ecological factors
Murray (1981)	Impala	Un	Not given	443	a + s	In the same group (group not defined)	Half-weight	Maximum spanning tree	Plot mean assoc. coeff. by age class
Myers (1983)	Sanderling	Bi	80–400	~25%	no	In the same flock (flock not defined)	Twice-weight	Histogram of observed and expected coherence distributions	Graph probability of remaining associated vs time (days) for three seasons
Nakagawa (1992)	Patas monkey	Pr	Not given	8 (this study)	a + s	In proximity (3 m); exchange contact calls; participants in grooming; rest in the same tree) night	Half-weight (proximity, calling & allogrooming); proportion of night coresting	Sociogram	Compare individuals of different age classes

(continues)

SUMMARY OF THE METHODS USED IN 88 STUDIES OF VERTEBRATE SOCIAL ORGANIZATION (*continued*)

Reference	Type of animal	Code	Population size	No. ind. ID'ed	Age or sex	Animals considered associated if	Index of association	Displays of association matrix	Treatment of temporal variability
Newberry and Wood-Gush (1986)	Domestic pig	Un	Not given (captive)	26 (this study)	a + s	Resting together; performing coincident behaviors; participants in butting or sniffing interactions; nearest neighbors	Half-weight; coincident behaviors; nearest neighbor occurrences and butting & sniffing interactions	Single link cluster analysis; sociograms	Compare associations at different ages of piglets
Norris et al. (1994)	Hawaiian spinner dolphin	Ce	~1000	36 (this study)	No	In the same school	Simple ratio (calculated for 1 pair)	Sighting history diagram	Discuss changes in observed associations
Pages-Feuillade (1988)	Grey lesser mouse lemur	Pr	Not given	9	a + s	Within 10 m of one another; home ranges overlap	Half-weight; % home range overlap; prop. of joint occurrences	Sociogram; map of home ranges; matrix only (joint occurrences)	Discuss varying sociability with ♀ estrus state
Palomares and Delibes (1993)	Egyptian mongoose	Ca	Not given	24	a + s	In the same resting site; <10 m apart	Simple ratio; home range overlap	Sociogram; map of home ranges	Compare home range overlap for 2 years
Parker et al. (1995)	Black vulture	Bi	Not given	17 (this study)	a	At the same roost	Simple ratio	Matrix only	Not considered
Penzhorn (1984)	Cape mountain zebra	Un	117–148	All	a + s	In the same group (= bachelor group of ♂'s < 5 but > 2 years old)	Half-weight	Principal components analysis	Compare associations in 10 3-month periods
Poole (1995)	Lynx	Ca	Not given	51	a + s	Home ranges overlap; S_c ???? O	Coefficient of sociality (S_c); % home range overlap	Table: assoc. coefficients; map of home ranges	Compare home range overlap in different years
Rayor (1988)	Gunnison's prairie dog	Ro	2 sites: 1000–1500; 125	Not given	a + s	Home ranges overlap; participants in agonistic or amicable interaction	% home range & space use overlap; counts of agonistic & amicable interactions	Table: association coefficient by age/sex class	Not considered
Reinhardt and Reinhardt (1981)	Zebu cattle	Un	47–108 (captive)	29 ♀'s (this study)	a + s	Participants in social grazing or social licking	Simple ratio; % social licking occurrences	Sociogram	Compare different years of study
Rood (1989)	Slender mongoose	Ca	6 adults + young on study site	6	a + s	Sighted in proximity	Counts of joint occurrences	Matrix only	Not considered

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Reference	Species	Code	Group size	N	a + s	Association definition	Index	Analysis	Purpose
Rowell and Rowell (1993)	Feral sheep	Un	40–60	All	a + s	Present in the same group (group not defined) in all 3 seasons	Occurrence in same group in 3 seasons	None	Compare group membership in 3 years
Schaller (1972)	Lion	Ca	2000–2400	216	a + s	Seen together; participants in head rubbing or social licking	Half-weight: occurrences of social licking and head rubbing	Matrices only	Compare association coefficient for 2 years
Schilder (1992)	Mixed group of Grant and Chapman plains zebras	Un	23–29 (captive)	All	a + s	Within 8 m of one another; participants in affiliative interaction	Simple ratio; occurrence of affiliative interactions	Sociogram	Compare pre- & postharem takeover periods
Shane and McSweeney (1990)	Short-finned pilot whale	Ce	Not given	Not given	a + s	In the same pod (pod not defined)	Half-weight	Sighting history diagram	Not considered
Shapiro (1986)	Coral reef fish	Fi	Not given	66	a + s	Together at one of three positions	Simple ratio	Matrix only	Measure changes in rate of movement between subgroups after experimental manipulation
Slooten et al. (1993)	Hector's dolphin	Ce	3000–4000	79	s	In the same group (group not defined) or cluster of groups (≤200 m)	Half-weight; simple ratio; standardized reassociation rate	Average linkage cluster analysis; rate plotted against time intervals	Plot reassociation rate as a function of time
Smith and Van Buskirk (1988)	Black-capped chickadee	Bi	Not given	114	a + s	In the same foraging group (=foraging together & separated from others)	Half-weight	Average linkage cluster analysis	Discuss frequent changes in group membership
Smolker et al. (1992)	Bottlenose dolphin	Ce	Not given	56 (this study)	a + s	Sighted in the same party (= within 10m of another member)	Half-weight	Sociogram and multi dimensional scaling	Present a sociogram for each of 5 years
Somers et al. (1995)	Warthog	Un	Not given	47	a + s	Participants in one of 8 types of interactions	Rates per hour of eight types of interaction	Matrix only	Discuss variation with season
Sugiyama (1988)	Chimpanzee	Pr	17–22	all	a + s	Participants in grooming interaction; in proximity (<1 m)	Counts of allogrooming and proximity interactions	Matrix only	Compare 2 study periods
Sullivan (1990)	Red junglefowl	Bi	35–50	27 (this study)	s	Within 20 m of one another seen together	Half-weight	Average link cluster analysis	Compare ♀ associations with & without chicks
Sun and Dai (1995)	Chinese water deer	Un	Not given	23	a + s	Within 20 m of one another and coordinating behavior	Twice-weight	Matrix of mean association coefficients by sex class	Discuss variations in association with mating phase

(continues)

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SUMMARY OF THE METHODS USED IN 88 STUDIES OF VERTEBRATE SOCIAL ORGANIZATION (*continued*)

Reference	Type of animal	Code	Population size	No. ind. ID'ed	Age or sex	Animals considered associated if	Index of association	Displays of association matrix	Treatment of temporal variability
Tilson *et al.* (1988)	Przewalski horse	Un	8 (captive)	8	a + s	Within 1 body length of one another; participants in agonistic interactions	Simple ratio; counts of agonistic interactions	Histogram of observed associations; matrix only (agonistic interactions)	Discuss uncertainty in longevity of association
Ueda (1986)	Fan-tailed warbler	Bi	Not given	786	s	Mate with one another	Counts of breeding attempts	Sighting history diagram	Compare 4 breeding seasons
Underwood (1981)	Common eland	Un	70–80	all >18 mo.	a + s	Sighted together	Half-weight	Maximum spanning tree	Plot prop. of companions remaining by day
Waser and Waser (1985)	White-tailed mongoose	Ca	Not given	24	a + s	Within 100 m of each other	Counts of joint occurrences	Matrix only	Not considered
Waterman (1995)	Cape ground Ro squirrel	Ro	68–79 in study site	All	a + s	Participants in one of 11 types of interactions	% of 11 diff. types of interactions	Bar chart: mean assoc. coeff. by sex class	Not considered
Weinrich (1991)	Humpback whale	Ce	not given	57 (this study)	a + s	Within 2 body lengths and behaving in a consistently coordinated manner	Twice-weight	Histogram: association coefficients	Discuss splitting and rejoining observed during study
Wells *et al.* (1987)	Bottlenose dolphin	Ce	~100	77 (this study)	a + s	Sighted together	Half-weight	Matrix of association coefficient by age/sex class	Compare association coefficients by age class

Reference	Species					Definition of association	Index	Analysis	Notes
White and Burgman (1990)	Pygmy chimpanzee	Pr	Not given	42	s	In the same party (party not defined); nearest neighbor (<5 m)	Twice-weight; proportion of nearest neighbor occurrences	Average linkage cluster analysis; principal coordinates analysis	Suggest party sighting data temporally autocorrelated
Whitehead et al. (1991)	Sperm whale	Ce	~3500	1295	No	Photographed within 2 h of one another	Standardized reassociation rate	Rate plotted against time intervals	Graph probability of remaining associated vs time (days)
Wilkinson (1985)	Common vampire bat	Ch	Not given	205 + 319 (two sites)	a + s	Roosting in the same tree	Half-weight	Matrix of obs. and exp. assoc. coefficients	Not considered
Williams (1986)	Short-tailed leaf-nosed bat	Ch	Not given	Not given	a + s	Roosting at the same site	Proportion of joint occurrences	None	Not considered
Würsig (1978)	Bottlenose dolphin	Ce	Not given	53	m/c prs noted	Surfaced within 3 sec of one another	Occurrence of joint surfacings	Table: observed associates; sighting history diagram	Compare surfacing association on two days
Yanagisawa (1993)	Cichlid fish	Fi	Not given	33	a + s	Forage together (< 50 cm); home ranges overlap; participant in agonistic encounter	% of total observation time in association: counts of home range overlap; rate of agonistic encounters	Map of home ranges; table: rate per hour of agonistic interactions by sex class	Not considered
Yeager (1990)	Proboscis monkey	Pr	Not given	Not given	a + s	Nearest neighbor	Square-root	Cluster analysis	Not considered

APPENDIX B

ASSOCIATION INDICES

Cairns and Schwager's Association Indices (Cairns and Schwager, 1987)
Half-weight

$$\frac{x}{x + y_{AB} + \frac{1}{2}(y_A + y_B)}$$

Twice-weight

$$\frac{x}{x + 2y_{AB} + y_A + y_B}$$

Simple ratio

$$\frac{x}{x + y_{AB} + y_A + y_B}$$

Square-root

$$\frac{x}{\sqrt{(x + y_A + y_{AB})(x + y_B + y_{AB})}}$$

where
x = individuals A and B are located together
y_A (or y_B) = only individual A (or B) is located
y_{AB} = individuals A and B are located separately

Cole's Association Index (Cole, 1949)
for $ad \geq bc$

$$\frac{ad - bc}{(a + b)(b + d)}$$

for $bc > ad$ and $d \geq a$

$$\frac{ad - bc}{(a + b)(a + c)}$$

for $bc > ad$ and $a > d$

$$\frac{ad - bc}{(b + d)(c + d)}$$

where
  a = both individuals present
  b = only individual B present
  c = only individual A present
  d = neither individual present

Coefficient of Sociality, S_c (Poole, 1995)

$$S_c = \frac{D_E - D_O}{D_E + D_O}$$

where
  D_O = observed distance between 2 individuals
  D_E = expected distance if they move randomly

Dimensionless Information Index, S (Kozhurina, 1993)

$$S = \frac{2I}{[H(A) + H(B)]}$$

where
  $I = H(A) + H(B) - H(A, B)$
  $H(A) = -\Sigma p_i(A) \log_2 p_i(A)$
  $H(B) = -\Sigma p_i(B) \log_2 p_i(B)$
  $H(A, B) = -\Sigma p_i(A, B) \log_2 p_i(A, B)$
and where
  $p_i(A)$ [or $p_i(B)$] = empirical probability of occurrence of individual A [or B] in roost i
  $p_i(A, B)$ = empirical probability of joint roosting for individuals A and B in roost i

Social Affinity Index (Lazo, 1994)

$$S = \frac{N_{A.B}}{\min(N_A, N_B)}$$

where
  $N_{A,B}$ = number of times individuals A and B located together
  N_A = number of times individual A located
  N_B = number of times individual B located

Mother-Offspring Relative Affinity (Le Pendu *et al.*, 1995)

$$P_m+ = \frac{N_{am}}{N_m} \times 100 \qquad\qquad P_o+ = \frac{N_{ao}}{N_o} \times 100$$

where

N_{am} (or N_{ao}) = the number of animals observed more frequently with the mother (or offspring) than was the offspring (or mother)

N_m (or N_o) is the number animals observed with the mother (or offspring)

Distance Coefficient (Lott and Minta, 1983)

DCOEF = 1 − (mean distance dyad/maximum distance between any dyad)

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