

CHAPTER 8

USING GROUP COMPOSITION DATA TO MEASURE SOCIAL AFFINITY: A NEW METHOD

ABSTRACT

Affinities between particular conspecifics are central to social organization and behavior. In species with variable group composition, frequency of shared group membership is a conspicuous and easily measured manifestation of social affinity. I review existing methods for measuring and statistically testing social affinity using group composition data, and find that they are not adequate for addressing the questions that are most often of interest. I describe a new method, based on computerized randomization of group composition, that overcomes these methodological difficulties. This technique provides measures of association preference between individuals or classes that can be compared across data sets, and also provides the first general statistical test for association preferences in group composition. The approach is widely applicable to studies of animal behavior, both for studies of social groups, and for other problems involving association between a set of entities within groups of variable size.

INTRODUCTION

The preferences that animals show in their patterns of association with conspecifics are a fundamental aspect of social organization. Association can be measured in various ways, but is perhaps most clearly manifested in the composition of temporary groups. A number of different “association indices” have been used to estimate two individuals’ level of association, or how much of their time they spend together, based on counts of how many times they are seen together and separately in groups (Cairns & Schwager 1987). Such indices are widely used to quantify basic parameters of social structure, including whether social groups are closed or open, whether they are stable or fluid, how association patterns differ between sexes or age classes, and whether there are “special relationships” based on individual recognition (e.g., tits, Ekman 1979; eland, Underwood 1981; bison, Lott & Minta 1983; zebras, Penzhorn 1984; bats, Williams 1986; reindeer, Hirotsu 1989; chimpanzees, White & Burgman 1990; dolphins, Smolker et al. 1992; feral cattle, Lazo 1994).

Association indices as measures of social affinity are used to examine other aspects of social behavior as well. For example, in studies of mating systems they are used to investigate whether there is general avoidance or affinity between the sexes, and whether there are heterosexual bonds between particular adults (e.g., chickadees, Ficken et al. 1981; ibex, Dunbar & Dunbar 1981; chimpanzees, Badrian & Badrian 1984; dolphins, Slooten et al. 1993; feral cattle, Lazo 1994). In studies of social development they are used to quantify the strength and persistence of maternal-offspring bonds (e.g., red deer, Guinness et al. 1979; bison, Green et al. 1989; dolphins, Smolker et al. 1992). Association levels are also evidence for kin recognition and discrimination, and association indices have been applied to questions such as whether reindeer show

association preferences for members of their own matrilineal group (Hirotsu 1989), whether hyenas maintain social bonds with their siblings (Smale et al. 1995), and whether adult vultures associate preferentially with relatives (Parker et al. 1995). Strong bonds between particular same-sex adults may reveal coalitions, and this has been investigated in eland (Underwood 1981), zebras (Penzhorn 1984), vampire bats (Wilkinson 1985), dolphins (Connor et al. 1992), squirrel monkeys (Mitchell 1994), and chimpanzees (Furuichi & Ihobe 1994). Finally, some species travel in mixed-species groups, and consistent associations may reveal mutualistic relationships between particular species (e.g., monkeys, Waser 1982; birds, Graves & Gotelli 1993; fish, Sakai & Kohda 1995).

Given the conceptual importance and widespread use of association indices, it is crucial to have reliable and powerful ways of analyzing such data. Current methods, however, are not adequate for addressing the questions that are often of greatest interest. These questions concern whether and how association patterns reveal animals' underlying social preferences. In the rest of this paper I explore these questions in detail, and review some of the most commonly used approaches and their deficiencies. I then describe a new approach using computer randomization that overcomes many current methodological limitations, and illustrate its application with several examples. Finally, I briefly discuss some applications of the method to other areas of animal behavior.

Group Composition Data and its Analysis

Throughout this paper I will use the term “association” to refer to common group membership, and “association level” to refer to any measure of the extent to which two individuals or classes share common group membership. I will use the term “association preference” to refer to any association pattern that discriminates among conspecifics. Thus if the probability of an animal being in a group is related to the identities of the other group members, it is showing an association preference. This can take the form of

either increased association (“affinity”), or reduced association (“avoidance”) between particular parties. Note that this definition of association preference is independent of overall sociality, or tendency to join groups. I will not define the term “group” here, because different definitions are most useful for different species and questions. Groups are most often defined in terms of physical proximity, but other kinds of interaction (e.g., affiliative, agonistic, communicative) can also be used as criteria.

As a simple example of group composition data, imagine that groups were observed on four occasions in a particular population containing five individuals (labeled A through D), as shown in Table 8.1. Three questions are likely to arise for any given pair of individuals: How often are they in the same group? How strong an affinity or avoidance does this represent? Is this apparent association preference likely to have arisen by chance if group composition is actually random? If the four individuals are members of two different classes (e.g., A and B versus C and D), one could ask the same questions about classes rather than individuals. I will refer to data in which group members are identified individually as “individual-based” data. In contrast, the same kind of data could be collected from groups whose members are identified only as members of particular classes, such as age or sex categories. The resulting data would still look like Table 8.1, but each letter would refer to a class rather than a specific individual, and thus could appear more than once in the same group. I will refer to this as “class-based” data. Note that individual-based data can be used to address questions about either individuals or classes, while class-based data can only address questions about classes. Although class-based data are often easier to acquire, they have been used less often than individual-based data to address questions about classes, because adequate methods have not been available.

Table 8.1. Example of group composition data. Each letter could represent either a different individual (individual-based data), or a different class of individuals (class-based data).

| <u>Group #</u> | <u>Size</u> | <u>Membership</u> |
|----------------|-------------|-------------------|
| 1 | 4 | A, B, C, D |
| 2 | 2 | A, B |
| 3 | 2 | C, D |
| 4 | 3 | A, B, D |

EXISTING METHODS

In this section I will briefly review some methods that have been used to address the three questions posed above. Answers to these questions take the form of measures of association level, association preference, and the probability of an observed preference arising by chance.

Measuring association levels

Individual association levels

The problem of measuring association between individuals has been solved reasonably well. There is one obvious and biologically relevant parameter that corresponds to the notion of “association level”, and that is the proportion of time two individuals spend together. Several related indices have been used to estimate this parameter from group composition data like those in Table 8.1. Each index consists of the number of times two individuals appear together, divided by some combination of the number of times they appear together and separately. They differ mainly in their

assumptions about the probability of observing two individuals while they are together versus apart. Cairns & Schwager (1987) review existing indices, discuss their relative merits, and offer some alternatives.

Class association levels

Measuring association levels between classes remains problematic. Unlike individuals, classes may be simultaneously apart in one group and together in another. Thus, in contrast to individuals, there is no single obvious candidate for what real-world parameter to estimate, and different studies have estimated different parameters. Individual association indices can be applied to class data (e.g., Wells et al. 1987), but the resulting numbers are not easily interpreted. Other studies have used the proportion of groups that contain both classes A and B (Halperin 1979, Badrian & Badrian 1984), or the proportion of groups containing class A that also contain class B (Wells et al. 1987). Unlike individual association indices, none of these class association indices estimate parameters of the social environment that animals experience directly. This makes them less easily interpreted, and potentially less biologically relevant.

Measuring association preference

Interest in association preferences is often the motivation for studying association, but no general methods exist for quantifying association preference. In order to measure deviation from chance levels of association, one needs an explicit model of random association, and this has proven difficult to generate. Instead, researchers have relied on various non-quantitative methods to indicate the extent of association preferences.

Individual association preference

If individuals join and leave groups randomly with respect to the identity of other group members, any two individuals in the same data set are expected to share the same

association level. If some dyads have higher association levels than others, this suggests positive association preferences, and low levels indicate negative preferences. Both the magnitude and the statistical significance of these differences are of interest; I will discuss the first issue here and the second in the next section. The major limitation of using association levels to quantify association preference is that they provide only relative, not absolute measures, and thus they only allow comparisons within a data set. Comparisons between data sets are not informative because the expected “baseline” association level in each data set depends on the number of individuals and the size distribution of groups. For example, it is not obvious whether two individuals show stronger affinity by staying together 25% of the time when the population is dispersed into many small groups, or 75% of the time when it is aggregated into a few large groups. For the same reason, the strongest affinity between individuals in one data set may be much weaker than the strongest affinity in another data set.

Class association preference

Unlike individuals, different classes are not expected to associate equally if group membership is random. This is because classes that make up a larger proportion of the population will occur together more frequently by chance alone. Therefore, unlike association indices that use individual-based data, those that use class-based data do not indicate association preference even within one data set. This is not always recognized, and class-based indices are sometimes mistakenly interpreted as measures of affinity (e.g., Halperin 1979, Badrian & Badrian 1984, Wells et al. 1987).

Because of this problem, workers interested in association preference between classes have previously been limited to using individual-based data. In addition to identifying all group members individually, this approach requires some way to summarize a large number of individual association levels in an easily interpreted form. (N different individuals generate $(N * (N-1)) / 2$ unique association levels.) To this end

authors have presented individual association data graphically in various ways, including matrices of numbers (Wilkinson 1985, Wells et al. 1987), sociograms (Goodall 1986, Smolker et al. 1992), maximum spanning trees (Morgan et al. 1976), dendrograms based on clustering algorithms (Morgan et al. 1976, Lott & Minta 1983, White & Burgman 1990), and scatter plots based on multidimensional scaling or principle components analysis (Morgan et al. 1976, Penzhorn 1984, White & Burgman 1990, Smolker et al. 1992). These graphical methods can suggest association preferences but cannot quantify them.

As a partial solution to the problem of quantifying class association preferences using individual-based data, one can use the mean of all individual association indices linking the two classes of interest. This method puts class association preference on the same footing as individual association preference; associations between pairs of classes can be ranked within a data set, but not compared between data sets.

Testing association preference statistically

Even if group composition is completely random, the association indices calculated from a finite data set will vary due to sampling error. When is an observed value sufficiently different from expected to reject the null hypothesis of no association preference? Few techniques are available for statistically testing association preferences. Modeling the null hypothesis of random group membership is a major obstacle. The expected level of association between two individuals or classes depends on many variables, including the number of individuals or classes, their relative frequencies in the data set, and the frequency distribution of group sizes. A second difficulty is that the association levels of different pairs are mutually dependent, which violates the assumptions of most statistical tests.

I am not aware of any existing method for testing the significance of individual association preferences within a data set. However, various authors have attempted to test for association preference between classes. For example, White (1988) used a hypergeometric distribution to generate the expected number of males and females for each group size observed, and performed a separate G test for each group size. This procedure only works if there are exactly two classes. It also creates the problem of how to combine the results of many tests if groups come in many sizes. Wells et al. (1987) performed a separate chi-square test on each class to test whether it associated equally with all other classes. This is not a valid test for association preference, however, because larger classes are expected to share higher association levels.

The most useful existing tests for association preference between classes are the Mantel test (Mantel 1967, Sokal & Rohlf 1995) and related matrix permutation tests (Dietz 1983, Hubert 1987, Hemelrijk 1990a, b). These procedures sidestep the problem of formulating a null hypothesis of random association, instead testing the null hypothesis that the observed association pattern is unrelated to another pattern generated as a theoretical prediction. The observed matrix of individual association indices is compared with a “prediction” matrix containing values of one for dyads predicted to have high association levels, and zero for dyads predicted to have low values. Repeated permutations by computer are used to determine whether the observed matrix is significantly correlated with the prediction matrix.

Although matrix permutation tests are very useful, they have some important limitations. One is that they cannot test for association preferences between individuals. A second is that they can only test hypotheses that can be formulated as a contrast between exactly two classes. A third is that they assume all differences in association levels reflect association preferences. Class-based indices do not meet this condition when classes contain different numbers of individuals, and thus individual identification

is required to assess preferences between classes. Finally, matrix permutation is not well suited to exploratory data analysis, because it can only test for a specific pattern predicted ahead of time, rather than for association preferences in general.

In summary, the state of the art in analyzing association preference from group composition is not satisfactory. There are no suitable methods for analyzing data in which animals are not identified individually. When animals are identified individually, there is no way to quantify absolute association preferences so that they can be compared between data sets. This makes it impossible to address many comparative questions, such as how affinity changes over successive time periods, under varying conditions, or between populations. Finally, no statistical tests are available for evaluating association preferences between individuals, and existing tests for association preference between classes are only suitable for a restricted set of *a priori* predictions. In the following section I describe solutions to each of these problems.

THE GROUP RANDOMIZATION APPROACH

The randomization method

A complete description of association preference should include measures of: (1) the observed level of association, (2) the level of association expected under the null hypothesis of random association, (3) a measure of how much the observed association level deviates from expected, and (4) the probability under the null hypothesis of obtaining a value as extreme as that observed. To obtain all but the first of these one must specify the frequency distribution of the association index under the null hypothesis. This can be generated by repeatedly randomizing the data using Monte Carlo simulation

(Manly 1991). In each iteration, the observed group structure is preserved but group membership is re-assigned randomly. The resulting simulated data set has the same distribution of group sizes and the same number of sightings of each individual or class as the original, but with the composition of each group randomized. The association index for each dyad is then calculated from the simulated data set. Repeating this assignment process many times builds up a frequency distribution for each dyad under the null hypothesis. The expected value of the association index is simply the mean of the simulated values. The ratio of observed to expected association levels, or “preference quotient”, provides a simple measure of association preference. Finally, the proportion of simulated association indices that are at least as extreme as the observed index provides a one-tailed p value for the observed association level. This procedure works equally well with any association index based on either individuals or classes.

The GROUPS program

I implemented the group randomization method in a computer program called GROUPS, which is available on request for IBM-compatible personal computers. The input is a text file listing the members of each group, as in the last column of Table 8.1. The user can select any of several association indices, direct the output to screen, printer or file, and specify the number of iterations to perform. Both the precision of the results and the time required increase with the number of randomizations performed. The user can also specify the number of individuals in each class if this is known, and which individuals or classes to analyze. To generate a simulated data set, the program randomly assigns each sighting of an individual or class member to an open slot in a group, without placing the same individual in one group twice or the same class in one group more times than there are class members.

Table 8.2 illustrates the program's output. The data in the last column of Table 8.1 were used as input, and treated as observations of known individuals. For this analysis I used the "Simple Ratio" index of individual association (Cairns & Schwager 1987), and randomized group membership 10,000 times. The resulting numbers answer the questions posed about these data in the beginning of this paper. For each dyad the observed values (O) indicate how much the two individuals associated in the original data, and the expected values (E) indicate the association level expected under random group composition. These two values indicate whether the dyad showed affinity ($O > E$), or avoidance ($O < E$). Finally, the p value for each dyad indicates the two-tailed probability, under the null hypothesis of random group composition, of an association level at least as extreme as that observed. Note that because the "Simple Ratio" index is symmetric (A associates with B at the same level as B associates with A), the resulting matrix is also symmetric. Although some dyads were always together and others usually apart, the data set was too small for any association preference to approach the 0.05 significance criterion.

The current version of the program treats each group as an independent sample, rather than distinguishing groups observed concurrently from those observed at different times. Therefore it cannot weight an observation of A without B differently depending on whether or not B was observed at the same time, as some association indices require. This limitation is not inherent in the group assignment approach, but only in the current version of the program. Cairns & Schwager (1987) found that the probability of locating only one versus both individuals when they are apart had a negligible effect on individual association indices, but the program is best suited for data sets in which each group represents an independent observation.

Table 8.2. Output from analysis of the data in Table 8.1 using the GROUPS program. A through D represent individuals, N = total number of sightings of row individual, O = observed association level, E = expected level, p = two tailed p value.

Input file: table1.dat
 11 sightings in 4 groups.
 Association index: Simple Ratio
 Iterations: 10000

| | | A | B | C | D | N |
|---|----|------|------|------|------|---|
| A | O: | | 1.00 | 0.25 | 0.50 | 3 |
| | E: | | 0.58 | 0.46 | 0.58 | |
| | p: | | 0.33 | 1.00 | 1.00 | |
| B | O: | 1.00 | | 0.25 | 0.50 | 3 |
| | E: | 0.58 | | 0.46 | 0.58 | |
| | p: | 0.33 | | 0.99 | 1.00 | |
| C | O: | 0.25 | 0.25 | | 0.67 | 2 |
| | E: | 0.46 | 0.46 | | 0.46 | |
| | p: | 1.00 | 0.99 | | 0.99 | |
| D | O: | 0.50 | 0.50 | 0.67 | | 3 |
| | E: | 0.58 | 0.58 | 0.46 | | |
| | p: | 1.00 | 1.00 | 0.99 | | |

For known individuals, the GROUPS program includes three commonly used association indices (Table 8.3), the relative merits of which are discussed by Cairns & Schwager (1987) and Ginsberg & Young (1992). All estimate the proportion of time that two individuals occur together, and all are symmetric (A associates with B at the same level that B associates with A). The “Twice-Weight” and “Simple Ratio” indices differ only in weighting simultaneous sightings of both individuals in different groups. Therefore they reduce to the same formula in this program (also known as Jacquard’s coefficient; Sneath & Sokal 1973). The program can also use as an index the number of

times two individuals occur together in the same group (“Co-occurrence Tally” in Table 8.3). This is useful for testing the overall goodness of fit between observed and expected values, as described below.

Table 8.3. Formulas for the association indices included in the GROUPS program. Names for the first three follow Cairns & Schwager (1987).

| | <u>Index</u> | <u>Formula</u> |
|-------------------------|------------------------------|--|
| Individual association: | Half-Weight | $\frac{x}{x + \frac{1}{2}(y_a + y_b)}$ |
| | Twice-Weight or Simple Ratio | $\frac{x}{x + y_a + y_b}$ |
| | Square Root | $\frac{x}{((x + y_a)(x + y_b))^{.5}}$ |
| | Co-occurrence Tally | x |
| Class association: | Frequency | $\frac{\sum a_i \text{ across all groups with } b_i > 0}{N_a}$ |
| | Mean Number | $\frac{\sum (a_i * b_i) \text{ across all groups}}{N_a}$ |

Definitions of variables:

x = number of groups containing both individuals A and B

y_a = number of groups containing only individual A

y_b = number of groups containing only individual B

a_i = the number of sightings of class "A" in group i

b_i = the number of sightings of class "B" in group i (b_i is replaced by a_i-1 for within-class association)

N_a = the number of sightings of class "A" in the data set

The program includes two association indices for data on classes (Table 8.3). The "Frequency" index is the frequency with which members of class A are observed in groups that also contain class B (ranging from 0 to 1). The "Mean Number" index is the average number of members of class B occurring with members of class A (ranging from 0 up). Unlike individual indices, class association indices are defined for each class with itself. Also unlike individual association indices, neither class index is symmetric. For example, the "Frequency" index might show that infants were always accompanied by adult females while the reverse was not true. Similarly, if females were more numerous, the "Mean Number" index might show that males had more female associates than females had male associates. Despite the asymmetry of the index itself however, the "Mean Number" index produces symmetric preference quotients and p values. In other words, if class A increases its contact with class B, then class B increases its contact with class A by exactly the same proportion, and with the same probability under the null hypothesis. This intuitively natural property arises because the denominator of the index does not change when group composition is randomized, and the numerator is symmetrical (see Table 8.3).

To obtain count data for an overall goodness of fit test, the program's output allows easy retrieval of the numerator of either class index. (Simply multiply each value of the association index by the number of sightings of the row class.)

Tests of overall significance

In some analyses the large number of dyads result in multiple tests, complicating the interpretation of p values. For example, 25 randomly associating individuals include 300 unique dyads, 15 of which are expected to show a significant association preference at the 0.05 level. This is not a problem if p values are used only as criteria for including dyads in descriptive analyses (e.g., Smolker et al. 1992). However, if one wishes to test

the null hypothesis that there are no association preferences in a data set, precautions may be necessary to avoid erroneously rejecting the null hypothesis. One approach is to lower the critical p value according to the number of tests, so that the risk of erroneously rejecting *any* null hypothesis does not exceed the critical value (e.g., Dunn-Sidak or Bonferroni methods; Sokal & Rohlf 1995). A less conservative alternative is to test for overall difference between observed and expected association levels before looking at dyads separately. A goodness of fit test such as a chi-square or G test is suitable for association indices that consist of counts, such as the number of co-occurrences in a data set. If the matrix of observed association levels deviates significantly from expected, one is justified in proceeding to examine which specific dyads are responsible for the preference. All of the association indices have counts as their numerators, and for the Simple Ratio index and both indices of class association, p values are unaffected if only the numerator is used instead of the whole index, because the denominator is not changed by randomizing group composition.

Finally, one may wish to test for similarity to a specific predicted pattern, rather than deviations from random association. Using a matrix of preference quotients rather than raw association levels makes it possible to use Mantel or related matrix permutation tests with class-based as well as individual-based association indices, because the expectation of equal values in all cells is then a valid representation of the null hypothesis of random association.

Interpreting association preference

Preference quotients should be interpreted with care, because factors other than active choice of associates can influence them. Different individuals may have different home ranges or daily activity patterns, or be attracted to different micro-habitats. Two individuals or classes may also show an apparent “affinity” for each if they are both

attracted to a third party, such as adult males congregating around estrous females. Finally, measures of association preference can only reflect association within a sample, and how well this reflects the population depends on the sampling methods used.

EXAMPLES

Because there is a much larger literature on the use of individual association indices, and an application of the GROUPS program to individual associations has already been published (Smolker et al. 1992), I will present here three examples of applications of the program to analyzing association between classes.

Example 1: Testing affiliation among the sexes using group composition data

Badrian & Badrian (1984) studied the group composition of wild bonobos (*Pan paniscus*), and reported their data in sufficient detail for re-analysis (Table 8.4). They note that, “the frequency of groups containing individuals of only one sex was low”, and “the predominance of mixed groups (groups containing both sexes) indicates that inter-individual affinity among pygmy chimpanzees is high”. They also use the frequency of mixed groups as an indicator of inter-sexual affiliation, as have other authors (e.g., Halperin 1979, Wells et al. 1987). However, these conclusions are not supported quantitatively. The proportion of mixed-sex groups reflects the size distribution of groups as well as association preferences, because larger groups are more likely to include both sexes. It is therefore not obvious what would constitute a “high” or “low” frequency of mixed-sex groups in a particular data set.

Because the indices of association included in the GROUPS program are designed to reflect the social environment experienced by individuals, none of them measure

association by counting groups, as Badrian & Badrian (1984) did. However, one of the indices in the program (“Frequency”) reflects how much time members of each sex spend in mixed-sex versus single-sex groups. The results of an analysis using this index show that although males did appear in single-sex groups 4% less often than expected, females actually appeared in single-sex groups 1% more often than expected. Neither of these differences were statistically significant, however (Table 8.5a). Note that preference quotients based on this index are not symmetric. Females were accompanied by males more often than expected, while males were accompanied by females less often than expected.

The authors conclude that, “The core of pygmy chimpanzee society is characterized by the presence of strongly bonded females, and males associating with them.” Is this conclusion supported by the data? The amount of time spent in groups containing at least one member of a given sex may not be the most appropriate or sensitive measure of affiliative tendency. A better measure may be the *number* of members of a given sex that individuals occur with on average (the “Mean Number” index). An analysis using this measure does indeed show that the strongest affinity (highest preference quotient) is among females, followed by males with females (Table 8.5b). The statistically significant avoidance among males suggests that they are only attracted to groups because they include females.

Table 8.4. Data from Badrian & Badrian (1984) on the size and adult sex composition of 190 groups of wild bonobos. Values in the table represent the number of groups observed of each type.

| | | Number of males in group | | | | | | | |
|----------------------------------|----|--------------------------|----|---|---|---|---|---|----|
| | | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 11 |
| Number of females in group | 0 | - | 24 | 7 | 2 | - | - | - | - |
| | 1 | 12 | 21 | 8 | 2 | 1 | - | - | - |
| | 2 | 2 | 12 | 4 | 8 | 3 | - | - | - |
| | 3 | 6 | 4 | 5 | 6 | 5 | 1 | - | - |
| | 4 | 1 | 2 | 1 | 2 | 1 | - | - | - |
| | 5 | 1 | 4 | 4 | 5 | 4 | 1 | - | - |
| | 6 | - | - | 2 | 3 | 1 | 3 | - | - |
| | 7 | - | - | 1 | 3 | 2 | 1 | 1 | - |
| | 8 | - | 1 | 1 | 1 | - | 2 | - | - |
| | 9 | - | - | - | - | - | 4 | 1 | - |
| | 10 | - | - | - | 1 | - | - | - | - |
| | 11 | - | - | - | - | 1 | - | - | - |
| | 12 | - | - | 1 | - | - | - | - | - |
| 18 | - | - | - | - | - | - | - | 1 | |

Table 8.5. Output of the GROUPS program using the data from Table 8.4 in 10,000 iterations. Values indicate association of row class (class A in Table 8.3) with column class (class B in Table 8.3). O = observed level, E = expected level, p = two tailed p value, N = total number of sightings of row class.

A. Association index = "Frequency"

| | | Female | Male | N |
|--------|------|--------|------|-----|
| Female | O: | 0.92 | 0.92 | 552 |
| | E: | 0.91 | 0.86 | |
| | O/E: | 1.01 | 1.07 | |
| | p: | 0.44 | 0.19 | |
| Male | O: | 0.89 | 0.83 | 390 |
| | E: | 0.91 | 0.86 | |
| | O/E: | 0.97 | 0.96 | |
| | p: | 0.19 | 0.02 | |

B. Association index = "Mean Number"

| | | Female | Male | N |
|--------|------|--------|------|-----|
| Female | O: | 4.65 | 3.05 | 552 |
| | E: | 4.25 | 3.01 | |
| | O/E: | 1.10 | 1.02 | |
| | p: | 0.04 | 0.42 | |
| Male | O: | 4.32 | 2.29 | 390 |
| | E: | 4.26 | 3.00 | |
| | O/E: | 1.02 | 0.76 | |
| | p: | 0.42 | 0.00 | |

Example 2: Measuring grooming preferences from participation in bouts

Badrian & Badrian (1984) present counts of mutual grooming bouts broken down by age and sex class (Table 8.6). They state that, “mutual grooming reflects the degree of affinity existing between individuals in great ape societies”, and that “male-female grooming partnerships were the most important between adults, female-female partnerships were the next most common, and male-male dyads the least common.” However, the frequency of grooming between two classes reflects not only affinities or preferences, but also the frequency with which each class participates in grooming. For example because males groom less frequently than females, male-male bouts would be relatively rare if grooming partners were paired randomly. Therefore the frequency of grooming between two classes does not necessarily correspond to their “degree of affinity”.

The GROUPS program solves this problem because different frequencies of grooming by different classes or individuals are incorporated into the model used to generate expected frequency distributions. I analyzed the data in Table 8.6 by treating each grooming bout as a group of size two, and using the “Frequency” index of class association (see Table 8.7 for output). To test for deviation from random association in the data set overall, I first examined the goodness of fit between observed and expected co-occurrence tallies. The observed values were very different from expected under random association ($p < 0.001$, see Table 8.8). Examining class dyads separately, the strongest grooming affinity among adults was actually between males, who groomed one another 77% more often than expected (although this preference did not reach statistical significance; Table 8.7). Female-female grooming rates occurred 43% less often than expected and constituted the only statistically significant level of avoidance. These results are somewhat counter-intuitive, and quite different from the authors’ interpretation based on the raw counts in Table 8.6.

Table 8.6. Counts of bonobo grooming bouts by age and sex of participants.
 From Badrian & Badrian 1984. M = adult male, F = adult female, J = juvenile, I = infant.

| | M | F | J | I |
|---|---|----|---|----|
| M | 5 | 18 | 0 | 1 |
| F | | 12 | 7 | 29 |
| J | | | 0 | 0 |
| I | | | | 0 |

Table 8.7. Analysis of the bonobo grooming data in Table 8.6 using the GROUPS program and 10,000 randomizations. I used the “Frequency” association index, which measures how frequently the row class occurred with the column class. M = adult male, F = adult female, J = juvenile, I = infant. See Table 8.5 for explanations of other abbreviations.

| | | M | F | J | I | N |
|---|------|-------|-------|-------|-------|----|
| M | O: | 0.345 | 0.621 | 0.000 | 0.034 | 29 |
| | E: | 0.194 | 0.547 | 0.049 | 0.210 | |
| | O/E: | 1.773 | 1.135 | 0.000 | 0.164 | |
| | p: | 0.224 | 0.558 | 0.395 | 0.011 | |
| F | O: | 0.231 | 0.308 | 0.090 | 0.372 | 78 |
| | E: | 0.203 | 0.538 | 0.049 | 0.210 | |
| | O/E: | 1.135 | 0.572 | 1.833 | 1.774 | |
| | p: | 0.558 | 0.000 | 0.029 | 0.000 | |
| J | O: | 0.000 | 1.000 | 0.000 | 0.000 | 7 |
| | E: | 0.203 | 0.546 | 0.044 | 0.208 | |
| | O/E: | 0.000 | 1.833 | 0.000 | 0.000 | |
| | p: | 0.395 | 0.029 | 1.000 | 0.381 | |
| I | O: | 0.033 | 0.967 | 0.000 | 0.000 | 30 |
| | E: | 0.203 | 0.545 | 0.049 | 0.204 | |
| | O/E: | 0.164 | 1.774 | 0.000 | 0.000 | |
| | p: | 0.011 | 0.000 | 0.381 | 0.038 | |

Table 8.8: The number of occurrences of row class individuals with column class individuals in the bonobo grooming data (Table 8.6). Values were calculated from Table 8.7 by multiplying the “Frequency” association index by the number of sightings of the row class. Juvenile and subadult categories were pooled to achieve large enough expected values for testing. The matrices are significantly different: $G = 26.8$, $d.f. = 5$, $p < 0.001$.

| | | Observed | | | | | Expected | | |
|-----|--|----------|----|-----|-----|--|----------|------|------|
| | | M | F | J/I | | | M | F | J/I |
| M | | 10 | 18 | 1 | M | | 5.6 | 15.9 | 7.5 |
| F | | | 24 | 36 | F | | | 42.0 | 20.2 |
| J/I | | | | 0 | J/I | | | | 7.9 |

Example 3: Development of sex-specific association patterns

In the final example I demonstrate the program’s use in exploratory data analysis, and also test its reliability through repeated measures from the same population. The data set consists of bottlenose dolphin groups observed over five years in Western Australia (see Smolker et al. 1992 for methodology). Although group members were identified individually, for this analysis I used only designations of age and sex class. I measured class association using the “Mean Number” index (Table 8.5). The results of a GROUPS analysis (summarized in Table 8.9b), illustrate the development of sex-specific association patterns through three life stages. Calves of both sexes associated preferentially with females and calves and avoided non-calf males. Subadults of both sexes associated preferentially with other subadults of both sexes, and avoided adult males. Some sex differences also emerge at this age; subadult females maintained their affinity with calves and adult females, while subadult males avoid them. By adulthood, the association preferences of the two sexes were almost opposite. Adult males showed an affinity with adult males and an avoidance of all other classes, while adult females

avoided non-calf males and preferred females and calves. Although not all of these preferences were present at a significant level in every year, none of the 56 significant preferences were reversed between years (Table 8.9a). This consistency provides a measure of confidence in the robustness and reliability of this approach to measuring social affinity.

Such an analysis of social affinity using class-based data would not be possible without the randomization method. Although one could undertake the analysis using individual-based indices, the very large matrices of several thousand pair-wise values that would result for each year would be awkward to manage and interpret. Thus even when individual identities are known, class-based analyses may be more practical and informative for some questions.

Table 8.9a. Association preferences among age-sex classes of bottlenose dolphins. The data from each year was subjected to 10,000 iterations of the GROUPS program. Results are shown as \log_2 transformed preference quotients, thus sign indicates direction of preference and each whole number increase represents a two fold increase in the preference quotient. Only preferences with $p < 0.01$ are shown. M = male, F = female, A = adult, S = subadult, C = calf. N = number of sightings per class per year.

| Year | | MA | MS | MC | FA | FS | FC | N |
|------|----|-----|------|------|------|------|------|-----|
| 1985 | MA | 1.0 | -1.4 | | | -0.4 | | 289 |
| | MS | - | 0.9 | | -0.8 | | -0.8 | 236 |
| | MC | - | - | | | | | 0 |
| | FA | - | - | - | | 0.4 | 1.0 | 178 |
| | FS | - | - | - | - | 0.4 | 0.5 | 237 |
| | FC | - | - | - | - | - | | 98 |
| | | | | | | | | |
| 1986 | MA | 0.8 | -0.6 | | -0.4 | -0.6 | -0.7 | 408 |
| | MS | - | 0.6 | | -0.4 | | | 258 |
| | MC | - | - | | | | | 6 |
| | FA | - | - | - | 0.4 | | 0.8 | 277 |
| | FS | - | - | - | - | | | 236 |
| | FC | - | - | - | - | - | | 101 |
| | | | | | | | | |
| 1987 | MA | 0.5 | | | -0.6 | -2.1 | -0.8 | 431 |
| | MS | - | 1.0 | | -0.6 | | -1.0 | 136 |
| | MC | - | - | | 0.9 | | 1.1 | 23 |
| | FA | - | - | - | 0.3 | 0.5 | 0.9 | 292 |
| | FS | - | - | - | - | | | 82 |
| | FC | - | - | - | - | - | | 99 |
| | | | | | | | | |
| 1988 | MA | 0.5 | -0.5 | | -0.8 | -0.4 | -0.6 | 375 |
| | MS | - | 1.8 | | -0.6 | 0.8 | | 90 |
| | MC | - | - | | 1.3 | | | 25 |
| | FA | - | - | - | 0.5 | 0.5 | 1.0 | 292 |
| | FS | - | - | - | - | | 0.7 | 69 |
| | FC | - | - | - | - | - | | 117 |
| | | | | | | | | |
| 1989 | MA | 1.0 | -0.6 | -3.0 | -0.7 | -0.8 | -1.1 | 245 |
| | MS | - | 2.1 | | -0.7 | | -1.5 | 93 |
| | MC | - | - | | | | | 30 |
| | FA | - | - | - | 0.4 | 0.8 | 0.6 | 266 |
| | FS | - | - | - | - | | | 68 |
| | FC | - | - | - | - | - | | 27 |
| | | | | | | | | |

Table 8.9b. Averages across all five years of log-transformed preference quotients from Table 8.9a. Positive values indicate affinities, and negative values indicate avoidances. M = male, F = female, A = adult, S = subadult, C = calf.

| | MA | MS | MC | FA | FS | FC |
|----|-----|------|------|------|------|------|
| MA | 0.8 | -0.8 | -3.0 | -0.6 | -0.9 | -0.8 |
| MS | - | 1.3 | | -0.6 | 0.8 | -1.1 |
| MC | - | - | | 1.1 | | 1.1 |
| FA | - | - | - | 0.4 | 0.5 | 0.9 |
| FS | - | - | - | - | 0.4 | 0.6 |
| FC | - | - | - | - | - | 0.0 |

OTHER APPLICATIONS OF THE GROUP RANDOMIZATION METHOD

Although I have emphasized applications involving social groups of animals, this is part of a larger family of problems involving the co-occurrence of elements that are repeatedly re-combined into groups of varying sizes. These problems share the same logical structure, and can all be addressed through the group randomization approach. For example, biases in the sex ratio of offspring have been studied in many species. To test the hypothesis that different mothers produce significantly different sex ratios, Sokal & Rohlf (1995, p. 706) recommend using a G test on a subset of the data consisting of sib groups of the same size. Although groups of offspring almost always vary in size, no existing method is applicable when family sizes vary. The GROUPS program can solve

this problem by using a class-based association index such as “Mean Number” to test for an “association preference” between sexes within sib groups.

Most of the individual association indices used in studies of animal behavior were originally devised by ecologists for studying the geographical co-occurrence of different species (Cairns & Schwager 1987), and they are still frequently used for this purpose. Species are scored as either present or absent in each location or sample plot, making them analogous to individuals in social groups. There is still no satisfactory general method for testing whether two species co-occur more often than expected by chance (Wilson 1987). The group randomization approach provides a solution for this problem.

More generally, any kind of entity that is repeatedly combined into “groups” of variable composition can be analyzed the same way, not just organisms. For example, in the gargle vocalization of the black-capped chickadee, certain note types tend to occur together in the same individuals’ repertoire more often than expected (Ficken & Popp 1995). The association of note types within repertoires fits into the same framework as the previous examples. In this application, the “group” is defined as the individual repertoire. If note types are scored as either present or absent, then individual-based indices are appropriate, while if the number of occurrences of a note type in a repertoire is relevant, then class-based indices are better suited.

Thus the group randomization approach is a general method for studying non-random patterns of co-occurrence in group composition data, and is applicable to a number of current problems in animal behavior and ecology.

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