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# 1 Generalized affiliation indices extract

## 2 affiliations from social network data

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15

16 **Abstract**

17 1. In the analysis of animal social networks, a common challenge has been distinguishing affiliations—  
18 active preferences of pairs of individuals to interact or associate with one another—from other,  
19 structural, causes of association or interaction. Such structural factors can include patterns of use of the  
20 habitat in time and space, gregariousness, and differential association rates among age/sex classes.

21 2. In an approach with similarities to the multiple regression quadratic assignment procedures test, we  
22 suggest calculating generalized affiliation indices as the residuals from a regression of the measures of  
23 association or interaction on structural predictor variables, such as gregariousness and spatiotemporal  
24 overlap. If the original data are association indices or counts of interactions, then generalized linear  
25 models with binomial or Poisson error structures, respectively, can be used in place of linear regression.  
26 Anscombe or deviance residuals can be used to assess the significance of particular affiliation indices.

27 3. Generalized affiliation indices can be used as the weights of links in a social network representation.  
28 They can then be portrayed in network diagrams or cluster diagrams, and used to calculate network  
29 statistics, to delineate communities by maximizing modularity, and to test for overall affiliation using  
30 data-stream permutation tests.

31 4. We evaluate the effectiveness of such generalized affiliation indices using simulated and real  
32 association data, finding that the method removes much of the effect of structural variables on  
33 association patterns, revealing real affiliations. While the approach is very promising, it is limited by the  
34 extent to which the input predictor variables represent important structural factors.

35

36

37 Keywords: Social structure; association; interaction; regression; residuals; multiple regression quadratic

38 assignment procedure; permutation test

## 39 **Introduction**

40 Among the potential goals of social network analysis, perhaps most fundamental is the description and  
41 investigation of preferred and avoided dyadic relationships, what we will call affiliations. A frequent  
42 objective of social network analysis has been testing the null hypothesis that there are no such  
43 affiliations in the study population, and, if this is rejected, identifying dyads with preferred or avoided  
44 relationships (Bejder, Fletcher & Bräger 1998; Croft *et al.* 2011).

45 Many, perhaps most, studies of the social networks of non-humans are built upon matrices of  
46 association indices, estimates of the proportion of time that pairs of individuals are associated  
47 (Whitehead 2008). In this approach, association should be defined such that is meaningful to the  
48 animals—how they interact and/or communicate—, but operationally association is usually based upon  
49 spatial, temporal, and/or behavioural metrics (Whitehead 2008). Using this approach, pairs of  
50 individuals may be delineated as associated if they are 1) communicating/interacting and making active  
51 decisions to associate with one another, 2) if they happen to be in the same place at the same time and  
52 so communicate/interact, or 3) if they happen to be in the same place at the same time and are not  
53 communicating or interacting. If interest is in disease transmission over the social network then all  
54 three of these forms of association are important. Forms 1) and 2), but not 3), allow for the  
55 transmission of cultural information transmitted through interactions or communication. However if we  
56 are interested in actively-maintained dyadic relationships, affiliation, only form 1) is relevant. In  
57 addition to true affiliation, factors that might affect association include spatial overlap (animals using  
58 the same parts of the population range associate more (e.g. Shizuka *et al.* 2014)), temporal overlap  
59 (animals using the study area at the same time are more likely to associate (e.g. Cantor *et al.* 2012)),  
60 gregariousness (animals that preferentially are found in large groups are more likely to associate with  
61 one another (Godde *et al.* 2013)), and gender (there may be preferential associations with the same or

62 the opposite sex). We shall refer collectively to such sources of association, which potentially mask the  
63 existence and strength of true affiliations, as structural variables.

64 Sometimes it is not clear whether a factor should be considered a structural factor predicting association  
65 or an element of affiliation. For instance, kinship could be deemed a structural factor if there is a  
66 preference to associate with kin, but kinship recognition is not linked to individual identification. If, on  
67 the other hand, kinship is perceived by the animals at an individual level (“One of the reasons I like X is  
68 because she is kin”), so affecting affiliation rather than association directly, then it might not be  
69 considered structural.

70 Disentangling true affiliations from other causes of association has led to the construction of structured  
71 permutation tests (Bejder, Fletcher & Bräger 1998; Croft *et al.* 2011; Whitehead 1999; Whitehead,  
72 Bejder & Ottensmeyer 2005). However such tests have limitations and challenges. They only give a  
73 perspective on the null hypothesis that there are no affiliations, or, in the case of a dyadic test (Bejder,  
74 Fletcher & Bräger 1998) that two animals are not affiliates. Furthermore as more structural factors that  
75 might cause association are accounted for, the tests become increasingly unwieldy. Additionally,  
76 network diagrams and network statistics include the non-affiliative causes of association, and so will be  
77 misleading if the primary goal is to study patterns of affiliation.

78 An alternative perspective pioneered by Godde *et al.* (2013) in the case of gregariousness is to correct  
79 the association index for the structural factor, and then carry out additional analyses—tests, diagrams  
80 and network statistics—on this new index. Here we extend this approach to include multiple structural  
81 factors, using a method closely allied with MRQAP (multiple regression quadratic assignment  
82 procedures).

83 MRQAP is itself an extension of the Mantel (1967) test in which the non-diagonal elements of two  
84 square matrices both indexed by the same objects (usually individuals in social network analysis) for

85 both rows and columns are tested for a linear relationship. So we might test whether there is an overall  
86 correlation between association indices of dyads and their genetic relatedness. Because of non-  
87 independence caused by the structure of the data, standard tests of correlation coefficients are invalid,  
88 but permutations of the object labels on one of the matrices allows a null hypothesis of no relationship  
89 to be tested. MRQAP extends this approach to situations in which the relationship between one  
90 dependent variable—typically an association index in social network analyses of animals—and an  
91 independent variable—such as kinship—is examined while controlling for other independent variables—  
92 such as range overlap or gender similarity. Because of potential collinearity among the independent  
93 variables, this is not as straightforward as in the case of the bivariate Mantel test. However, there are  
94 effective permutation methods for MRQAP tests (Dekker, Krackhardt & Snijders 2007).

95 Here we propose that the residuals following a multiple regression of the association index on various  
96 structural variables using generalized linear models, be used as generalized indices of affiliation among  
97 pairs of individuals. We consider possible structural variables that might be included as predictors of  
98 association, how to measure the significance of structural variables, and, having removed the structural  
99 factors, how to test for the presence of affiliation both at the dyadic level and globally. We illustrate the  
100 method using simulated and real data.

## 101 **Methods**

### 102 **Calculating generalized affiliation indices**

103 We start with a square matrix representing associations or interactions between individuals. This will  
104 often be a matrix of association indices, such as the simple ratio index (Ginsberg & Young 1992), which  
105 estimates the proportion of time members of a dyads are associated:

$$106 \quad y(\text{simple ratio})_{ij} = \frac{\text{No. sampling periods } i \text{ and } j \text{ associated}}{\text{No. sampling periods } i \text{ or } j \text{ or both observed}} \quad (1)$$

107 where  $y_{ij}$  is the simple ratio association index between individuals  $i$  and  $j$ , given definitions of  
108 “association” (e.g. seen within 3 body lengths of one another) and “sampling period” (e.g. hour ). Also  
109 frequently used is the half weight index in which the denominator of the simple ratio index is replaced  
110 by half the sum of the sampling periods in which each individual was observed. However the matrix  
111 could list counts of, say, touches between individuals, and it could be asymmetric.

112 If the non-diagonal elements of the association matrix are listed in an  $n$ -element vector  $Y$  (if asymmetric  
113 all non-diagonal values are entered and  $n$  is twice the number of dyads; if symmetric only the upper or  
114 lower triangle is needed and  $n$  is the number of dyads), and the corresponding elements of  $v$  structural  
115 predictor variables for each dyad are given in the  $n$ -by- $v$  matrix  $X$ , the generalized linear model is:

$$116 \quad f(Y) = \alpha X + E \quad (2)$$

117 where  $f$  is a link function,  $\alpha$  is a vector of the regression coefficients, and  $E$  an  $n$ -element vector of  
118 residuals. Following the regression,  $E$  is then recast as a square matrix in which the  $ij$  element gives the  
119 generalized affiliation index,  $e_{ij}$ , between individuals  $i$  and  $j$ . A high positive value of  $e_{ij}$  suggests  
120 affiliation—i.e. that the dyad are more associated than expected given the structural predictor  
121 variables—and a negative value indicates avoidance.

122 If the elements of  $Y$  are simple counts of interactions—as may be appropriate with small populations  
123 when all interactions can be observed—then a Poisson generalized linear model, with a log link function  
124 can be used. If an association index (e.g. equation 1), the numerator and denominator of the index can,  
125 with the assumption of independence, be considered to be from the binomial distribution. Hence we  
126 can use a binomial version of the generalized linear model and a logit link function, with the vector  $Y$  in  
127 equation 2 becoming a  $n$ -by-2 matrix giving the numerator and denominator of each association index.  
128 This formulation is useful in that it corrects for variable amounts of effort directed towards different  
129 dyads.



130 If using a linear model then the residuals from the regression model can be used straight as affiliation  
131 indices. When using a binomial model, they should be divided by the denominator of the original  
132 association index (as in the denominator of equation 1). With a Poisson model the straight residuals  
133 seem to work reasonably (see Results).

134 We can transform the residuals, for instance into Anscombe residuals or deviance residuals (Pierce &  
135 Schafer 1986), which should be distributed as the standard normal distribution. These indicate the  
136 statistical significance of particularly large positive or negative affiliations. In our evaluations of real and  
137 simulated data (see below), we found that Anscombe and deviance residuals were very similar to one  
138 another.

### 139 **Structural variables and their significance**

140 Structural variables may be continuous, ordinal, categorical, or binary. Here are some that might be  
141 employed:

142 *Range overlap:* Concurrent use of space is necessary for association or interaction. Thus range overlap  
143 (within the study area) will often be a structural variable of concern. Utilization distributions describe  
144 how animals use habitat, the probability that they are in a particular place, and can be estimated from  
145 real locational data in a variety of ways. Getz et al. (2007) recommend the local convex hull  
146 nonparametric kernel method, and its variants, as being superior to other current techniques. We are  
147 interested in the extent to which the utilization distributions of different individuals overlap, for which  
148 there are several potential statistics, including the utilization distribution overlap index and  
149 Bhattacharyya's affinity (Fieberg & Kochanny 2005). These could be appropriate measures of range  
150 overlap.

151 *Temporal overlap:* Animals may move into and out of the study area where association is observed, and  
152 can only be observed associating when they are both inside it. Short time scale temporal overlap, i.e. at

153 a scale similar to the sampling period being used, might be considered an element of affiliation—  
 154 animals choosing, or not, to be together. Longer time scale emigration/immigration, or birth/death, is  
 155 perhaps more of a structural factor affecting association. A suitable measure might be an association  
 156 index, as in equation 1, but using a long sampling period, say a month or year, and defining association  
 157 broadly as both individuals identified, not necessarily associated, in that sampling period. This gives an  
 158 estimate of the proportion of time that two individuals were both in the study area during the research.  
 159 In some cases, such as when data are collected non-continuously in several study locations that are  
 160 small relative to the ranging patterns of the animals, spatial and temporal overlap might be covered by  
 161 one predictor variable, similar to the temporal predictor just proposed.

162 *Gregariousness*: Godde et al. (2013) correct standard association indices for gregariousness using the  
 163 expected values of the association index for a pair, given the estimated gregariousness of each. We  
 164 could use this as a measure of mutual gregariousness, and a structural variable in the estimation of  
 165 affiliation:

166 
$$x(\text{gregariousness})_{ij} = \frac{\sum_k y_{ik} \cdot \sum_k y_{jk}}{\sum_k \sum_l y_{kl}} \quad (3)$$

167 where  $y_{ij}$  is the association index between individuals  $i$  and  $j$ , and  $y_{kk}$  is set to zero for all  $k$ . As we are  
 168 supposing that the association indices may depend on structural factors, including gregariousness itself,  
 169 this formulation is somewhat circular: a high value of an association index between two individuals  
 170 increases their joint gregariousness. To remove this effect, we propose removing each dyadic  
 171 association index when calculating the joint gregariousness of that particular dyad:

172 
$$x(\text{gregariousness})_{ij} = \text{Log}(\sum_{k \neq i, j} y_{ik} \cdot \sum_{k \neq i, j} y_{jk}) \quad (4)$$

173 *Gender/class similarity*: The simplest version of a gender similarity structural variable is:  $x(\text{gender})_{ij}=1$  if  $i$   
 174 and  $j$  are the same gender;  $x(\text{gender})_{ij}=0$  if of different gender. This implies that in gender relationships

175 same and different are the primary factors. Alternatively a categorical variable, with three values,  
176  $(x(\text{gender})_{ij} = \text{MM}, \text{MF}, \text{or FF})$  can be defined giving different possible association rates for males with  
177 males and females with females, as well as between the sexes. If the population is delineated into other  
178 classes that might affect association, for instance age classes, reproductive status or classes based upon  
179 mitochondrial haplotypes or characteristic behaviour, then structural variables can be defined in a  
180 similar manner.

181 *Social unit membership:* If animals are allocated to social units we can use these units as classes to  
182 define a structural variable. One possibility is a simple binary same/different unit categorization. A more  
183 nuanced categorization, using up more degrees of freedom, would give distinctive values for  
184 associations within each unit, and between members of each pair of units.

185 *Kinship:* As noted in the Introduction, it may sometimes be appropriate to consider the kinship between  
186 two animals as a structural variable influencing, likely positively, their probability of association. Kinship,  
187 as measured by relatedness, can be calculated if the genealogy of the population is known, but will  
188 more often be estimated using molecular genetic markers such as microsatellites (van de Castele, Galbusera & Mattysen 2001). However, often kinship may most appropriately be considered as a factor  
189 influencing affiliation itself and therefore one would not want to factor it out before calculating  
190 affiliation, rather seeing how kinship relates to the output affiliations.  
191

192 The relative significance of the different structural variables can be assessed in several ways. For  
193 instance, we can present standardized partial correlation coefficients of each predictor variable with the  
194 association index, controlling for the other predictor variables. Being dimensionless, these give easily-  
195 interpretable measures of the relative significance of the predictors. We can also carry out MRQAP tests  
196 for each predictor, controlling for the others. These can be the basis of stepwise procedures aimed at  
197 delineating an efficient subset of structural factors that affect association.

## 198 **Using affiliation indices**

199 With a few exceptions, generalized affiliation indices can be analyzed much as association indices. We  
200 can display them as a printed matrix, as a network diagram, or using multidimensional scaling or  
201 hierarchical cluster analysis (Whitehead 2008). We can examine the distribution of the generalized  
202 affiliation indices or network statistics derived from them, such as strength (gregariousness),  
203 connectedness and affinity (Croft, James & Krause 2008; Wey *et al.* 2008). We can see how these  
204 measures differ between classes of animal, such as the sexes, and how they may correlate with one  
205 another. We can look for fairly closed communities of affiliated individuals by techniques such as  
206 maximizing modularity (Newman 2006). We can use data-stream permutation tests to test null  
207 hypotheses that there is no real affiliation in the population (Bejder, Fletcher & Bräger 1998). For these  
208 tests, first the gregariousness values (if being used as a predictor), then the generalized affiliation  
209 indices, and finally the test statistic (e.g. the standard deviation of the indices) are recalculated after  
210 each permutation of the data. The value of the test statistic on the real data is compared with that for  
211 the permutations, giving a P-value.

212 Unlike association indices or counts of interaction, generalized affiliation indices can be negative. Thus,  
213 they cannot be used as input for principal coordinates analysis; further, some standard test statistics of  
214 permutation tests, such as the coefficient of variation of the indices, are inappropriate. (The standard  
215 deviation of the indices is an appropriate test statistic for both association and affiliation indices.)

216 Negative generalized affiliation indices are also an issue when using network diagrams to illustrate the  
217 generalized affiliation indices. They can be omitted, or perhaps illustrated in a different way (different  
218 colour or line style) from the positive indices.

## 219 Evaluating generalized affiliation indices

### 220 Simulated data

221 We used simulated data to investigate to what extent the generalized affiliation indices produced by the  
222 method described above mirror input affiliations, and to examine whether the significance of the  
223 predictor variables suggested by the proposed method matched their input significance.

224 We constructed simulated data sets with the following characteristics:  $m$  individuals, each with a 50%  
225 probability of being male or female,  $s_i=0$  or 1 respectively, a gregariousness,  $g_i$ , drawn from the uniform  
226 random distribution on  $[1 G]$ . There are  $n=m(m-1)$  dyads. Each dyad has a probability  $p$  of being  
227 designated a pair of “affiliates”:  $f_{ij}=1$  if  $i$  and  $j$  affiliates,  $f_{ij}=0$  otherwise. Each pair of individuals may, or  
228 may not, associate during any of  $T$  sampling periods.

229 At the beginning of the simulation (sampling period 0), individuals have a 50% probability of being inside  
230 the study area. At the start of each sampling period individuals outside the study area have probability  $q$   
231 of entering it, and those inside the study area probability of  $q$  of leaving, giving sequences:  $b_{it}=1$  if  
232 individual  $i$  was in the study area in sampling period  $t$ ,  $b_{it}=0$  if not.

233 Then, for individuals  $i$  and  $j$  in sampling period  $t$  we define a propensity for association:

$$234 u_{ijt} = g_i \cdot g_j \cdot b_{it} \cdot b_{jt} \cdot (1 + \sigma \cdot (s_i == s_j)) \cdot (1 + \phi \cdot f_{ij}) \quad (5)$$

235 This is dependent on the gregariousness of each individual ( $g_i, g_j$ ), requires both to be in the study area  
236 during the sampling period ( $b_{it}=b_{jt}=1$ ), and is increased if both are of the same sex (by a factor of  $1+\sigma$ ), or  
237 both are affiliates (by a factor of  $1+\phi$ ). The probability that individuals  $i$  and  $j$  are associated in sampling  
238 period  $t$  is proportional to the propensity for association,  $u_{ijt}$ , with the constant of proportionality  
239 adjusted so that the maximum probability of association is  $a_{max}$ . This procedure then gives a record of

240 associated/not associated for each pair of individuals in each sampling period, from which we calculated  
241 association indices as in equation 1.

242 Assuming that we knew the sexes of each individual, but not their actual gregariousness, actual  
243 presence in the study area, or who were affiliates with whom, we estimated affiliation indices as  
244 described above using the following predictors: sex similarity, estimated dyadic gregariousness  
245 (equation 4), an estimate of temporal overlap (a simple ratio index using sets of five consecutive  
246 sampling periods as the new long sampling period, and defining association as both animals identified in  
247 a long sampling period), and a nuisance variable with uniform random numbers from the [0 1] interval  
248 chosen for each dyad with no relationship to association. We used the linear model on the association  
249 indices, the binomial model on the numerator and denominator of the association indices, and the  
250 Poisson model just on the numerator of the association indices.

251 At the end of each run we retrieved the information on which pairs were affiliates, and compared the  
252 association indices and affiliation indices of affiliated pairs and non-affiliated pairs. The success of an  
253 index in identifying affiliates was indicated by Cohen's  $d$ , the difference between the mean of the index  
254 for affiliated pairs and that for non-affiliated pairs divided by the pooled standard deviation.

255 For each data set we also calculated the partial correlation coefficient between the association indices  
256 and each of the predictor variables, controlling for the other predictor variables. These partial  
257 correlation coefficients were also the test statistic for MRQAP double semi-partiailling (Dekker,  
258 Krackhardt & Snijders 2007) tests for each predictor (null hypothesis that the predictor was linearly  
259 unrelated to association, given the other predictors), with 1,000 replicates.

260 For each data set we tested for preferred/avoided associations using the 'permute associations within  
261 sampling periods' methodology in which pairs of associates within sampling periods are flipped  
262 maintaining the number of associates of each individual as well as the total number of associations

263 within each sampling period (Whitehead, Bejder & Ottensmeyer 2005). We tested both the association  
264 indices and generalized affiliation indices using this method (calculating generalized affiliation indices  
265 anew for each random data set), with 1,000 permutations and each permutation being made up of  
266 1,000 flips. The null hypothesis of no preferred association/affiliation was rejected if the standard  
267 deviation of the real indices was greater than at least 950 of the standard deviations of the sets of  
268 random indices.

269 Initial runs were made using a “standard” set of parameters:  $n=20$ ,  $G=2$ ,  $T=50$ ,  $\rho =0.09$ ,  $q=0.1$ ,  $\sigma=0.9$ ,  
270  $\phi=2.0$ ,  $a_{max}=0.6$ . In subsequent sets of runs, we changed the number of individuals ( $n=10, 40$ ), number  
271 of sampling periods ( $T=25, 100$ ), and mean rate of association ( $a_{max}=0.3, 0.85$ ) to check the robustness of  
272 the results for smaller, larger, or differently-sampled data sets. Then we effectively removed any  
273 preference for affiliates ( $\phi=0.0$ ), gregariousness differences ( $G=1$ ), and sex preferences ( $\sigma=0.0$ ). In the  
274 final set of runs we increased the rates of movement into and out of the study area ( $q=0.4$ ) effectively  
275 making our measure of temporal overlap (calculated over 5 consecutive sampling periods) no longer  
276 relevant. There were 100 runs with each set of parameters.

### 277 **Bottlenose whale data**

278 We used a data set on the social relationships of northern bottlenose whales (*Hyperoodon ampullatus*)  
279 based upon photoidentifications collected in three submarine canyons on the edge of the Scotian Shelf  
280 between 1988-2003, an extended version of the data set analyzed by Gowans et al. (2001). We used  
281 only those animals: a) with markings considered “reliable” allowing consistent matching between years;  
282 b) who could be allocated to age-sex classes as either mature males, subadult males or females based  
283 upon photographs of their foreheads; and c) who were identified on 15 or more different days (see  
284 Gowans, Whitehead & Hooker 2001). There were 16 animals in this data set. Sampling periods were  
285 days, and dyads were considered associated on a day if they were identified within 1 hour of each other.

286 We constructed half-weight indices between individuals using these data. We also calculated several  
287 predictor measures:

288 'Gregariousness': as in equation 4.

289 'Age-Sex': 1 if pair of same age-sex class; 0 otherwise.

290 'Temporal overlap': Proportion of years in which at least one of the individuals in the dyad was  
291 identified that both were identified.

292 'Spatial overlap': Proportion of those years in which both were identified, that both were  
293 identified in the same canyon.

294 We examined the significance of these predictor variables using MRQAP tests and partial correlation  
295 coefficients, sequentially removed predictors with non-significant ( $P > 0.10$ ) MRQAP tests, and then  
296 calculated generalized affiliation indices using a binomial model. We compared association and  
297 generalized affiliation indices for these whales using network diagrams, network statistics, as well as  
298 tests for age-sex class effects (Mantel tests) and overall affiliation (data-stream permutations).

## 299 **Results**

### 300 **Simulated data**

301 Results of the runs with simulated data are given in Supplemental Table 1.

302 For the first run with the standard set of parameters, network diagrams generated using the original  
303 simple ratio association indices as well as the generalized affiliation indices (binomial method) are  
304 shown in Fig. 1. When compared with the association indices, affiliation indices show true affiliations  
305 more prominently (red links are generally wider, and so less often dashed, on the lower, affiliation,  
306 diagram), are less affected by gregariousness (number of links less related to size of node in lower



307 diagram), and do not segregate genders (compare lower and upper diagrams). In Fig. 2 the distributions  
308 of association indices and affiliation indices (binomial, linear and Poisson) are compared for true  
309 affiliates and other dyads using box plots. The distinction between affiliated and non-affiliated dyads is  
310 much stronger—the boxplots are less overlapped—for all three types of affiliation index than for  
311 association indices. This difference was quantified using Cohen’s  $d$ , with  $d=1.57$  for association indices  
312 and  $d=2.30$ ,  $2.36$  and  $2.68$  for binomial, linear and Poisson affiliation indices, respectively.

313 In all runs with simulated data, except those where affiliations were effectively disabled ( $\phi=0$ ), the  
314 affiliation indices better discriminated between affiliates and non-affiliates than association indices, with  
315 a mean increase in Cohen’s  $d$  of  $0.70$ ,  $0.62$ , and  $0.98$  for binomial, linear and Poisson runs respectively.  
316 When affiliations were effectively disabled ( $\phi=0.0$ ) the distinctions were virtually erased, with near zero  
317 values of Cohen’s  $d$  for both associations and affiliations. The affiliation indices performed better with  
318 more sampling periods, and worse with a smaller population size, fewer sampling periods, and fewer  
319 associations.

320 The partial correlation coefficients and MRQAP tests clearly showed the irrelevance of the nuisance  
321 variable with near-zero partial correlation coefficients, and the null hypothesis of no relationship to  
322 association rejected in only about 5% of the runs, as expected. The analysis also clearly indicated the  
323 significance of the gender predictor variable, with strong partial correlation coefficients and universal  
324 rejection of the null hypothesis except when the gender similarity effect was removed ( $\sigma=0.0$ ), when the  
325 partial correlation coefficient fell to nearly zero and the null hypothesis was rejected at the expected  
326 rate. The results were similar with the temporal predictor, although the partial correlation coefficient  
327 and null hypothesis rejection rate were not entirely reduced to zero by decoupling the migration rate  
328 from the length of the longer sampling periods. The most obvious discrepancy was for gregariousness

329 which was signalled as a useful predictor of association in many runs, including some of those in which  
330 no gregariousness effect was input ( $G=1$ ).

331 The permutation tests for preferred/avoided associations almost always rejected the null hypothesis of  
332 no preferred/avoided associations for both the simple ratio indices and the generalized affiliation  
333 indices. There were some failures to reject the null hypothesis with a population of only 10 individuals,  
334 and with fewer associations (less dense network) for the generalized affiliation indices. The primary  
335 distinction though is for the runs without built in affiliations ( $\phi=0$ ): the null hypothesis was generally  
336 rejected when testing the simple ratio index, but not when testing the generalized affiliation index,  
337 which had mean P-values of about 0.3. This shows that the generalized affiliation index had effectively  
338 removed the non-affiliation sources of association, exposing cases when there was true affiliation  
339 among individuals. Thus the generalized affiliation index fulfilled its mandate.

#### 340 **Bottlenose whale data**

341 MRQAP tests indicated that age-sex class and temporal overlap were useful in explaining patterns of  
342 association in the northern bottlenose whales (Table 1), with gregariousness and spatial overlap being  
343 removed by the stepwise procedure. Using age-sex class and temporal overlap as predictors we  
344 calculated generalized affiliation indices. Network diagrams of the association indices and generalized  
345 affiliation indices are compared in Fig. 3. The primary distinction is that the network as portrayed by  
346 half-weight indices is much more prominently structured by age-sex class than is the network of  
347 generalized affiliation indices. The mature males appear to form a clique with their associations. The  
348 network of generalized affiliation indices does not obviously show this characteristic, as might be  
349 expected with age-sex class used as a structural factor in the calculation of the generalized affiliation  
350 indices. However some strong relationships, for instance between mature males #1 and #3 are  
351 maintained with the transformation into generalized affiliation indices.

352 We also compared several characteristics of the association indices to those of the generalized affiliation  
353 indices (Table 2). In most respects the pattern of generalized affiliation indices appears less structured  
354 than that of the half-weight association indices: there was less modularity, lower correlations between  
355 strength (i.e. gregariousness for association indices) and other nodal network metrics, no support for  
356 age-sex class structuring associations (versus a strong matrix correlation and significant Mantel test for  
357 the same comparison with associations), and a permutation test did not reject the null hypothesis of no  
358 preferred or avoided affiliations (versus a significant result for associations). However when the test just  
359 included the 7 mature males, the test was marginally significant for generalized affiliation indices and  
360 the original half-weight association indices (Table 2). (The structure of the data was not suitable for a  
361 similar test of the 7 females.) Large deviance residuals (greater than 2.5) indicated two strongly  
362 affiliated dyads: mature males #1 and #3 (2.81); subadult male #267 and female #102 (3.82). While the  
363 relationship between #1 with #3 is clearly strong in the original association data (Fig. 3), that between  
364 #267 and #102 had not been previously recognized as significant. There were no deviance residuals less  
365 than -2.5 so little evidence for avoidance.

366

## 367 **Discussion**

368 Disentangling true affiliations from association or interaction data has been a major challenge in the study  
369 of animal social networks (Bejder, Fletcher & Bräger 1998; Croft *et al.* 2011). In this paper we build on  
370 the ideas of Godde *et al.* (2013) by removing structural predictors in the calculation of new indices that  
371 reflect true affiliations (Fig. 4). The results of the evaluations of generalized affiliation indices with both  
372 simulated and real data illustrate how the method can remove structural determinants of association,  
373 leaving what appear to be fundamental affiliations that can be analyzed using a wide range of  
374 techniques.

375 It is impossible to cover all potential scenarios with simulations, but from the consistency of the results  
376 within the range that we covered, and the basic logic of the approach, we expect that within much or all  
377 of the range of scenarios used to study animal societies generalized affiliation indices will provide  
378 insight. Perhaps the most significant omission in our simulations are “gambit of the group” data, when  
379 associations are defined by group membership (Whitehead 2008), and thus have extra dependencies.  
380 Evaluating these scenarios is a next step.

381 Our methodology identifies affiliation using the residuals after removing structural predictors of  
382 association. This definition-by-elimination is philosophically unsatisfactory, but avoiding it would need a  
383 completely different approach. Practically it leads to two issues. The first is whether particular factors  
384 should be included as structural predictors. Kinship could drive association directly or through  
385 affiliation. Large-scale temporal use of the study area will usually be a structural factor, whereas small-  
386 scale temporal patterns may be better considered elements of affiliation. In cases of uncertainty, we  
387 suggest calculating the generalized affiliation indices with and without the ambiguous factor.

388 The second issue deriving from our negative connotation of affiliation constitutes the primary limitation  
389 of the technique: it can only be only as effective at removing structural determinants of association as  
390 these determinants are represented by the predictor variables entered into the model. Structural non-  
391 affiliative factors that affect association but are not represented by the predictor variables will remain.  
392 Our simulations suggested that even imperfect predictor variables (such as the temporal overlap  
393 predictor used for our simulated data sets) can do a good job of exposing true affiliations. Predictors  
394 can also fill in for one another, and mask each other. For instance, the gregariousness predictor includes  
395 how available individuals are to observation. This, we think, is why gregariousness was sometimes found  
396 to be a useful predictor in our simulations even when input gregariousness was disabled ( $G=1$ ). Our

397 measure of gregariousness was covering some of the variation in association rates produced by different  
398 individual use of the study area.

399 Another concern is when predictor variables are calculated from the association data. For this reason,  
400 we used a “jackknife” definition of gregariousness (equation 4). A similar problem of circularity, and  
401 potential resultant loss of power for generalized affiliation indices as indicators of true affiliation, arises  
402 if memberships of social units are used as predictor variables (see above) when these social units are  
403 themselves delineated from the association data using cluster analysis or maximization of modularity.

404 The model that we have postulated (equation 2) assumes additivity of predictor variables. So, for  
405 instance, the range overlap effect is added to the gregariousness effect to produce an expected value of  
406 the association index. In some situations multiplicative effects may be more appropriate, so that if there  
407 is little range overlap between a pair, the possible effect of their similarity in gregariousness is  
408 proportionally reduced. This could be achieved by logging the structural variables (as in our definition of  
409 gregariousness, equation 4), and possibly changing the link function. However using an additive model  
410 (equation 2) on our simulated data which were produced using a multiplicative model (equation 5),  
411 seemed to work effectively.

412 In their quest to control the structural factors affecting association, current data stream permutation  
413 tests—that of Bejder et al. (1998) and its successors—are quite complex and time consuming. As the  
414 generalized affiliation index specifically removes the effects of the structural factors, performing the  
415 data stream permutation tests on the generalized affiliation indices seems overkill—the structural  
416 factors are apparently being removed twice. Simpler node-permutations of the data in each sampling  
417 period do not work, as predictor variables, such as spatial overlap, no longer match the data. Using our  
418 random data, we have explored the possibility of using the fit of the binomial generalized linear model  
419 (indicated by deviance) to the association data as a test for underlying affiliations. If there are no

420 affiliations then the binomial model should fit. Although, in our explorations, this method had high Type  
421 I error rates, there may be other relatively-simple ways to test for underlying affiliations in a social  
422 network using generalized affiliation indices. It would also be very useful good to have an overall “effect  
423 size” for the degree of affiliation in the population. The social differentiation (estimated coefficient of  
424 variation of true association indices, before sampling) attempts this for association indices (Whitehead  
425 2008), but much more useful would be a counterpart for affiliation indices.

426 The technique that we have explored could easily be extended in a variety of ways. It could be used on  
427 interaction counts (perhaps using the Poisson version of the generalized linear model) or rates (perhaps  
428 using time spent observing each dyad as an offset predictor variable). It could be used on asymmetric  
429 data (e.g. grooming), and on rectangular rather than square association matrices (e.g. males versus  
430 females). Categorical variables (a category for each dyad) could be used as predictors.

431 One of us (HW) has incorporated the calculation and analysis of generalized affiliation indices, including  
432 all the features used in our examples, into the next (soon to be released) version of SOCPROG, a  
433 MATLAB-based package for the analysis of animal social structure (Whitehead 2009). Other social  
434 analysis packages, such as the R program asnipe (Farine 2013), might be integrated with this  
435 methodology, or extended to use it directly.

## 436 **Conclusion**

437 Generalized affiliation indices provide a new route for uncovering affiliations in animal social networks.  
438 They can be used instead of structured data-stream permutation tests, or in conjunction with them.  
439 They are more flexible than currently available data-stream permutation tests in how they deal with  
440 structural factors affecting association, and can be used for a wide range of purposes, including the  
441 production of affiliation-based network diagrams, network statistics, division into communities, and  
442 testing for overall affiliation.

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451 Society, the Canadian Whale Institute, the Island Foundation, Fisheries and Oceans Canada and World  
452 Wildlife Fund Canada.

453

454 **Data Accessibility**

455 In the supporting information are:

456 Data\_scripts.pdf: Explains script and data files

457 MATLAB\_scripts.zip: MATLAB scripts producing and analyzing random data

458 SOCPROG2.6.zip: files for the latest draft, unreleased, version of SOCPROG (including generalized  
459 affiliation indices), as well as SOCPROG files with the northern bottlenose whale data.

460 Table\_S1.pdf: Results of simulation analysis

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508

509 Table 1. Efficiency of predictor variables in explaining association indices among bottlenose whales, as  
510 shown by partial correlation coefficients and results of MRQAP tests (1,000 replications).

511

Predictor	Partial correlation	MRQAP P-value
Gregariousness	0.068	0.300
Age-sex	0.292	0.001
Temporal overlap	0.295	0.002
Spatial overlap	0.117	0.109

512

513

514 Table 2. Statistics and tests of half-weight association indices and generalized affiliation indices for 16  
 515 northern bottlenose whales.

	Association indices	Generalized affiliation indices
Differences between age-sex classes:		
Matrix correlation	0.413	0.008
Mantel test, P-value (1,000 permutations)	0.000	0.569
Correlation coefficients among network statistics <sup>1</sup> :		
Strength by clustering coefficient	0.653	0.077
Strength by affinity	0.710	0.030
Modularity <sup>2</sup> :		
Communities identified using modularity	2	4
Modularity	0.235	0.112
Tests for preferred associations <sup>3</sup>		
All whales ( <i>n</i> =16)		
sd (indices), real : random (mean)	0.094 : 0.090	0.079 : 0.079
P-value	0.002	0.439
Mature males ( <i>n</i> =7)		
sd (indices), real : random (mean)	0.132 : 0.125	0.124 : 0.117
P-value	0.094	0.082

516 <sup>1</sup>Network statistics are: strength (sum of association indices or generalized affiliation indices linking each  
 517 individual); clustering coefficient (a measure of how well the associates of an individual are themselves

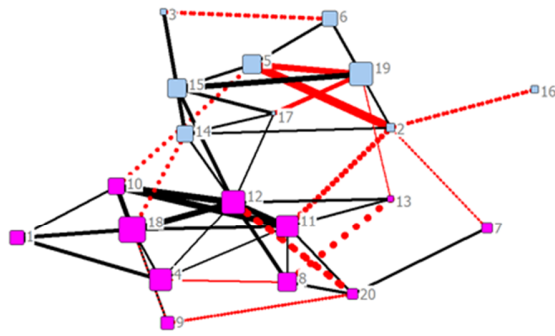
518 associated using the matrix definition of clustering coefficient for weighted networks of Holme et al.  
519 (2007)); affinity (the strength of an individual's associates, weighted by the association index between  
520 the individual and each of them).

521 <sup>2</sup>Modularity indicates how well a network can be divided into communities. We use Newman's (2006)  
522 eigenvector-based method. Modularities above 0.3 indicate substantial support for the division  
523 (Newman 2004).

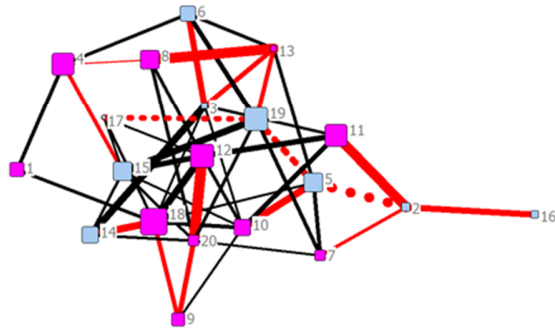
524 <sup>3</sup>Permutation tests using flips of pairs of associations within sampling periods with 1,000 permutations,  
525 1,000 flips/permutation (Whitehead 2008, 129-130). Test not possible just using females because of  
526 data structure.

527

Associations



Affiliations



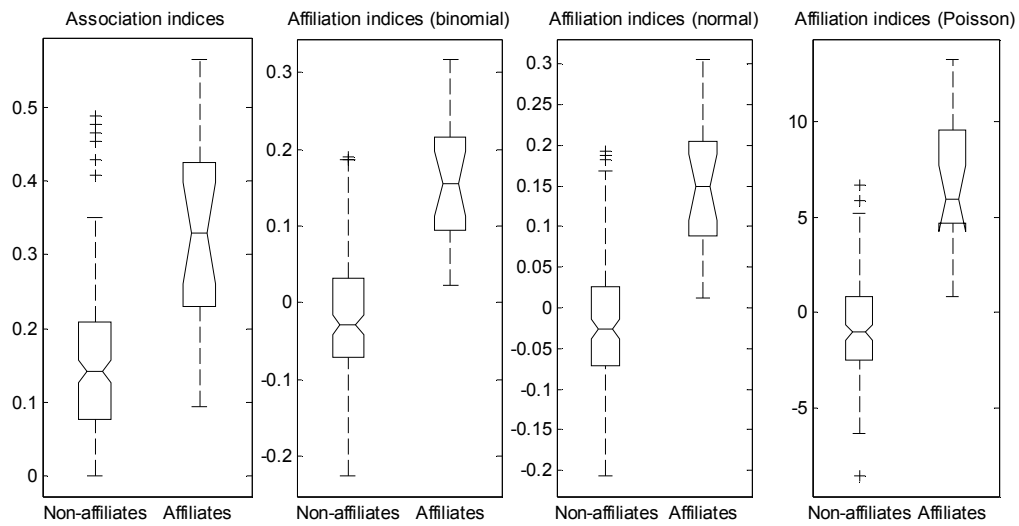
528

529 **Figure 1**

530 Network diagrams using one run of simulated data (for parameters, see main text), using association  
531 indices (above) and generalized affiliation indices (below). Arrangements are optimized using the default  
532 spring-embedding algorithm of NetDraw. The colour of each node indicates its gender, size its  
533 gregariousness. Only links representing indices in the upper 25% percentile are shown, and link width is  
534 proportional to index weight. Input dyadic affiliations are shown by red links. When the standardized  
535 (mean 0; SD 1) association indices are greater than the standardized generalized affiliation indices for  
536 dyadic affiliations, the red links are dotted in the lower diagram, and when the standardized generalized

537 affiliation indice are larger than the standardized association indices, the red links are dotted in the  
538 upper diagram.

539



540

541 **Figure 2**

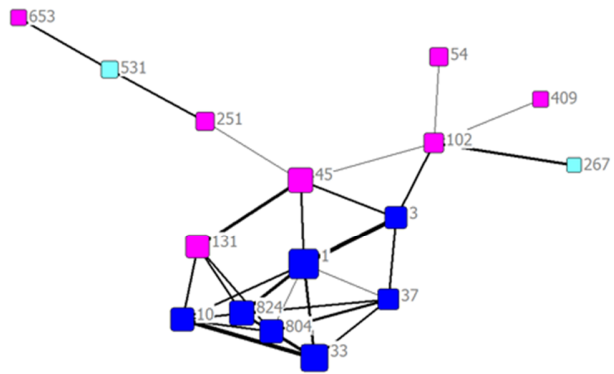
542 Boxplots comparing the distribution of association and (binomial, linear, Poisson) generalized affiliation  
543 indices for true affiliates and non-affiliates using the same simulated data that produced the network  
544 diagrams in Figure 1.

545

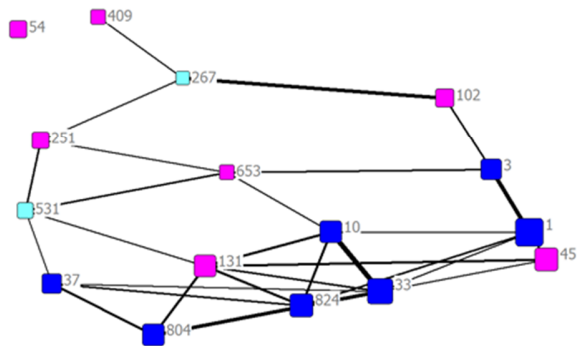
546



## Associations



## Affiliations

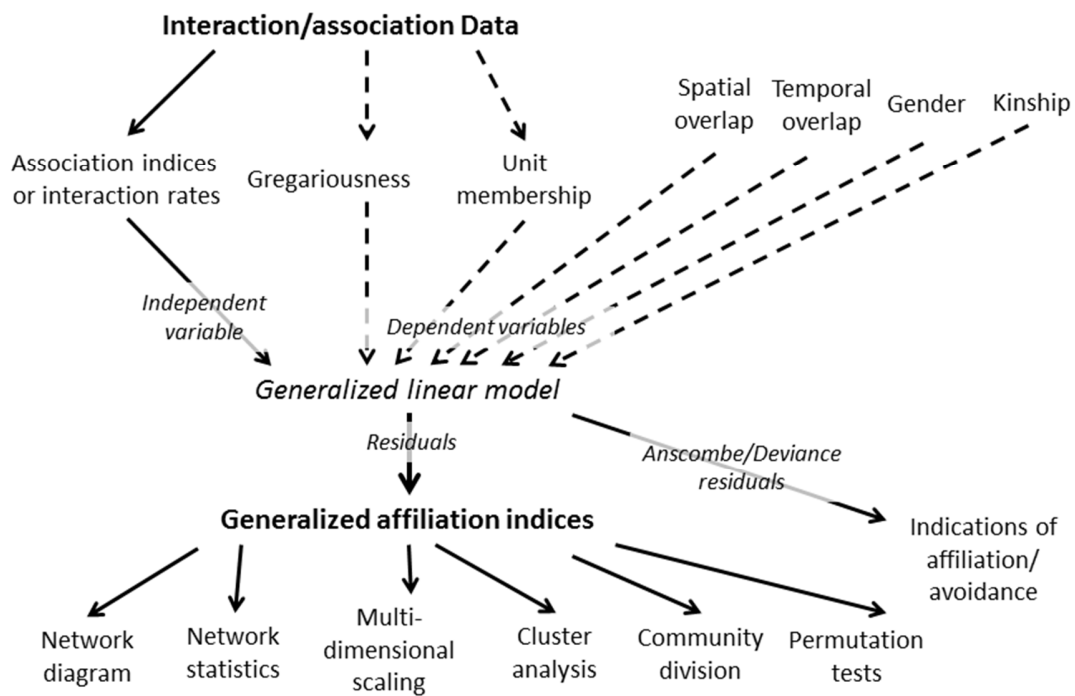


547  
548 **Figure 3**

549 Network diagrams for 16 northern bottlenose whales using association indices (above) and generalized  
550 affiliation indices (below). The colour of each node indicates its age-sex class (pink females; dark blue  
551 mature males; light blue subadult males), the size of each node its gregariousness. Other attributes as in  
552 Figure 1.

553

554



555

556 **Figure 4**

557 The construction and usage of generalized affiliation indices.