



A method for testing association patterns of social animals

LARS BEJDER*, DAVID FLETCHER† & STEFAN BRÄGER*

*Department of Marine Science and †Department of Mathematics & Statistics, University of Otago

(Received 20 October 1997; initial acceptance 9 December 1997;
final acceptance 18 February 1998; MS. number: 5686)

ABSTRACT

Association indices were originally developed to describe species co-occurrences, but have been used increasingly to measure associations between individuals. However, no statistical method has been published that allows one to test the extent to which the observed association index values differ from those of a randomly associating population. Here, we describe an adaptation of a test developed by Manly (1995, *Ecology*, 76, 1109–1115), which uses the observed association data as a basis for a computer-generated randomization. The observed pattern of association is tested against a randomly created one while retaining important features of the original data, for example group size and sighting frequency. We applied this new method to test four data sets of associations from two populations of Hector's dolphin, *Cephalorhynchus hectori*, using the Half-Weight Index (HWI) as an example of a measure of association. The test demonstrated that populations with similar median HWI values showed clear differences in association patterns, that is, some were associating nonrandomly whereas others were not. These results highlight the benefits of using this new testing method in order to validate the analysis of association indices.

© 1998 The Association for the Study of Animal Behaviour

Historically, association indices were developed to describe the co-occurrence of (plant) species within a community or habitat (Dice 1945; Sørensen 1948). During the last 25 years, zoologists have adopted the method to measure the strength of associations between individuals, especially in social vertebrates (e.g. Schaller 1972). The underlying assumptions are that physical proximity (i.e. membership of the same group) signifies social affiliation, and that amount of time together correlates with the strength of affiliation. Hubálek (1982), Sailer & Gaulin (1984) and Whitehead (1997) provided the theoretical background to measuring social affiliations with association indices. The more common indices have been evaluated by Cairns & Schwager (1987) and Ginsberg & Young (1992).

An association index is calculated for each dyad (pair of individuals) in the population. The majority of indices are defined so that they range between zero (two individuals never seen together) and one (two individuals always seen together). The higher the value of the index, the greater the level of association between that pair of individuals. It is common to summarize the results of an analysis of association by presenting the frequency distribution of index values for all dyads (e.g. Fig. 1), together with a summary statistic such as the median. In addition, an ordination technique such as cluster analysis can be

used to investigate any patterns in the indices that might help in understanding the social structure of the population (e.g. Slooten et al. 1993).

There is a major drawback to using the indices in this descriptive manner. As Whitehead (1997) pointed out for analyses of association in general, '... it is often important to distinguish real features from methodological artefacts and random noise'. For example, a cluster analysis might be used to infer existence of particular social groups within the population, the dyads concerned having relatively high values for the association index; but could such apparently strong associations have occurred by chance alone given the number of individuals in the population, individual sighting histories and the number of individuals per group? This question must be answered before any inferences can be drawn from descriptive summaries of association index values.

A test of random association can be performed using a Monte Carlo method (Manly 1997), in which testing is carried out using simulated data sets. These data sets are randomly generated in such a way as to retain important features of the original data. This general approach has been used by a number of authors in the analysis of association (Whitehead et al. 1982; Lott & Minta 1983; Myers 1983; Wilkinson 1985; Mitani et al. 1991; Smolker et al. 1992; Slooten et al. 1993). None of these authors, however, discussed the details of the algorithm they used for generating data sets. The choice of a suitable algorithm is not trivial. This is clear from the literature on

Correspondence: S. Bräger, Department of Marine Science, University of Otago, P.O. Box 56, Dunedin, New Zealand (email: stefan.brager@stonebow.otago.ac.nz).

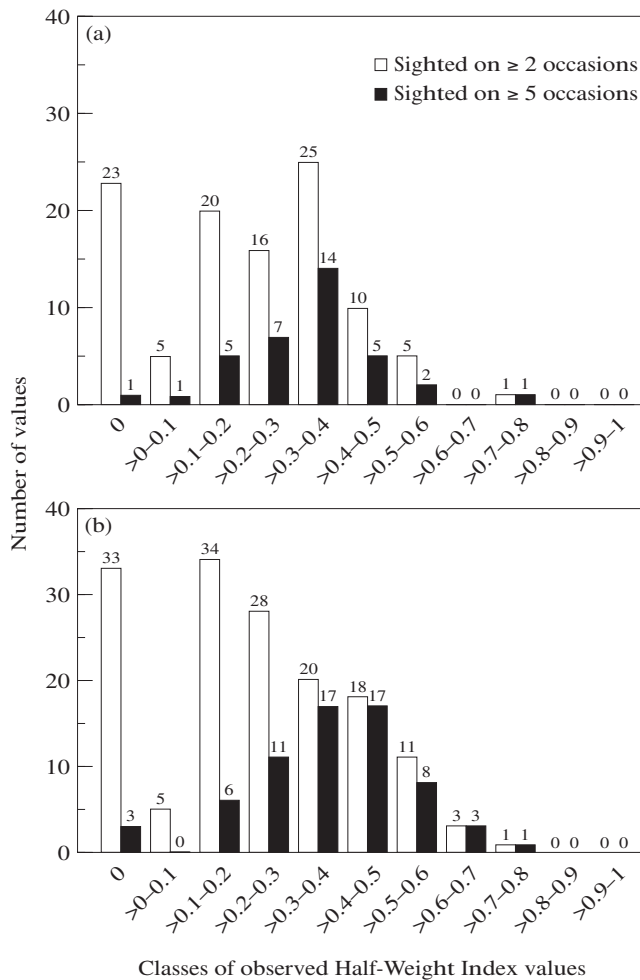


Figure 1. Observed frequency distributions of values of the Half-Weight Index for four populations of Hector's dolphins in Porpoise Bay, New Zealand. (a) 1995–1996; (b) 1996–1997.

randomization testing for species co-occurrences on islands, a mathematically equivalent problem.

We present a simple algorithm that can be used to perform a Monte Carlo test of random association. It is based on one suggested by Manly (1995) for analysing species co-occurrences on islands. We adapt his method of testing and discuss the calculation of P values in detail. We also show how this type of analysis can highlight those dyads for which the association index is higher than would be expected from random association. We demonstrate the method using data for two populations of Hector's dolphin, *Cephalorhynchus hectori*, in New Zealand.

METHODS

Field Methods and Data Collection

We used photographs to identify individuals. This is a noninvasive tool frequently used to study the social structure of cetaceans and other social mammals (Würsig

& Würsig 1977; Würsig & Jefferson 1990). Our data come from two studies carried out on distinct populations of Hector's dolphins in the inshore waters of the South Island of New Zealand. The estimated sizes of the two populations differ considerably. That in Porpoise Bay, at the southern tip of the South Island, is estimated to contain 50–70 individuals (L. Bejder, unpublished data), whereas the size of the Banks Peninsula population (at the central East Coast of the South Island) is about an order of magnitude greater (500–1000 individuals; S. Bräger, unpublished data). The average group sizes were 11.0 and 11.6 in Porpoise Bay in the summers of 1995–1996 and 1996–1997, respectively (L. Bejder, unpublished data), and 10.9 for Banks Peninsula during 1986–1989 (S. M. Dawson, personal communication).

Hector's dolphins are most often observed in groups of two to eight individuals. These groups often fuse together and split up over periods of less than an hour to several hours (Slooten et al. 1993). Individuals were considered associated if they were members of the same group or cluster of groups, as defined in Slooten et al. (1993). Groups of dolphins were considered part of the same cluster of groups if groups merged in the time span when photographs were being taken during an encounter. An encounter was defined as a time period spent with the same group or cluster of groups (usually 10–120 min).

Photo-identification surveys in Porpoise Bay (46°39'S, 169°6'E) were carried out on 44 days between 3 December 1995 and 6 April 1996 and on 35 days between 21 November 1996 and 15 April 1997. Three vessels, ranging from 3.8 to 6 m long, were used. Only surveys that allowed complete coverage of the bay were included in the analysis. Field work at Banks Peninsula (centre at 43°40'S, 173°E) was conducted by S. M. Dawson and E. Slooten between November 1984 and April 1988 from a 3.9-m inflatable boat (see Slooten et al. 1993 for field effort). Here we use Banks Peninsula data from the 1985–1986 and 1987–1988 seasons. Surveys at both sites were conducted at slow planing speeds (10–15 knots), with the vessel slowing to less than 3 knots for photography once dolphins were sighted. Photographs were taken using 35 mm cameras with various lenses, at ranges of less than 10 m. Group size, location and time were recorded for each encounter (field methods following Slooten et al. 1993). Analyses presented here are based entirely on photographic records; individuals seen but not photographed were not included. Because the composition of analysed individuals changed between years, we refer below to four statistical populations from the two biological populations.

Calculation of Association Index

It is common practice to include in the analysis only those individuals seen at least a certain number of times. This helps to guarantee that those individuals can be reidentified. In studies we have seen, this minimum has ranged from two to six sightings (e.g. Underwood 1981; Myers 1983; Penzhorn 1984; Metcalfe 1986; Weinrich 1991; Whitehead et al. 1991; Slooten et al. 1993; Bräger

et al. 1994; Würsig & Lynn 1996). In addition, sightings are usually required to be spaced at least a day apart so as to provide independent evidence of association.

We chose to use two values for the required minimum number of sightings (≥ 2 and ≥ 5), to assess the effect that this number had on the analysis. Following Cairns & Schwager (1987), we used the Half-Weight Index (*HWI*) with a range of possible values between 0 and 1), which has been commonly used in studies of dolphin social structure (e.g. Wells et al. 1987). This index appears to be appropriate, because photographic identification studies are likely to underestimate the number of joint sightings (Smolker et al. 1992; Slooten et al. 1993). However, the approach we describe applies equally well to any other measure of association.

The *HWI* is calculated as follows:

$$HWI = x / (x + y_{ab} + 0.5(y_a + y_b))$$

where x = number of encounters including both dolphin A and B in the same group or cluster of groups; y_a = number of encounters including dolphin A but not dolphin B in the same group or cluster of groups; y_b = number of encounters including dolphin B but not dolphin A in the same group or cluster of groups; and y_{ab} = number of encounters including dolphin A and B in different clusters of groups at the same time.

In our case y_{ab} is always zero: dolphins A and B could not be scored as in different groups or cluster of groups at the same time, owing to our definition of groups together with the criterion that dolphins needed to be photographed to be included in the analysis.

Testing the Hypothesis of Random Association

The hypothesis is tested by randomly generating alternative data sets, involving the same number of dolphins and the same number of groups as in the observed data. Furthermore, in each of these data sets, the number of times each dolphin is sighted and the number of dolphins in each group are both constrained to be the same as in the original data. This has the advantage of retaining important features of the original data in all the randomly generated alternatives. This constrained-randomization approach has also been used by Whitehead et al. (1982), Smolker et al. (1992) and Slooten et al. (1993) in analysing association patterns. Unfortunately, none of these authors provided details of the algorithm used to implement this approach.

First, the *HWI*s are calculated for each dyad from the observed data, and an overall summary statistic S derived from them. The statistic we use here is the one suggested by Manly (1995) for testing the randomness of species co-occurrences. In our context, this is written as

$$S = \sum_{i=1}^D \sum_{j=1}^D (o_{ij} - e_{ij})^2 / D^2$$

where D is the total number of individuals included in the analysis, o_{ij} is the *HWI* for individuals i and j , and e_{ij}

is its expected value under the hypothesis of random association.

Second, S is calculated in the same manner for each randomly generated set of data. This set of values of S provides a randomization distribution. If the hypothesis of random association is true, the observed value of S should appear to be a typical value from this distribution. The proportion of all the values of S (observed and randomly generated) that are as large as or larger than the one observed is the Monte Carlo P value. If this P value is less than 0.05 (say), we reject the null hypothesis of random association. As usual, failing to reject this hypothesis does not imply that association is random: it simply means that there is no evidence against it in the data. To calculate S , we need to determine the expected value (e_{ij}) of the *HWI* for individuals i and j under random association. As suggested by Manly (1995), we use the mean value of o_{ij} over all randomly generated data sets as an estimate of e_{ij} .

If we reject the overall hypothesis of random association, it is natural to consider each dyad separately, to identify individuals that are interacting nonrandomly. This can be achieved by testing the hypothesis of random association separately for each dyad. For individuals i and j , the P value is the proportion of all the o_{ij} (observed and randomly generated) that are at least as large as the observed value of o_{ij} . A small P value implies that individuals i and j are seen together more often than would be expected under random association. By calculating the proportion of all the o_{ij} that are as small as or smaller than the observed value of o_{ij} , we can also obtain a P value for assessing whether individuals i and j are seen together less often than would be expected under random association. With many pairs of individuals there is the option of using a Bonferroni adjustment in order to reduce the overall Type I error rate, although this will naturally lead to an increase in the overall Type II error rate (Manly 1995, page 1113). Even if overall there is no evidence of nonrandom association in the population, the dyad P values can still be used to allow key animals and group compositions to be studied in detail.

Data sets are generated from the observed data in a sequential manner, as follows. Starting with the observed data matrix (Table 1), a new matrix is generated by (1) randomly selecting two rows (i and j) and two columns (m and n) for which the elements of the matrix have either of the following patterns:

		Column				Column	
		m	n			m	n
Row	i	0	1	Row	i	1	0
	j	1	0		j	0	1

(an example of such a pattern is highlighted in Table 1 for $i=11$, $j=17$, $m=D$, and $n=K$); and (2) changing these four elements by replacing the zeros with ones and the ones with zeros.

This step has the effect of randomly swapping two individuals between groups in such a way as to keep fixed the number of times an individual was sighted and the number of individuals per group. *HWI* values are calculated for this new data matrix, and the process is repeated

Table 1. Sightings of identifiable Hector's dolphins in Porpoise Bay in 1996–1997 for 40 groups (1=present, 0=absent)

Group number	Individuals																		Total number of identifications in group
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	
1	0	1	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	6
2	0	1	1	1	1	0	1	0	0	1	0	1	0	0	1	1	0	0	9
3	0	1	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	7
4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
5	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	3
6	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3
7	1	1	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	6
8	1	1	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	6
9	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
10	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
11	1	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	7
12	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
13	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
14	1	1	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	6
15	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	4
16	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
17	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	4
18	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	4
19	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	1	1	0	6
20	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	5
21	1	1	0	1	1	1	1	0	0	1	1	0	1	0	0	1	0	0	10
22	1	1	1	0	1	1	1	0	0	0	1	0	1	0	0	1	1	0	10
23	1	1	0	1	1	1	1	0	0	0	0	1	1	1	0	1	0	0	10
24	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	2
25	1	0	0	1	1	1	1	0	1	0	0	1	1	0	0	1	0	0	9
26	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0	5
27	0	1	0	1	1	0	1	0	0	0	0	1	1	0	0	0	0	0	6
28	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
29	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
30	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
31	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	3
32	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	4
33	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
34	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
35	1	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	5
36	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	4
37	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	3
38	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	5
39	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	4
40	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	5
Total no. of sightings	20	24	7	12	18	8	9	5	2	9	3	15	24	2	2	11	4	2	177

Outlined cells demonstrate the randomly chosen specific pattern $\begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$ that is switched to its inverse $\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$ during the randomization test.

a large number of times, each time starting with the matrix generated at the previous step. Manly (1995) discussed the theoretical background to this method, and pointed out that the resulting P value may be positively biased if the number of randomizations is not large enough, as the data matrices that are generated are too close to the original observed matrix. He suggested replicating the test 100 times (say) to obtain a mean P value, together with a standard error. We prefer not to use this approach, as the amount by which the mean P value is biased is unknown. Instead we prefer to replicate the test a small number of times for each of a number of randomizations. For example, we might replicate the test 5–10 times for each of 1000, 5000 and 10 000 randomizations. The pattern in the resulting mean P values (with standard errors) allows us to assess whether the underlying true P value (the one we would obtain

if we used an infinite number of randomizations) is sufficiently small.

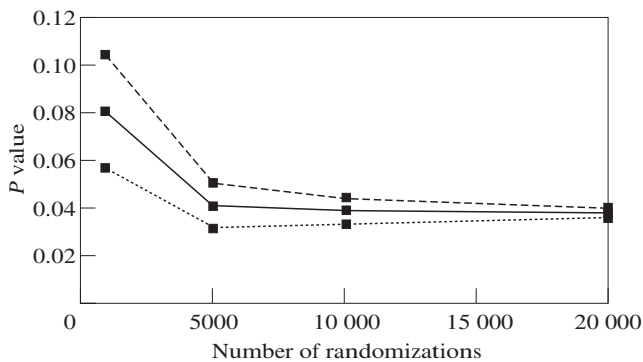
RESULTS

Table 2 summarizes the sighting histories of Hector's dolphins around Banks Peninsula and Porpoise Bay. At each site, individuals included in the analyses in one season were not necessarily included in the analyses of the subsequent season if they failed to meet the sighting criteria. Thus, the 52 individuals sighted twice or more around Banks Peninsula in 1985–1986 and in 1987–1988 are not all the same individuals.

The HWI values for Banks Peninsula contain a large proportion of zeros (range 67–91%), in contrast to those for the Porpoise Bay population (range 3–22%; Table 2). If we consider only those dyads with nonzero HWI values,

Table 2. Association summaries and mean *P* values for testing the hypothesis of random association for four populations of Hector's dolphins, based on five replicates of 20 000 randomizations

Sampling area and period (sample size for individuals with $\geq 2/\geq 5$ sightings)	Percentage of zero values of the observed <i>HWI</i> values for all individuals sighted		Median of all observed <i>HWI</i> values for all individuals sighted		Median of observed <i>HWI</i> values (>0) for all individuals sighted		Mean <i>P</i> values for testing the hypothesis of random association for all individuals sighted	
	≥ 2 times	≥ 5 times	≥ 2 times	≥ 5 times	≥ 2 times	≥ 5 times	≥ 2 times	≥ 5 times
Banks Peninsula 1985–1986 (<i>N</i> =52/5)	91	80	0.000	0.000	0.286	0.130	0.72	0.64
Banks Peninsula 1987–1988 (<i>N</i> =52/17)	89	67	0.000	0.000	0.250	0.167	0.08	0.07
Porpoise Bay 1995–1996 (<i>N</i> =15/9)	22	3	0.250	0.348	0.290	0.348	0.006	0.03
Porpoise Bay 1996–1997 (<i>N</i> =18/12)	22	5	0.207	0.376	0.280	0.380	0.83	0.25

**Figure 2.** Effect of the number of randomizations on the mean *P* value (—; upper and lower confidence intervals are also shown) for testing the hypothesis of random association (Porpoise Bay 1995–1996 for ≥ 5 sightings). The sets of 1000 and 5000 randomizations were replicated 10 times, and the sets of 10 000 and 20 000 randomizations were replicated five times.

the medians are similar in the four populations for dolphins sighted on at least two occasions (0.25–0.29). Using the more stringent criterion of five or more sightings led to increases in the median *HWI* for the Porpoise Bay population, but decreases for the population at Banks Peninsula (compared to the ones from ≥ 2 sightings). Furthermore, the more stringent criterion drastically reduced the number of dolphins included in the analyses by 35–90%. It also reduced the proportion of zero *HWI* values by 11–22% (Banks Peninsula) and 17–19% (Porpoise Bay).

The effect of the number of randomizations is seen most clearly for the Porpoise Bay population in 1995–1996 (Fig. 2). The upper and lower 95% confidence intervals decrease as the number of randomizations is increased, giving an indication as to when one is approaching the underlying true *P* value and so whether or not to reject the hypothesis of random association. Figure 2 suggests that the mean *P* value based on 20 000 randomizations is reliable.

There was evidence for nonrandom association at Porpoise Bay in 1995–1996, regardless of the criterion

used for including individuals (Table 2). There was also evidence (although not quite significant at the usual 5% level) for nonrandom association at Banks Peninsula in 1987–1988, again regardless of the inclusion criterion. There was no evidence for nonrandom association at Banks Peninsula in 1985–1986 nor at Porpoise Bay in 1996–1997. In both cases the *P* value decreased as a result of using the more stringent inclusion criterion.

In comparing the left and right sides of Table 2, it is clear that inference about association using just the median (nonzero) *HWI* could be misleading. For example, for Porpoise Bay, the frequency distributions are similar for the two seasons (regardless of the inclusion criterion) and yet there is evidence for nonrandomness of association in only one of the seasons (Fig. 1). This emphasizes the fact that a high median *HWI* does not necessarily imply nonrandom association and that one needs to distinguish between random noise and actual features when drawing conclusions from social structure analyses. At Porpoise Bay in 1995–1996, 12 and four dyads were associating nonrandomly for two or more and five or more sightings, respectively. In the next season, when the overall pattern showed no evidence of nonrandomness, two and one dyads were associating nonrandomly, respectively.

DISCUSSION

Testing for Nonrandomness

Analyses of association based solely on the values of an index are limited, in that they do not provide any evidence as to whether the observed index values are higher than would be expected under random association. Thus, simple threshold values of 0.2 or 0.4 (say) for the median index value seem to be of little use without testing for nonrandomness.

Whitehead et al. (1982) and Slooten et al. (1993) both used a Monte Carlo method to test for nonrandomness in the temporal nature of association patterns, amongst humpback whales, *Megaptera novaeangliae*, and Hector's dolphins, respectively. Smolker et al. (1992) tested for sex

differences in the association patterns of bottlenose dolphins, *Tursiops truncatus*, and Wilkinson (1985) tested for an interaction of sex with strength of roost association among vampire bats, *Desmodus rotundus*; again both used a Monte Carlo approach similar to the one described here. A key component in such an approach is the algorithm used to generate alternative data sets, yet none of these authors provided details of the algorithm they used. We have presented an algorithm that is straightforward to implement, and avoids some of the potential complexities inherent in alternative algorithms: Manly (1995) provided a good discussion of the alternatives that have been used in the context of analysing species co-occurrences on islands.

Impact of Sighting Threshold

In selecting a criterion for including individuals in the analysis, there is a trade-off between including as many animals as possible and ensuring that the data are reliable. For the Hector's dolphin populations considered here, we used two criteria. The effects on the tests for nonrandomness were small, with no change in the conclusions for either population, whereas the changes in the median nonzero HWI values were quite different for the two populations. Note that changing the inclusion criterion will not affect the HWI values for individual dyads, only whether those dyads are included in the analysis.

Effect of Sighting Rate

The number of identifiable individuals per group will vary between populations and within populations at different times. In general, a low sighting rate necessitates a greater number of randomizations to detect nonrandomness. In the extreme case where there is only one identifiable individual per group (i.e. no observed associations), it is impossible to detect nonrandomness with the method presented here, as all randomly generated data matrices are equivalent to the observed one. Another extreme case, where all identifiable individuals belong to every group, cannot be assessed by this method as no random swaps are possible. However, these limitations are simply a consequence of using species association indices to measure affiliations between individuals (sensu Cairns & Schwager 1987, page 1458).

When are the Values of an Association Index Meaningful?

In assessing association patterns, some authors have used the value of the association index for each dyad to determine the strong associations (e.g. Slooten et al. 1993; Bräger et al. 1994). As indicated earlier, these values can be misleading unless they are compared to what would be expected by chance. We have shown that of two populations with similar HWI values, one has nonrandom associations while the other does not. This would suggest that the HWI alone provides little information about association strength. Thus, it is possible for a

relatively high index value to be not significantly different from what would be expected under random association, given the observed group sizes and numbers of sightings per individual. Similarly, a relatively low index value can be significantly different from what would be expected under random association, for example when two individuals are actively avoiding each other (i.e. the test is two-tailed). The same argument applies to the use of any index.

The test of the hypothesis of random association presented here does not provide a direct comparison of two sets of observed index values. An indirect comparison is clearly possible by comparing their *P* values for the overall test. It is natural to consider how we might directly compare the association patterns in two populations, of different species or of the same population at different times, in a manner that allows for differences in population size and group size distribution. This will be our objective in a future publication.

Acknowledgments

We are grateful to S. M. Dawson and E. Slooten for allowing us to use their data for the analysis. This paper could not have been completed without their input. We also thank them as well as B. Würsig, J. Lazarus and two anonymous referees for constructive comments on the manuscript. B. Manly and J. Harraway provided helpful comments on various statistical aspects. Furthermore, we thank L. Dahl, B. Gee, N. Gee and S. Heinrich for their help in the field. Financial and logistic support was provided by World Wide Fund for Nature (New Zealand), New Zealand Department of Conservation and PADI—Project Aware.

References

- Bräger, S., Würsig, B., Acevedo, A. & Henningsen, T. 1994. Association patterns of bottlenose dolphins (*Tursiops truncatus*) in Galveston Bay, Texas. *Journal of Mammalogy*, **75**, 431–437.
- Cairns, S. J. & Schwager, S. J. 1987. A comparison of association indices. *Animal Behaviour*, **35**, 1454–1469.
- Dice, L. R. 1945. Measures of the amount of ecologic association between species. *Ecology*, **26**, 297–302.
- Ginsberg, J. R. & Young, T. P. 1992. Measuring association between individuals or groups in behavioural studies. *Animal Behaviour*, **44**, 377–379.
- Hubálek, Z. 1982. Coefficients of association and similarity, based on binary (presence-absence) data: an evaluation. *Biological Review*, **57**, 669–689.
- Lott, D. F. & Minta, S. C. 1983. Random individual association and social group instability in American bison (*Bison bison*). *Zeitschrift für Tierpsychologie*, **61**, 153–172.
- Manly, B. F. J. 1995. A note on the analysis of species co-occurrences. *Ecology*, **76**, 1109–1115.
- Manly, B. F. J. 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. 2nd edn. London: Chapman & Hall.
- Metcalf, N. B. 1986. Variation in winter flocking associations and dispersion patterns in the turnstone *Arenaria interpres*. *Journal of Zoology*, **209**, 385–403.

- Mitani, J. C., Grether, G. F., Rodman, P. S. & Priatna, D. 1991. Associations among wild orang-utans: sociality, passive aggregations or chance? *Animal Behaviour*, **42**, 33–46.
- Myers, J. P. 1983. Space, time and the pattern of individual associations in a group-living species: sanderlings have no friends. *Behavioral Ecology and Sociobiology*, **12**, 129–134.
- Penzhorn, B. L. 1984. A long-term study of social organisation and behaviour of Cape mountain zebras *Equus zebra zebra*. *Zeitschrift für Tierpsychologie*, **64**, 97–146.
- Sailer, L. D. & Gaulin, S. J. C. 1984. Proximity, sociality, and observation: the definition of social groups. *American Anthropologist*, **86**, 91–98.
- Schaller, G. B. 1972. *The Serengeti Lion*. Chicago: University of Chicago Press.
- Slooten, E., Dawson, S. M. & Whitehead, H. 1993. Associations among photographically identified Hector's dolphins. *Canadian Journal of Zoology*, **71**, 2311–2318.
- Smolker, R. A., Richards, A. F., Connor, R. C. & Pepper, J. W. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour*, **123**, 38–69.
- Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. *Kongelige Danske Videnskabernes Selskabs Skrifter*, **5**, 341–354.
- Underwood, R. 1981. Companion preference in an eland herd. *African Journal of Ecology*, **19**, 341–354.
- Weinrich, M. T. 1991. Stable social associations among humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine. *Canadian Journal of Zoology*, **69**, 3012–3018.
- Wells, R. S., Scott, M. D. & Irvine, A. B. 1987. The social structure of free-ranging bottlenose dolphins. In: *Current Mammalogy 1* (Ed. by H. H. Genoways), pp. 247–305. New York: Plenum.
- Whitehead, H. 1997. Analysing animal social structure. *Animal Behaviour*, **53**, 1053–1067.
- Whitehead, H., Silver, R. & Harcourt, P. 1982. The migration of humpback whales along the northeast coast of Newfoundland. *Canadian Journal of Zoology*, **60**, 2173–2179.
- Whitehead, H., Waters, S. & Lyrholm, T. 1991. Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. *Behavioral Ecology and Sociobiology*, **29**, 385–389.
- Wilkinson, G. S. 1985. The social organization of the common vampire bat. *Behavioral Ecology and Sociobiology*, **17**, 111–121.
- Würsig, B. & Jefferson, T. A. 1990. Methods of photo-identification for small cetaceans. *Reports of the International Whaling Commission (Special Issue)*, **12**, 43–52.
- Würsig, B. & Lynn, S. K. 1996. Movements, site fidelity, and respiration patterns of bottlenose dolphins on the central Texas coast. *NOAA Technical Memorandum NMFS-SEFSC-383*, 1–111.
- Würsig, B. & Würsig, M. 1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science*, **198**, 755–756.