

Statistical comparison of proximity matrices: applications in animal behaviour

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Abstract. Animal behaviour studies often require the diagnosis and statistical evaluation of patterns among individuals of a group. However, association values derived for all pairs of individuals are mathematically interrelated and, hence, difficult to evaluate. A general method of matrix comparison, called the Mantel test, is described which accounts for such interdependencies. In this test, two square difference matrices are compared to determine whether a statistical association exists between corresponding elements. For example, distances in one of the matrices might represent differences in songs for each pair of a group of birds, while distances in the other matrix could be the geographic distances between each of the same bird pairs; the test would assess whether or not birds close to one another have songs that are more similar than those pairs that are located further apart geographically. Distances in the matrices can be of a variety of sorts (depending on the application), including for instance geographic distances, morphological differences, or behavioural differences. The test has wide applicability in studies of animal behaviour, and we present three examples. First, dialects of splendid sunbirds (*Nectarinia coccinigaster*) were investigated to determine whether local or regional patterns of geographic variation in song were present, and whether birds with similar dialects were concentrated within the same habitat. Second, dominance hierarchies of white-throated sparrows (*Zonotrichia albicollis*) and dark-eyed juncos (*Junco hyemalis oreganus*) were analysed by constructing appropriate hypothesis matrices that were contrasted against a matrix summarizing behavioural interrelationships of flock members. In the third application, involving progressions of yellow baboons (*Papio cynocephalus*), an approach was developed to assess whether members of a given sex occur adjacent (or at least closer) to one another in progression order more often than expected by chance, and also whether individuals of a given sex tend to be found at or near the end of a progression more frequently than predicted. Other possible applications of the Mantel test are discussed, and a detailed computational example is included.

Ethologists frequently need to evaluate associations among individual animals in a group or population. For instance, investigations of song dialects in birds can be approached by comparing the geographic distances between individuals against measures of song dissimilarities for the same birds. Also, studies of dominance hierarchies frequently involve factors such as age or plumage, which influence social interactions among individuals in a group. Other researchers are interested in the geometric arrangement of individuals—for example, the positions of primates in progressions with respect to age, sex or status.

These examples represent rather disparate kinds of research problems, but have in common the fact that they involve comparisons between all pairs of

individuals to determine whether a pattern exists in the inter-associations of group members. Since association values between all possible pairs are mathematically related to one another, statistical techniques typically used to test for significant differences become inappropriate. Therefore, statistical methods must be chosen that take into account and correct for the presence of interdependencies.

Mantel (1967), while investigating temporal and spatial clustering of disease, developed a general method of matrix comparison which can be applied to each of the behavioural research problems mentioned above. In Mantel's procedure, two square difference matrices, each representing inter-individual distances of some type, are compared to determine whether there is a statistical association between corresponding elements.

The general approach has been applied by animal systematists studying geographic variation (e.g. Sokal 1979; Jones et al. 1980) and may be of

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use for certain problems in geography (Glick 1979). Schnell et al. (in press) used the test in an analysis of wildlife data, while Douglas & Endler (1982) and Ryman et al. (1980) applied the technique in evolutionary analyses of population differentiation. Cothran & Smith (1983) evaluated chromosomal and genic divergence in mammals using the test. In a computer simulation study of population genetics and the isolation-by-distance model, Sokal & Wartenberg (1983) used the Mantel test essentially as an analysis of variance for distances that could not be analysed by conventional means because of the lack of independence of the individual distances. Huber (1978, 1979, 1983) pointed out further generalizations and extensions of these procedures, and Dietz (1983) has examined a broad class of appropriate permutation tests.

In this paper we briefly outline Mantel's (1967) method and then demonstrate its application in the following ethological examples: (1) dialects of splendid sunbirds (*Nectarinea coccinigaster*); (2) dominance hierarchies in white-throated sparrows (*Zonotrichia albicollis*) and dark-eyed juncos (*Junco hyemalis oreganus*); and (3) progressions of yellow baboons (*Papio cynocephalus*).

THE MANTEL TEST

The test of Mantel (1967) is a generalized regression technique that looks for associations of inter-individual distances based on one characteristic (or set of characters) with those calculated from a second characteristic. It is a non-parametric test (in terms of the distribution-free requirements of matrix cell contents) and, if desired, one set of distances can be artificially constructed to reflect a particular hypothesis of inter-individual associations (see below, as well as Douglas & Endler 1982). In an investigation of n individuals, each matrix would be of size $n \times n$ and composed of distances between all pairs of individuals, with distances along the diagonal (i.e. distances of individuals from themselves) set at zero. All other elements in each matrix must have quantities assigned: there can be no missing values. Zero distances in non-diagonal cells are treated like any other distance value. Usually, and in all of our examples, matrices are symmetric (i.e. the distance from individual i to j is the same as from j to i), although asymmetric matrices can be compared.

One matrix, for example, may represent differ-

ences in song between each pair of 10 birds, while the other matrix could indicate geographic distances separating each bird pair. The null hypothesis would be that there is no association between song differences and geographic distances (i.e. the songs of birds located far apart geographically are not any more or less different than those of birds close together).

The sum of the products of corresponding elements of the two distance matrices $\mathbf{X}$ and $\mathbf{Y}$ is calculated as

$$Z = \sum_i \sum_j X_{ij} Y_{ij}$$

for all rows i and columns j . The expected value of Z is based on the null hypothesis of random permutations of the rows and columns of matrix $\mathbf{Y}$, and is calculated as (or estimated for) the inner product of each of these permutations with the $\mathbf{X}$ matrix. Thus, the observed association between sets of differences is tested relative to their permutational variance. Operationally, one computes Z , subtracts the expected value of Z , and divides this difference by the standard error of Z . The resulting statistic (a t -value) is compared against a standard normal distribution (which of course is equivalent to a t -distribution with infinite degrees of freedom). A detailed computational example of the Mantel test is supplied in the Appendix using data from one of the behavioural applications presented later in this paper.

When small numbers of individuals (less than about 20) are involved in comparisons, the asymptotic normality of the Mantel test might be too crude an approximation. In such cases, an investigator may wish to test the significance of the Mantel statistic by means of a Monte Carlo test. When the results are borderline, statistical conclusions may be different for the two approaches to testing. Sokal & Wartenberg (1983) used such a Monte Carlo test in their application of the technique. Besag & Diggle (1977) have discussed, in a very general way, some simple Monte Carlo tests for the analysis of spatial patterns. These authors refer to several types of research questions that can be or have been assessed using the Mantel test.

It should also be noted that Mielke (1979) has demonstrated that departures from normality can occur with null distributions of the type used in the Mantel test. Thus one can expect that some additional refinements in testing procedures may be employed in the future. His findings, however,

do not detract in a substantive way from the considerable practical utility to animal behaviourists of the Mantel test as it is now designed.

We performed computations using GEOVAR, a library of computer programs written by David M. Mallis and furnished by Robert R. Sokal. We also computed the matrix correlation (Sneath & Sokal 1973) by matching pairs of common elements in the two difference matrices; the resulting value is equivalent to the product-moment correlation of the corresponding matrix elements (ignoring the diagonal entries). The statistical significance of these coefficients cannot be tested using standard techniques, because difference values for all pairs of individuals are not statistically independent. However, the resulting quantity, taken in conjunction with the Mantel *t*-value, provides another indication of the degree of matrix concordance.

DIALECTS IN SUNBIRDS

An obvious ethological application of Mantel's test is the analysis of geographic variation in bird song, since the research problem is very similar to those encountered by systematists using morphological and other types of characteristics. Payne (1978) has evaluated microgeographic variation in vocalizations of splendid sunbirds from a 6-km² area on the campus of Cape Coast University in Ghana. He recorded songs of individual birds to test whether sunbirds exhibit 'dialects'. The first step in such an analysis is to demonstrate geographic variation coupled with local homogeneity in songs. Sunbirds have relatively simple songs, and Payne recorded five temporal and six sound-frequency measurements for the songs of 39 birds. He also recorded the geographic locations of these birds and the type of habitat in which they were found. An assessment was made of the song differences against geographic distances but, as indicated by Payne (1978), without a valid statistical test.

Using the Mantel test, we evaluated the following questions. (1) Is there an overall association of song differences and geographic distances? (2) Is there local patterning of song variation? (3) Is there an association of song differences with differences in habitat?

Our treatment of Payne's (1978) data was different from his in that we standardized each of the 11 frequency and temporal characters for the 39 birds, which resulted in each character having a mean of

zero and standard deviation of one. Product-moment correlations were calculated between all pairs of birds, and then, to obtain distance measures like those used by Payne, we subtracted all correlations from one. The resulting 'song-distance' values were non-negative, with low values indicating similarity. In Payne's original study, he reanalysed the songs to exclude three birds at the edge of the study area which may have had nearest neighbours that were overlooked. Therefore, we computed a second song distance matrix for the 36 remaining birds following the procedures outlined above.

Using a map of bird locations (Fig. 1 of Payne 1978), we calculated kilometric distances between all bird pairs, thus forming geographic distance matrices for the 36- and 39-bird samples. These matrices were tested against matrices of song distances to determine if a regional geographic pattern was present in the songs—that is, whether songs for the closest birds were the most similar, and those of the most widely separated birds had the greatest divergence. This would be indicated in the Mantel test by a positive association (i.e. positive *t*-value) of geographic distances and song distances.

We also tested whether local geographic patterning was evident, by comparing song distances against the reciprocals of geographic distances (as done by Jones et al. 1980; Schnell et al., in press). A significant negative association (negative because a reciprocal scale is reversed from that of kilometric distances) would indicate that—given the song differences for all pairs of birds—close birds would have more similar songs than expected by chance alone. When employing reciprocals of geographic distances, all larger distances are considered to be effectively equal, while that portion of the scale involving smaller distances is expanded. Therefore, the use of reciprocals increases the power of the analysis to reveal geographic patterns that are local in nature (Mantel 1967), whereas tests involving linear distances evaluate broader, regional trends. Positive associations of frequency differences and geographic distances are indicated by positive *t*-values from the Mantel test, while negative *t*-values denote such associations when the reciprocals of distances are used.

It is possible to have both kinds of patterns or to have only local associations. For instance, birds at two ends of an elongated study area could have similar songs, although songs of birds from inter-

mediate locations are quite different. This is not a regional pattern by our operational definition, but would be an example of local patterning if birds at either end and in the centre of the study area had songs similar to their relatively close neighbours. While hypothetically one could find regional but not local patterning using our test criteria, this is an improbable result for biological populations.

Payne (1978) identified two broad habitat types within the study area that supported sunbirds—one included the residential and administrative areas on the campus, with well manicured lawns, shrubs and gardens; the other encompassed cropland and brushy areas within the immediate vicinity of the campus. He wanted to determine whether birds with similar dialects were concentrated in similar habitats. In order to evaluate this idea statistically using the Mantel test, we first constructed a 'habitat matrix' involving all birds: a zero was entered for each pair of birds found in the same habitat, while a one was used for all dyads where the birds were in different habitats. The habitat matrix is considered a hypothesis matrix, indicating on the basis of some criteria (in this case, habitat) the song distances predicted to be larger (i.e. those corresponding to one placed in the hypothesis matrix) and those expected to be smaller (where zeros were placed). A positive association between the habitat and song-distance matrices would indicate that songs were more different between rather than within habitats. This approach is similar to that used by Douglas & Endler (1982) in constructing hypothesis matrices that reflect models of population differentiation.

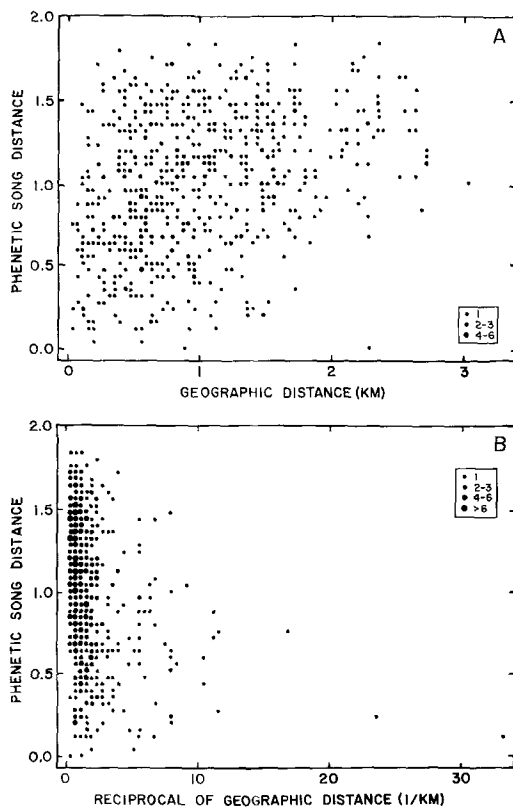


Figure 1. Relationship of song differences based on 11 sound frequency and temporal characters for 36 splendid sunbirds with (A) geographic distances and (B) the reciprocals of these distances. A total of 630 difference and distance values are depicted in each graph, involving comparisons of all bird pairs. As indicated, some of the graph points represent more than one comparison.

Table 1. Association of inter-individual song distances with geographic distances (km), reciprocals of distances (1/km), and contrasting habitat indices: results of Mantel tests (*t*) and matrix correlations (*r*)

Song distance characters	Distance (km)		Reciprocal of distance (1/km)		Contrasting habitats	
	<i>t</i>	<i>r</i>	<i>t</i>	<i>r</i>	<i>t</i>	<i>r</i>
39 birds						
All 11 characters	5.45***	0.176	-6.95***	-0.252	0.40	0.014
36 birds						
All 11 characters	9.21***	0.336	-7.20***	-0.285	0.33	0.012
Frequencies only (6)	9.54***	0.396	-6.96***	-0.278	0.54	0.023
Temporal characters only (5)	6.32***	0.223	-5.67***	-0.224	0.83	0.029

*** $P < 0.001$.

In Fig. 1, plots are provided for the 36-bird sample showing the association of song distances (based on 11 characters) with geographic distances and reciprocals of distances. The relatively wide scatter of points is not unexpected, given that all pairs of distances are considered—the trends relative to distances and reciprocals are marked and significant. Table I presents the *t*-values resulting from Mantel tests and the matrix correlations for song-distance matrices against those for geographic distances and the reciprocals, as well as for the one contrasting habitats. Whether considering 36 or 39 birds for the 11 song characters or either of the character subsets, the tests involving geographic distances indicate that there was a relatively strong regional pattern, with birds geographically distant having the most dissimilar songs. Tests with reciprocals of geographic distance are also significant, demonstrating that birds sang songs that were relatively more similar to those of their close neighbours than predicted by chance. There was no relationship between song differences and differences in habitat. Our conclusions agree with those reached by Payne (1978), but now we are able to attach measures of statistical significance to the evaluation.

DOMINANCE HIERARCHIES

White-throated Sparrows

One of us (Watt 1983) has been analysing dominance behaviour in flocks of white-throated sparrows, as a function of plumage and other characteristics. Such studies involve extensive analyses of inter-individual associations, and the Mantel test can be helpful in addressing questions about the interactions of group members.

Birds were captured in the wild, fitted with coloured leg bands to facilitate identification, and introduced into an aviary (circa 2 m on a side, with food and water dishes on a shelf in one corner). The sparrows were observed for 120 to 165 min each day for several days to determine (on the basis of numbers of interactions) the positions of individual birds in the group's social hierarchy. Watt (1983) recorded several different types of encounters including: (1) 'supplantings', where a bird chased or displaced another bird from the vicinity of the feeding dish; and (2) 'shares', where two birds

would 'share' the food, both eating from the food dish at the same time.

Experiment 1

After a hierarchy of 16 birds was established by the birds, Watt recorded the frequency of supplanting in order to evaluate two related hypotheses: first, that individuals tend to supplant birds adjacent to them in dominance rank less often than they supplant others; and second, that individuals are more aggressive (as indicated by supplanting) towards birds distant from them in the social hierarchy than towards those close in rank.

The upper right portion of Table II gives supplanting frequencies—the number of times each of the 16 birds supplanted another. For example, the 13 in row 5 and column 7 of Table II indicates the number of times the fifth bird supplanted the seventh bird. Birds are listed in order relative to their position in the hierarchy, with bird 1 being the highest. No 'reversals' occurred, where a bird supplanted one higher than it in the hierarchy.

The hypothesis matrix for the first supposition was constructed with zeros for the immediately off-diagonal elements and ones for the rest (except the diagonal values, which are always zeros). Thus, zeros were placed in the cells associating bird 1 with bird 2 (there are two of these cells in the complete symmetric matrix), and ones for bird 1 with birds 3–16; bird 2 had zeros with bird 3 and ones with the rest, etc. The lower left portion of Table II gives values (rank difference indices) for the second hypothesis matrix. They indicate how many birds separate any given pair in the social hierarchy.

For the first hypothesis, there was a significant negative association between supplanting frequencies and corresponding elements in the hypothesis matrix. The *t*-value for the Mantel test was -2.31 ($P < 0.05$) and the matrix correlation -0.198 , demonstrating that within the hierarchy, supplanting occurred more often between adjacent birds than between birds that were separated by one or more birds in the hierarchy.

For the second hypothesis, Fig. 2 indicates a relatively strong negative association of supplanting frequencies with rank difference indices. The Mantel test yielded a *t* of -3.84 ($P < 0.001$), while the matrix correlation was -0.377 . Clearly, dominant birds supplanted those relatively close to them in social rank much more frequently than they did birds quite different from them in status.

Table II. Frequency of supplanting in a group of 16 white-throated sparrows (upper right*), and numbers in hypothesis matrix (rank difference indices) to test if birds are more aggressive towards birds more distant from them in the hierarchy (lower left)

Bird	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	×	4	2	2	5	4	2	6	1	—	2	—	2	1	2	—
2	0	×	5	3	2	11	7	1	8	2	2	1	2	—	3	2
3	1	0	×	4	4	7	7	6	4	—	1	1	1	—	3	2
4	2	1	0	×	6	5	2	5	2	2	—	1	2	—	3	3
5	3	2	1	0	×	7	13	5	10	—	—	3	5	—	4	1
6	4	3	2	1	0	×	9	7	4	2	1	5	1	1	1	—
7	5	4	3	2	1	0	×	6	—	2	5	5	6	2	6	—
8	6	5	4	3	2	1	0	×	10	—	2	2	2	—	1	1
9	7	6	5	4	3	2	1	0	×	2	2	1	2	—	3	1
10	8	7	6	5	4	3	2	1	0	×	1	1	5	3	3	4
11	9	8	7	6	5	4	3	2	1	0	×	3	6	3	1	—
12	10	9	8	7	6	5	4	3	2	1	0	×	4	2	2	14
13	11	10	9	8	7	6	5	4	3	2	1	0	×	2	3	9
14	12	11	10	9	8	7	6	5	4	3	2	1	0	×	—	3
15	13	12	11	10	9	8	7	6	5	4	3	2	1	0	×	5
16	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	×

* Birds are listed numerically as to their positions in the social hierarchy, with tabulations indicating how many times a lower-ranking (i.e. higher-numbered) bird was supplanted by one of higher rank.

Experiment 2

In a different group of 17 white-throated sparrows, the number of times birds shared the feeding dish (i.e. were close to the dish and within about 15

cm of one another) was recorded. A summary is provided in the upper right of Table III, where sparrows are ordered according to their rank in the social hierarchy.

The first hypothesis was that individuals would share less often with those adjacent to them in the hierarchy than with other birds. As with the initial test in experiment 1, the hypothesis matrix contained zeros in the immediate off-diagonal elements and ones in the rest of the matrix.

White-throated sparrows have variable plumages (Thornycroft 1975), and we were particularly interested in the nine 'bright-morph' males in this group of 17 sparrows (see Table III). We wanted to determine whether bright-morph males shared less often with each other than did other combinations of birds. Thus, the hypothesis matrix contained zeros for cells involving two bright-morph males and ones for all other elements (lower left of Table III).

For the initial test concerning sharing with adjacent birds in the hierarchy, the Mantel *t*-value of 1.89 was slightly less than the critical value at the 0.05 level (1.96), while the matrix correlation was 0.156. Thus, we were unable to demonstrate any statistical relationship of the sharing frequencies between adjacent birds as contrasted to those for

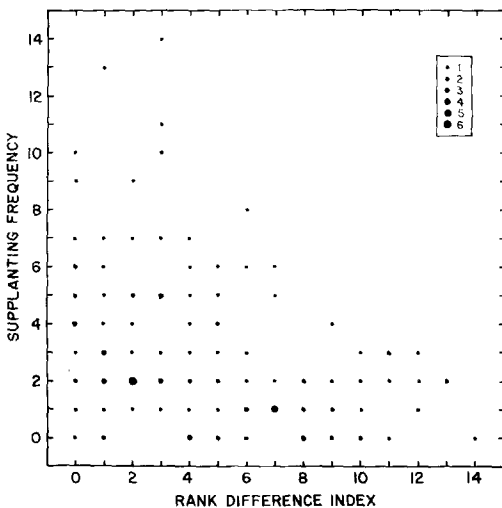


Figure 2. Association of supplanting frequency with an index representing the difference in social rank of interacting white-throated sparrows. All possible pair combinations of the 16 sparrows are plotted, with some graph points representing more than one comparison.

Table III. Frequency of sharing the food dish by pairs of 17 white-throated sparrows (upper right), and hypothesis matrix with zeros indicating pairs of bright-morph males and ones for all other combinations (lower left) (birds are listed according to their positions in the social hierarchy)

Bird	1*	2*	3*	4*	5*	6*	7*	8	9	10*	11	12	13	14*	15	16	17
1*	×	—	—	—	—	—	—	—	—	1	—	2	—	—	1	1	—
2*	0	×	—	—	—	1	—	—	—	—	—	1	2	—	3	—	3
3*	0	0	×	—	—	—	—	3	1	1	—	1	—	—	—	—	2
4*	0	0	0	×	—	—	—	—	—	—	—	—	1	—	—	—	—
5*	0	0	0	0	×	—	—	—	—	—	—	—	—	—	—	—	—
6*	0	0	0	0	0	×	—	1	—	—	—	—	2	—	—	—	—
7*	0	0	0	0	0	0	×	—	3	2	1	1	1	—	5	—	1
8	1	1	1	1	1	1	1	×	—	1	—	—	—	—	—	—	1
9	1	1	1	1	1	1	1	1	×	1	1	1	—	—	—	—	—
10*	0	0	0	0	0	0	0	1	1	×	—	1	—	—	—	—	1
11	1	1	1	1	1	1	1	1	1	1	×	—	—	—	2	2	1
12	1	1	1	1	1	1	1	1	1	1	1	×	—	—	—	—	1
13	1	1	1	1	1	1	1	1	1	1	1	1	×	—	—	—	1
14*	0	0	0	0	0	0	0	1	1	0	1	1	1	×	—	—	—
15	1	1	1	1	1	1	1	1	1	1	1	1	1	1	×	—	1
16	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	×	—
17	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	×

* Bright-morph bird.

other combinations of birds. Instead of analysing the frequency of sharing, one can evaluate simply whether sharing was observed (one or more times)—thus producing a data matrix of zeros and ones, with ones replacing all non-zero entries in the upper right of Table III. In this case, the test against the adjacency hypothesis matrix is significant ($t=2.16$, $P<0.05$) and the matrix correlation is 0.172, suggesting that adjacent birds are not as likely ever to engage in sharing as birds of all other pair combinations. Such a statement covers only whether or not they were observed to share at least once.

The frequency of sharing between bright-morph males was not significantly different from that for other bird combinations, although the t of 1.94 for the Mantel test approached the critical value. The matrix correlation was 0.200. The test against the data matrix indicating only whether sharing was observed at least once was also non-significant ($t=1.92$, $P>0.05$; $r=0.217$). Thus, the data at hand do not demonstrate differences in sharing for pairs of bright-morph males as compared to the other pairs of the 17 sparrows.

Dark-eyed Juncos

Sabine (1959) conducted studies of dominance

and subordination in a winter flock of dark-eyed juncos in the Deep Springs Basin, Inyo County, California. The 27 members of a flock that frequented a feeding station were colour-marked, and dominance (as indicated by pecks and retreats) between pairs of birds was recorded (Fig. 1 in Sabine 1959). A basically linear social hierarchy existed in the flock. There were 'reverse pecks', where a typically subordinate individual would win a particular encounter with a dominant bird; however, these were relatively infrequent, and we did not consider them in our calculations.

We analysed a total of 2414 interactions taken from the upper right portion of the matrix in Fig. 1 of Sabine (1959). As with our data for white-throated sparrows (Table II), the matrix was organized by listing birds on the basis of dominance from the highest (alpha bird) on the left and top to the lowest on the right and bottom. For the juncos, we tested the two hypotheses evaluated in experiment 1 above for the white-throated sparrows. The hypothesis matrices were the same, except for being enlarged to accommodate the 27 juncos in the flock.

As with the white-throated sparrows, a statistically significant negative association was found for the first hypothesis, where we evaluated whether birds had fewer aggressive encounters with those

juncos adjacent to them in dominance rank than with others. The Mantel t -value was -2.85 ($P < 0.01$) and the matrix correlation -0.128 . Encounters occurred more often between adjacent juncos in the hierarchy than between birds separated by one or more birds.

The second hypothesis suggests that birds are more aggressive towards those distant from them in the social hierarchy than those close in rank. As with the white-throated sparrows, a significant negative association was found between the elements in the junco data matrix and those in the hypothesis matrix (which has zeros in the immediately off-diagonal elements and progressively larger numbers as one proceeds away from the diagonal). We obtained a t -value of -2.79 ($P < 0.01$) and a matrix correlation of -0.203 . Thus there are progressively fewer interactions between birds as one serially considers pair combinations of more distant birds in the social hierarchy.

BABOON PROGRESSIONS

As indicated by Altmann (1979), troops of yellow baboons often progress in an elongated formation, which in the extreme becomes a single file. He analysed numerous progressions of baboons in terms of the positions of individuals relative to their sex, age or social status. In addition, Altmann (1979) discussed a number of statistical techniques for the analysis of group geometry and demonstrated that some of these are insensitive to subtle spatial patterning.

The Mantel test can be particularly useful in the analysis of progressions. We demonstrate its use in approaching the following questions, which are addressed separately with respect to each sex. (1) Do members of a sex occur adjacent to one another more often than expected by chance? (2) Overall, do individuals of a sex occur closer together in a progression than would be expected on the basis of chance? (3) Do individuals of a sex tend to occur at or near the ends of progressions more often than expected if progression positions were randomly determined?

Altmann (1979) noted that, while many claims had been made as to the adaptive group geometry found within baboon troops, no author had published the order of individuals in even a single progression. He provided 20 examples of progression orders involving eight different groups of

baboons. In Table IV, we have summarized baboon positions for 17 of these progressions, indicating whether an individual was an adult male, adult female, juvenile or infant. The other three progressions listed by Altmann involved groups with 15 or fewer individuals; typically, a troop of this size or smaller includes so few individuals of any particular sex or age class that one has insufficient information to show statistically significant deviations from random progression orders.

Hypothetical Example

As in our other applications of the Mantel test, we constructed hypothesis matrices to evaluate the three questions posed above. The actual baboon progressions involve numerous animals, and thus result in large matrices. Therefore, a shorter hypothetical progression of six animals is presented in Fig. 3A to assist in the explanation of our procedures. For this example, we consider only questions concerning female-female associations; inter-male associations were tested in a similar way.

Our initial hypothesis concerned whether females in a progression occurred adjacent to one another more often than expected by chance. Our data matrix consisted of zeros to identify female-female pairs and ones for all other combinations (see upper right of Fig. 3B, which is half of the symmetric matrix tested). The hypothesis matrix contained zeros for elements just off the diagonal and ones for the rest of the elements (half of this matrix is represented in lower left of Fig. 3B). The zeros in the hypothesis matrix represent all pairs of adjacent individuals in the progression (i.e. animals 1 and 2, 2 and 3, etc.). If females typically occurred adjacent to each other, the zeros in the upper right of Fig. 3B would be nearer the diagonal. In such a case, there would be a positive matrix correlation involving corresponding elements of the data and hypothesis matrices, as well as a positive t -value from the Mantel test. A negative association and negative t -value would be found if females were less often found adjacent to one another than predicted from chance.

Clearly, the second hypothesis—whether females tend to be closer to one another in the progression than expected by chance—is related to the first. However, in this hypothesis matrix we were not interested in differentiating only between adjacent versus all other combinations of animals, but wished to incorporate information about

Table IV. Examples of progression orders of yellow baboons taken from Table II of Altmann (1979)

Progression no.*	No. baboons	Order (front to back)†
1	37	F-M-F-j-F-j-j-F-F-j-M-j-F-F-j-j-i-i-M-i-F-i-j-i-i-M-F-M-F-M-M-M-F
2	37	F-M-j-j-j-F-j-F-M-i-F-F-j-j-j-M-i-j-F-j-M-F-M-j-i-i-F-i-F-i-F-M-F-F-i-M-M
3	37	M-F-j-j-F-i-F-j-j-F-j-i-j-F-j-M-M-M-i-i-j-i-F-F-i-j-F-i-M-F-M-M-F-i-j-M-F
4	37	F-M-F-M-M-j-j-j-j-F-F-j-M-j-j-j-F-F-i-j-i-i-F-F-F-i-F-i-j-F-i-M-F-M-F-M-M
5	25	M-M-F-i-i-j-j-F-j-F-M-F-j-i-j-j-j-i-F-j-M-F-M-j-j
6	18	M-F-M-F-F-i-F-i-i-i-F-i-j-F-F-j-F
7	18	F-j-M-F-F-M-F-F-j-M-i-j-F-i-j-F-i-F
8	18	M-M-i-i-M-F-F-F-F-i-j-F-F-j-i-i-F-i
9	18	M-F-F-j-M-i-i-i-j-F-F-i-i-F-F-M-F-i
10	21	M-F-M-F-i-j-F-i-M-j-F-j-M-j-j-j-F-i-M-j-j
11	19	F-j-F-M-F-M-F-i-i-i-i-F-j-F-i-F-M-j
12	19	F-M-j-F-F-F-j-j-F-j-F-i-j-i-j-M-F-i-j
13	35	j-F-j-M-i-i-F-j-j-F-j-F-M-j-M-j-F-i-F-i-i-F-i-j-M-F-j-F-F-M-M-F-i-M
14	29	F-F-M-F-i-F-M-i-j-j-j-j-M-i-i-M-j-M-F-i-F-j-M-F-F-i-M-F-j
15 (18)	25	j-F-j-M-j-j-i-F-F-i-F-j-M-F-F-F-j-F-i-i-M-M-F-i-F
16 (19)	39	j-F-F-j-F-M-F-j-j-F-M-j-j-F-j-F-j-F-i-j-F-M-F-j-j-F-j-F-F-M-i-F-i-F-M-M-F
17 (20)	18	F-M-j-F-j-j-j-F-i-F-i-M-j-M-j-i-F-F

* Numbers in parentheses refer to Altmann's (1979) where they differ from ours.

† M = adult male, F = adult female, j = juvenile, i = infant. Altmann (1979) further divided the latter category into small and large infants.

exactly how close or how far away animals were from one another in the progression. Our data matrix (upper right of Fig. 3C) was the same as in the previous test, but the hypothesis matrix differed (lower left of Fig. 3C). The numbers in the latter represent differences in the progression positions of each pair of baboons. For example, the positions of the first and second baboons are one apart, while those of animals 1 and 6 are five apart. If females tend to be relatively close to one another, zeros in the data matrix (upper right) will correspond to small values in the hypothesis matrix (lower left), with the result being a positive matrix correlation coefficient and a positive *t*-value. When females are more uniformly distributed throughout the progression than predicted from chance, a negative coefficient and negative *t*-value will result. (A detailed computational example for this second hypothesis and our hypothetical data is presented in the Appendix.)

In order to evaluate the third hypothesis (e.g. that females occur near the ends of progressions more often than expected by chance), we first established a hypothesis matrix that contrasted

pairs of animals where both were near the ends (or even at the same end) of the progression with pairs where both were in the middle. For this hypothesis matrix (lower left of Fig. 3D), calculations were made of what we have termed reflected distances between positions in the progression. Such a distance is in effect the difference between two positions in the progression, but counted by going from one position to the centre of the progression and then back to the other position. In our hypothetical example (Fig. 3A), the centre of the progression is between positions 3 and 4. Thus, the reflected distance between animals 1 and 6 (which are the most extreme with respect to being on the ends of the progression) is five. In addition, this distance is also relatively great (a value of 4) for animals 1 and 2, which are near one end of the progression. The shortest distance (e.g. 1) is between animals 3 and 4, which are the most central pair. The overall result is that the hypothesis matrix has high values where both animals are near the ends of the progression and low values where both are in the centre.

For this hypothesis the same data matrix was

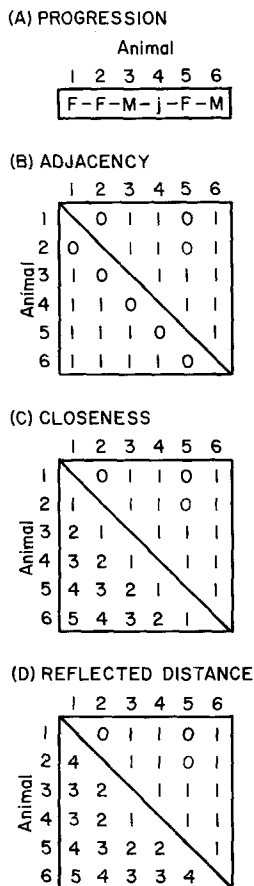


Figure 3. Hypothetical example used to explain our approach in evaluating associations in baboon progressions. (A) Progression of three females, two males and one juvenile. Below this progression are three matrices containing data to assess three hypotheses involving female-female relationships: (B) adjacency of females; (C) closeness of females; and (D) whether females tend to occur near the ends of progressions. The upper right portion of each matrix contains zeros for pair associations that are female-female and ones for all other combinations of individuals. The lower left half of each matrix represents half of a symmetric hypothesis matrix. See text for further explanation.

used (upper right of Fig. 3D), with zeros for the female-female pairs. If females tend to occur at or near the ends, these zeros in the data matrix will correspond with high values in the hypothesis matrix, and the matrix correlation coefficient and t -value will be positive if females are found near the centre of the progression more often than expected by chance.

Evaluation of Progressions

The results of Mantel test (t -values) and matrix correlations for evaluations of data matrices representing female-female and male-male associations against hypothesis matrices for adjacency, closeness and reflected distance are presented in Table V. When adjacency was assessed for females, 15 of the 17 progressions produced negative t -values and correlations. Progressions 8 and 9 (see Table IV), which resulted in positive values, had females adjacent to one another somewhat more often than the expected frequency of such pairings. However, the deviation is not statistically significant in either case. For all other progressions, the trend is in the opposite direction, indicating that the females were found next to other females less often than expected on the basis of chance. Two of these progressions (11 and 16) exhibit statistically significant deviations from chance expectations. None of the females in progression 11 were next to one another, while in progression 16 there was only one pair of adjacent females (Table IV).

For male-male pairs, seven progressions produced positive values, while 10 resulted in negative values (Table V). None of the t -values were even close to being statistically significant. It appears as if, for this sample of progressions, the males showed no tendency to occur next to one another, nor were they spaced out in progressions.

The evaluations of closeness in females gave five positive and 12 negative t -values and correlations (Table V). Only one progression (no. 14) produced a t -value close to being statistically significant (-1.94 , with the 0.05 level being at -1.96). Overall, more progressions showed a tendency for females to be more uniformly distributed along the line of individuals than showed a grouping tendency.

Analysis of male-male closeness in progression positions produced three positive and 14 negative values (Table V). Progression 4 is the only one with a statistically significant t -value (-2.55). For most of the progressions, male-male differences in position were somewhat greater than the null expectation.

Table V shows that, with respect to reflected distances, the data matrices for female-female pairs produced seven positive and 10 negative t -values. The value for progression 14 was statistically significant and negative, indicating that females were closer to the ends of the progression

Table V. Association of inter-individual difference matrices for progression positions of female and male yellow baboons with hypothesis matrices indicating adjacency, closeness, and reflected distance: results of Mantel tests (*t*) and matrix correlations (*r*)

Progression no.	Female-female						Male-male					
	Adjacency		Closeness		Reflected distance		Adjacency		Closeness		Reflected distance	
	<i>t</i>	<i>r</i>	<i>t</i>	<i>r</i>	<i>t</i>	<i>r</i>	<i>t</i>	<i>r</i>	<i>t</i>	<i>r</i>	<i>t</i>	<i>r</i>
1	-0.16	-0.004	-0.82	-0.050	-1.26	-0.149	0.49	0.016	-0.54	-0.029	-1.92	-0.183
2	-1.19	-0.035	-0.67	-0.040	-0.52	-0.060	-0.52	-0.017	-1.23	-0.066	-0.74	-0.071
3	-1.58	-0.048	-1.12	-0.066	-1.02	-0.112	1.50	0.049	-0.38	-0.020	-0.15	-0.014
4	-0.16	-0.004	-0.18	-0.011	0.14	0.016	0.49	0.016	-2.55*	-0.136	-3.03**	-0.289
5	-1.38	-0.068	0.00	0.000	0.44	0.053	0.27	0.014	-1.83	-0.127	-1.60	-0.175
6	-1.05	-0.060	-1.16	-0.122	-1.25	-0.234	-0.35	-0.029	1.05	0.086	-1.69	-0.137
7	-1.05	-0.060	-1.05	-0.110	-0.89	-0.167	-0.65	-0.050	0.66	0.057	0.71	0.080
8	1.66	0.101	1.58	0.162	1.82	0.322	1.30	0.100	-1.46	-0.126	-1.67	-0.186
9	0.66	0.040	-0.59	-0.060	-0.36	-0.064	-0.65	-0.050	1.46	0.126	-1.43	-0.160
10	-1.21	-0.073	-0.04	-0.003	0.03	0.004	-1.21	-0.073	-1.06	-0.087	-0.63	-0.081
11	-2.20*	-0.128	-0.85	-0.082	-0.98	-0.165	-0.63	-0.046	-1.00	-0.082	-0.84	-0.089
12	-0.21	-0.012	0.34	0.033	0.03	0.004	-0.34	-0.026	-1.69	-0.129	-1.20	-0.092
13	-1.34	-0.041	0.01	0.001	0.13	0.016	-0.22	-0.008	-0.87	-0.047	0.97	0.092
14	-0.43	-0.017	-1.94	-0.134	-2.24*	-0.284	-1.52	-0.064	-0.20	-0.013	0.48	0.054
15 (18)†	-0.50	-0.021	0.34	0.028	0.82	0.124	0.86	0.046	-0.63	-0.041	-0.15	-0.015
16 (19)	-2.58*	-0.063	-0.64	-0.040	-0.25	-0.031	0.30	0.010	-1.03	-0.049	-1.21	-0.095
17 (20)	-0.72	-0.047	-1.68	-0.166	-0.94	-0.155	-0.65	-0.050	-0.66	-0.057	-0.24	-0.027
No. positive‡	2		5		7		7		3		3	
No. negative	15		12		10		10		14		14	

* $P < 0.05$; ** $P < 0.01$.

† Numbers in parentheses refer to Altmann's (1979, Table II) numbers where they differ from ours.

‡ Tabulated before *t*-values and correlations were rounded to two and three decimal places, respectively. In all cases, the numbers of positive and negative values were the same for *t*-values and correlations.

than would be predicted by chance alone; as indicated in Table IV, there were a number of immature and juvenile animals in this progression. However, when considering all 17 progressions, it is clear that no strong tendency exists for females to be near the ends (as indicated by negative values) of progressions, nor toward the centre (positive values).

However, a different result was found when analysing male-male pairs in terms of reflected distances. Only two progressions produced positive *t*-values, while 15 resulted in negative *t*-values. In progression 4, where males were clearly concentrated near the ends of the progression, the negative *t*-value is very highly significant ($P < 0.001$).

One obvious finding from the analysis of female-female and male-male pairs of baboons, with respect to the three hypotheses, is that with the Mantel test it was seldom possible for us to show a statistically significant deviation from chance expectations in the positionings of such pairs in any

single progression. In fact, the number of progressions that exhibited significant deviations for any particular hypothesis (for example, that female-female pairs would be found adjacent to one another more often than predicted) was typically not much higher than one would expect by chance alone: that is, 2 of 17 progressions produced significant deviations for the first hypothesis when considering female-female pairs (Table V), while we would expect 1 of 20 by chance at the 0.05 probability level.

The reason for not obtaining more conclusive results when considering a single progression is not because of the Mantel test itself, but is related to properties of individual progressions per se and the information contained in them. Typically, considerably fewer than half of the individuals in a given progression were adult and of one sex (because of the presence of immatures and juveniles). In such cases, the changing of positions of one or two individuals in a progression could

substantially modify inter-pair associations. Statistical power would be greater in those situations where the type of individuals in question constitute close to 50% of the total number of individuals. Of course, the opportunity for showing statistically significant deviations from chance expectation increases as the length of progressions increases (assuming the same proportion of males and females).

Sometimes an investigator will wish to evaluate positioning in a single progression and, as shown above, this can be statistically analysed. However, often one would want to determine only whether a trend exists for a series of progressions. This kind of problem can be approached simply by using the inter-individual data and hypothesis matrices, as has been done in our baboon examples. A series of *t*-values and/or matrix correlation coefficients would be calculated as indices to be analysed for statistical trends.

For example, when considering the 17 progressions (Table IV) it is clear that a statistically significant trend exists for female-female pairs not to occur adjacent to one another. The probability of getting two positive and 15 negative *t*-values or a more extreme deviation from a 50% split by chance alone is only 0.0023 (exact binomial probability; Sokal & Rohlf 1981). The probabilities of obtaining the numbers of positive and negative *t*-values for the other hypotheses evaluated (see Table V) are as follows: female-female closeness, 5 positive and 12 negative, $P=0.1435$ (NS); female-female reflected distance, 7 and 10, $P=0.6291$ (NS); male-male adjacency, 7 and 10, $P=0.6291$ (NS); male-male closeness, 3 and 14, $P=0.0127$; male-male reflected distance, 3 and 14, $P=0.0127$. Thus our general conclusions for this set of progressions are that: (1) females tend not to be next to one another; (2) males occur farther apart from one another than expected by chance; and (3) males show a tendency to occupy positions near the ends of progressions.

DISCUSSION

These examples demonstrate a range of potential applications of this matrix approach in behavioural investigations. In some cases, like the evaluation of sunbird vocalizations, there are other statistical techniques like spatial autocorrelation (for examples of its application in geographic

variation analyses, see Sokal & Oden 1978a,b) which can be extremely helpful when used separately or in conjunction with the Mantel test to elucidate geographic or ecological patterning.

There are also a number of other kinds of questions posed by animal behaviourists that can profitably be investigated using the Mantel test or one that employs a similar approach. For example, Wampold & Margolin (1982) have recently applied the cross-product notion to test for independence of behavioural states in sequential data. Their techniques are conceptually related to those we have presented.

When evaluating spatial geometry within animal groups, there are additional questions related to those posed above that could be considered using this matrix approach. For instance, one could just as easily investigate the two-dimensional or three-dimensional positioning of individuals, and not restrict an investigation to linear progressions. In fact, it appears as if a major reason for previous workers analysing progressions instead of two-dimensional positioning of primates was because the former was the simpler case with fewer methodological problems. However, primates in groups most often do not position themselves in a straight-line arrangement, and questions of interest are often investigated more realistically when the worker is not limited to situations where a linear arrangement of individuals is produced. The matrix approach described here can be used to study metric distances in addition to rank ordering, which would allow one to evaluate a much wider range of questions concerning individual spacing within a group.

For most sets of data on inter-individual associations, there are a considerable number of possible and reasonable hypothesis matrices. Testing a single data matrix against a large number of such hypotheses can, of course, lead to concerns about the statistical interdependencies of these multiple tests. Thus, if numerous hypotheses are of interest, it may be necessary to repeat experiments in order to test multiple questions for a given group of organisms. In this way the data required and the requirements for avoiding multiple testing are not different from those of other statistical tests. However, Hubert (1983) has outlined procedures of matrix construction that can be used to determine whether a given set of data better supports one hypothesis in contrast to another. His methods may be of considerable interest to ethologists.

One other refinement that can be employed when conducting multiple tests is the Dunn-Sidak method (Sokal & Rohlf 1981) used by Sokal & Wartenberg (1983). It evaluates results on the basis of experimentwise error rate rather than having the error rate set for individual tests in a series. In this way, inter-associations of tests are taken into account, and repetition of an experiment or set of observations—which is often impossible or at least impractical in behavioural studies—is not required.

As indicated earlier, the test does not require any particular statistical distribution of matrix elements and is in this sense a non-parametric test. However, as is clear from some of our examples, the Mantel test is sensitive to the choice of metric. For instance, in the case where we analysed sunbird songs for geographic patterning, a slightly different test value would result if we represented distances in miles instead of in kilometres. This statistical property can be obviated by using tests like those outlined by Dietz (1983), where ranks of differences are analysed, rather than the actual differences. The resulting statistics are invariant under monotone transformations of matrix elements, a desirable property when comparing distance measures whose actual magnitudes may be arbitrary.

However, for a number of kinds of research problems, one may well not wish to remove sensitivity to the choice of metric, but instead use this property to one's advantage in discriminating between different types of patterns. As an example, if the tests employed by Dietz (1983) were applied to Payne's (1978) sunbird data, identical test statistics would result if one used kilometric distances or their reciprocals. In our analysis of Payne's data, we have used the Mantel test to tease apart what can be considered to be very different aspects of spatial patterning (see also Jones et al. 1980; Schnell et al., in press).

We have in effect employed different metrics for what amount to different hypotheses, thus at least suggesting that this sensitivity could lead to some subtleties of interpretation. One might ask whether or not every admissible metric, of which there exist an uncountable number, represents a different biological hypothesis. While technically the answer to such a query is probably yes, in practice it has been our experience that the test is not dangerously sensitive to the choice of distance measure.

When we first became interested in differentiating between regional and local patterning in geo-

graphic data, numerous transformations of distance measures were tried. A variety of transformations of kilometric distances—logs, squares, cubes, squared reciprocals, etc.—expand small distances and de-emphasize large ones. In our empirical evaluations, all gave essentially the same results for a wide variety of data sets. Likewise, while there were slight differences when we used kilometres rather than miles as a distance measure, the differences in resulting test statistics were so minor as to be inconsequential. An awareness of possible subtleties related to the metric chosen can help one avoid making unwarranted inferences and, for certain problems, can allow the investigator to extend his or her analyses in profitable ways.

A chief benefit of following the kinds of matrix procedures outlined in this paper for the study of problems of inter-individual or inter-group associations may be simply in the clear delineation of the research questions. The process of determining the correct hypothesis matrix can in itself have considerable heuristic value and result in more precisely defined hypotheses. We foresee considerable use of this test and believe that it (or a similar one) is likely to become a standard statistical method widely applied in animal behaviour.

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APPENDIX: COMPUTATIONAL EXAMPLE OF THE MANTEL TEST

Actual calculations are included below for the hypothetical example of baboon progressions (Fig. 3A), to evaluate whether females in a progression occurred closer to one another than expected by chance (Fig. 3C). This exercise is for illustrative purposes only, since given such small matrices the

asymptotic normality of the Mantel test would be too crude an approximation and a more appropriate way of testing the Mantel statistic would be to use a Monte Carlo procedure. The outlined procedures assume that matrices are symmetric, which will be the case in essentially all behavioural applications. Refer to Mantel's (1967) original paper if asymmetric matrices are to be compared.

The complete data matrix (**X**; Table VI), expanded from that in the upper right half of Fig. 3C, has zeros for female-female pairs and ones for all other combinations. The hypothesis matrix (**Y**; Table VI) is the expanded form of the one in the lower left portion of Fig. 3C. The **X** and **Y** matrices are both symmetric in that row 1 equals column 1, row 2 equals column 2, etc. Also, both have zeros for their diagonal elements.

For the test, as detailed in the following paragraphs, we must compute the test statistic *Z*, as well as its permutational variance, standard error, and expected value. The expected value is subtracted from the test statistic and the result divided by the standard error to provide a *t*-value that can be compared against a *t*-distribution with infinite degrees of freedom (i.e. the standard normal distribution).

The sum of products of the corresponding elements of the two matrices is computed in the final column of Table VI and is the test statistic *Z*. A number of other calculations required for the test are shown in Table VI. Symbols for summations are given at the bottom of the table (with subscripts *x* or *y* to indicate the matrix). In words, these variables are the: (*A*) grand total of all elements; (*B*)

sum of squares of all elements; and (*D*) sum of squares of the row totals. In addition, the squares of the grand total for each matrix are

$$G_x = (A_x)^2 = 576$$

and

$$G_y = (A_y)^2 = 4900$$

and the sum of squares of row totals minus the sum of squares of all elements are

$$H_x = D_x - B_x = 78$$

and

$$H_y = D_y - B_y = 644$$

We then calculate *K* for each matrix,

$$K_x = G_x + 2B_x - 4D_x = 216$$

and

$$K_y = G_y + 2B_y - 4D_y = 1904$$

The following are needed:

$$L = 2B_xB_y = 10\,080$$

$$O = 4H_xH_y/(n-2) = 50\,232$$

$$P = K_xK_y/((n-2)(n-3)) = 34\,272$$

$$Q = G_xG_y/(n(n-1)) = 94\,080$$

and

$$R = L + O + P - Q = 504$$

where *n* is the number of rows which is equivalent to the number of columns (in our example *n*=6).

Table VI. Symmetric **X** (data) and **Y** (hypothesis) matrices expanded from Fig. 3C, along with initial computations*

X matrix	ΣX_j	ΣX_j^2	$(\Sigma X_j)^2$	Y matrix	ΣY_j	ΣY_j^2	$(\Sigma Y_j)^2$	ΣX_jY_j
0 0 1 1 0 1	3	3	9	0 1 2 3 4 5	15	55	225	10
0 0 1 1 0 1	3	3	9	1 0 1 2 3 4	11	31	121	7
1 1 0 1 1 1	5	5	25	2 1 0 1 2 3	9	19	81	9
1 1 1 0 1 1	5	5	25	3 2 1 0 1 2	9	19	81	9
0 0 1 1 0 1	3	3	9	4 3 2 1 0 1	11	31	121	4
1 1 1 1 1 0	5	5	25	5 4 3 2 1 0	15	55	225	15
Totals	24	24	102		70	210	854	54
Notation	$\Sigma \Sigma X_{ij}$	$\Sigma \Sigma X_{ij}^2$	$\Sigma_i (\Sigma_j X_{ij})^2$		$\Sigma \Sigma Y_{ij}$	$\Sigma \Sigma Y_{ij}^2$	$\Sigma_i (\Sigma_j Y_{ij})^2$	$\Sigma \Sigma (X_{ij}Y_{ij})$
Symbols	<i>A_x</i>	<i>B_x</i>	<i>D_x</i>		<i>A_y</i>	<i>B_y</i>	<i>D_y</i>	<i>Z</i>

* Notation and symbols from Mantel (1967). An *i* designates rows, while a *j* refers to columns.

The permutational variance is

$$S = \text{Var } Z = R/(n(n-1)) = 16.8$$

and the standard error is

$$T = SE \, Z = S^{0.5} = 4.09878$$

The expected value (or null expectation for random association of elements in **X** with those in **Y**) is

$$U = \exp Z = A_x A_y / (n(n-1)) = 56$$

and

$$V = Z - \exp Z = Z - U = -2$$

The latter quantity is divided by the standard error of Z to provide the t -value,

$$W = t = V/T = -0.4880$$

After comparing this result against the standard normal distribution (or t -distribution with infinite degrees of freedom; $t = 1.96$ and -1.96 at the 0.05 probability level), we conclude that for our example there is no indication that females are closer to one another more often than expected by chance alone. In fact, the negative t -value shows that the females are slightly further apart than expected although, as indicated above, this is not a statistically significant deviation from chance expectations.

In our analyses, we have also presented the matrix correlation (r). It is the product-moment correlation of corresponding entries in the two matrices, ignoring the diagonal elements (i.e. the zeros that indicate the association of an individual with itself). For this example, the matrix correlation is -0.134 .

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