Non-parametric Estimates of Interaction from Radio-tracking Data

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Some non-parametric methods of resolving static interaction between the utilizations of two home ranges, and dynamic interaction between the movements of two individuals, are evaluated and shown to be useful tools in the analysis of radio-tracking data on overlapping ranges and concurrently tracked animals. The methods described are independent of sampling intensity and, with few underlying assumptions, they are suitable for quantitative comparisons between different pairs of animals. The interpretive value of analyses of interaction is illustrated with data obtained on the mobile ranges of foxes living in Oxford city.

1. Introduction

Numerous analytical techniques have been developed for transforming data on the successive positions of an animal into graphical reconstructions of home range configuration and the animal's distribution in time within the range (reviewed in Kenward, 1987). They have proved particularly useful in radio-tracking studies on animals that are otherwise difficult to observe in their natural habitat. The typically high frequency data generated by radio-telemetry also provide a suitable data base for analysing of interactions between individuals when two or more have been tracked in the same area. However, few empirical studies have attempted either to quantify the degree of concordance in the utilization of shared areas (Adams & Davis, 1967; Rasmussen & Rasmussen, 1979; Webster & Brooks, 1981 and C. P. Doncaster, unpublished thesis) or to évaluate the manner of interactions between concurrently tracked individuals (Dunn, 1979; Macdonald *et al.*, 1980; Webster & Brooks, 1981; Doncaster & Micol, 1989 and C. P. Doncaster, unpublished thesis), despite the obvious biological interest of such analyses.

Spearman's coefficient of rank correlation is a strong candidate for an index of concordance in the utilization of home ranges, because it takes into account both the overlap of two ranges and their utilizations. However, Rasmussen (1980) noted that it gives a non-linear response for varying degrees of overlapping utilization, and therefore cautioned its use for comparing the extent to which areas are shared.

Parametric tests for dependency in the concurrent movements of two individuals have been developed by Dunn (1979) and Macdonald *et al.* (1980). Both tests require that the utilization of each range is distributed about a single centre of activity and violation of this assumption, which has no obvious biological basis, can produce large errors (Macdonald *et al.*, 1980).

The aims of this paper are (a) to explore the behaviour of Spearman's coefficient under different degrees of utilization and concordance in overlapping home ranges,

and (b) to describe a non-parametric reduction of Macdonald *et al.*'s (1980) test of dependency in the movements of two individuals tracked at the same time. The utility of the two non-parametric techniques is demonstrated with examples from red foxes (*Vulpes vulpes* L.) living in the city of Oxford and occupying group ranges that are continually drifting across the town (C. P. Doncaster, unpublished thesis).

2. Definitions

The spatial overlap of two home ranges and congruence in at least part of their utilization distributions is termed "static interaction", while dependency in the simultaneous movements of a pair of individuals is termed "dynamic interaction". Implicit in both the notions of utilization distribution and simultaneous movements is the assumption that the interval data from which they have been estimated are independent and regularly sampled in time. That is, the time interval between successive fixes is approximately constant and such that the animal being followed would normally have had sufficient opportunity to move to any other part of its range between one fix and the next (see Swilhart & Slade, 1985 for techniques of estimating independence).

3. Static Interaction

Rasmussen (1980) identifies three criteria for a desirable "index of consistency" to compare patterns of range use: (1) it should assess similarity in the location of intensively used clumpings; (2) it should not be influenced by differences in the total amount of data available for each animal; (3) its evaluation should not be affected by differences in the size of the spatial frame of reference (the sum of cells to be compared) between pairs under consideration.

The percentage overlap of two home ranges provides a first approximation of static interaction and is most useful for identifying ranges with congruous borders (Macdonald *et al.*, 1980). Such an index, however, is of limited value because it takes no account of the utilization distribution within the shared parts of each range. For example, two ranges might overlap by less than 50% although the shared area contains the most utilized parts of both ranges. Alternatively, two individuals may concentrate their activities in different parts of a largely shared range.

This problem can be overcome by testing for correlation in the utilization distributions of each range. Positive correlation indicates similar utilizations (attraction) and negative correlation separate utilizations (repulsion). A simple and non-parametric estimate of the utilization distribution is obtained from the grid-cell method of range analysis (Siniff & Tester, 1965). For a chosen scale of grid, and fixes collected at fairly regular time intervals during the animal's period of activity, utilization through the range is obtained from the sum of fixes in each cell (or a probability estimate based on these frequencies: Ford & Krumme, 1979; Anderson, 1982). The size of grid-cells must clearly be large enough that some cells contain several fixes, but not so large as to obscure the overall configuration of the range.

A Spearman's coefficient, calculated on the pairs of fix scores (or probability estimates) obtained from all the grid-cells frequented by one or both animals, tests for correlation between the two utilization distributions. For all unshared cells, one value of the pair of utilization scores will be zero and Rasmussen (1980) points out that these zero scores give a non-linear relationship between the coefficient and the extent of overlap. In other respects, however, rank correlation meets the three criteria given above for indexing concordance in range use.

In order to determine the behaviour of Spearman's coefficient as an index of static interaction, it was modelled on hypothetical ranges of ten grid-cells each. Figure 1 shows how the coefficient responds to varying overlap of ranges of equal size (a) and (b) and ranges in which one is a subset of the other (c) and (d). The coefficient r was calculated from 0–100% overlap of two ranges. In addition, the rank scores (no tied scores) in the shared cells of one range underwent ten step-wise changes between maximum concordance and maximum discordance with respect to the rank scores in the cells shared with the other range [lines numbered 1–10 in Fig. 1(a) and (b); same sequence for (c) and (d)]. For example, two ranges of ten grid-cells each, of which the seven most utilized are shared, had the following scores:

Scores for range 1:	1	2	3	4	5	6	7	8	9	10	0	0	0
Ranked utilization:	4	5	6	7	8	9	10	11	12	13	2	2	2
Region of overlap:													
Scores for range 2:	0	0	0	4	5	6	10	9	8	7	3	2	1
Ranked utilization:	2	2	2	7	8	9	13	12	11	10	6	5	4

Four of the seven most frequented cells (with scores of 7, 8, 9 and 10) were not utilized in complete concordance, and line 4 in Fig. 1(a) is determined by this arrangement under varying degrees of range overlap. In this example, the percent overlap of ranges is $7/13 = 53\cdot85\%$ and the correlation coefficient for the 13 ranked scores is $0\cdot78$.

At 100% overlap, Fig. 1 shows that r is sensitive to the full extent of affiliations between two utilization distributions, from complete concordance (perfectly matched utilization distributions) giving a maximum r of $+1\cdot0$ to complete discordance (areas used heavily by one animal are avoided by the other) giving a minimum r of $-1\cdot0$.

For ranges of equal size, if the shared area is only 50% of the combined area of both ranges, but contains the most utilized parts of each range, the index should reflect attraction: r has a value between $+0\cdot54$ and $+0\cdot79$, depending on the degree of concordance within the shared area [Fig. 1(a)]. If the shared area is still 50% of the combined area of both ranges, but it contains only the least utilized parts of each range, the index should reflect repulsion: r lies between $-0\cdot73$ and $-0\cdot98$ [Fig. 1(b)]. For ranges of equal size and no overlap, r is constant at $-0\cdot86$ (all the ranked scores in one range are correlated with the rank corresponding to a zero utilization score in the other range). The value of r is not affected by sample size (number of grid-cells), and equivalent results are produced from similar manipulations of 20 or 100 grid-cells. Moreover, the behaviour of r changes little when the two ranges are not exactly equal in size: for comparisons of overlapping home
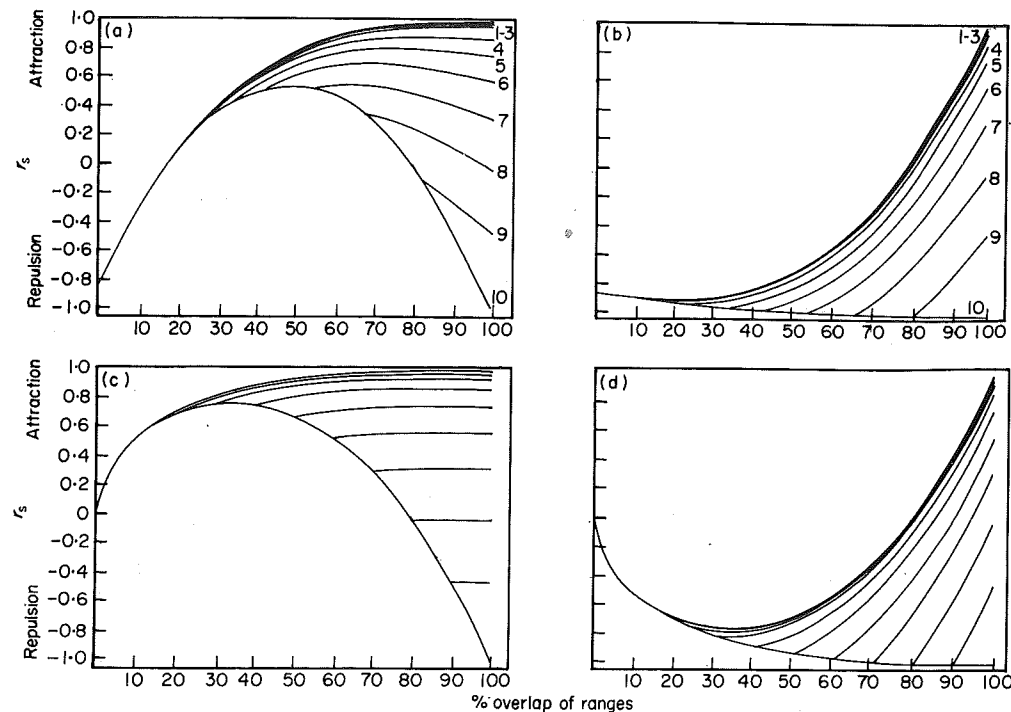
FIG. 1. The behaviour of Spearman's *r* as an index of interaction between two overlapping home ranges: (a) both covering ten grid-cells and sharing the most utilized cells of each range; (b) both covering ten grid-cells and sharing the least utilized cells of each range; (c) and (d) as for (a) and (b) but one range a subset of the other, which covers ten grid-cells. The lines numbered 1–10 show increasing discordance in utilization of shared cells, from perfectly matched (1) to perfectly opposing (10).

FIG. 2. The behaviour of Spearman's *r* for two ranges of ten grid-cells each, in which the most utilized parts of one range are shared with the least utilized parts of the other. Line numbers 1–10 show increasing discordance in utilization of shared cells.

ranges in which one is 20% larger than the other, the magnitude of *r* varies by ≤ 0.01 from that given in Fig. 1(a)–(b).

Figure 1(c)–(d) models the behaviour of Spearman's *r* for varying overlap of two ranges in which one is a subset of the other. For the purposes of modelling, one range was set to ten grid-cells, and the other was made smaller in incremental steps within its boundary (giving 100, 90, 80 . . . 0% overlap). This situation might correspond to a juvenile animal having access only to a proportion of the parental range (see example below). If the smaller range is half the size of the larger (50% overlap), and it covers the most utilized parts of the larger range, *r* lies between $+0.68$ and $+0.94$ [Fig. 1(c)]; if it covers only the least utilized parts of the larger range, *r* lies between -0.68 and -0.94 [Fig. 1(d)].

In further tests on ranges of equal size, for which the most utilized parts of one range are shared with the least utilized parts of the other (Fig. 2), *r* lies between the two limits of values shown in Fig. 1(a) and (b) for a given overlap ($+1$ to -1 at 100%; -0.16 to -0.41 at 50%; -0.86 at 0%).

Spearman's *r* therefore provides an unambiguous index of concordance in utilization, even for ranges that overlap relatively little. Some examples of the usefulness
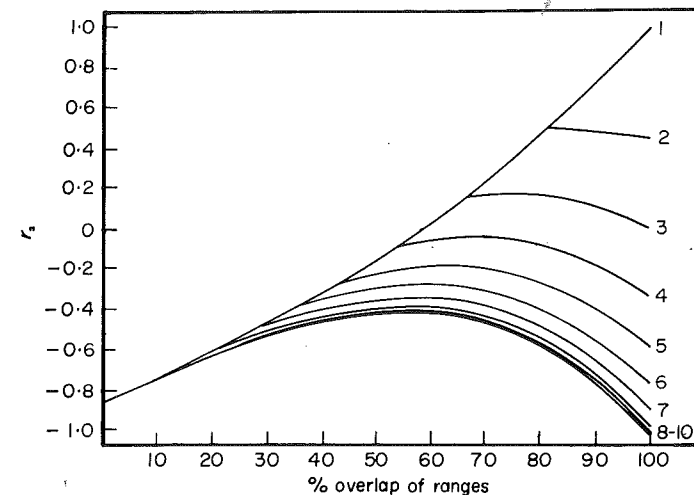
of the index are illustrated by analysis of the spatial organization of fox home ranges in Oxford city. Range sizes and configurations were calculated from 50×50 m grid-cells, including the eight influence cells surrounding each non-peripheral cell in which an active fix was located (Voigt & Tinline, 1980), and utilization distributions were obtained from the sum in each cell of independent fixes and influences (given 1/8 the value of fixes). Radio-tracking of 17 resident foxes for periods of 2–25 months revealed home ranges that averaged 39 ha at any one time. Although these ranges remained relatively constant in size throughout an individual's lifetime, they were not spatially stable, drifting across the town landscape by 30–40 ha year^{-1} (C. P. Doncaster, unpublished thesis). In consequence, a simple plot of home range configurations gave a blurred picture of static interaction from which it was not possible to ascertain the relationships between foxes.

For example, the home ranges of two foxes that were known to be a mated pair overlapped by 32% and had a Spearman's *r* of -0.23 for the 27 consecutive months of data in which first the male (m1) and then his mate (f2) had been tracked. However, when the pattern of overlap was compared only for the 2 months in which both foxes had been tracked together, the two ranges covered less than half their corresponding total areas, at 35 and 40 ha, and overlapped by 82%. A Spearman's *r* of $+0.76$ indicated sharing of the more heavily frequented parts of their ranges, and strong concordance in the utilization of these shared areas [Fig. 1(a)].

The poor concordance of their total ranges had been due in large part to the vixen expanding and shifting her range after the death of her mate. This is illustrated in Fig. 3 by changes in the size, and the areas covered by, the prevailing range of the vixen throughout her tracking history. For any given night, an animal's prevailing range was defined retrospectively to cover only those parts of its total home range
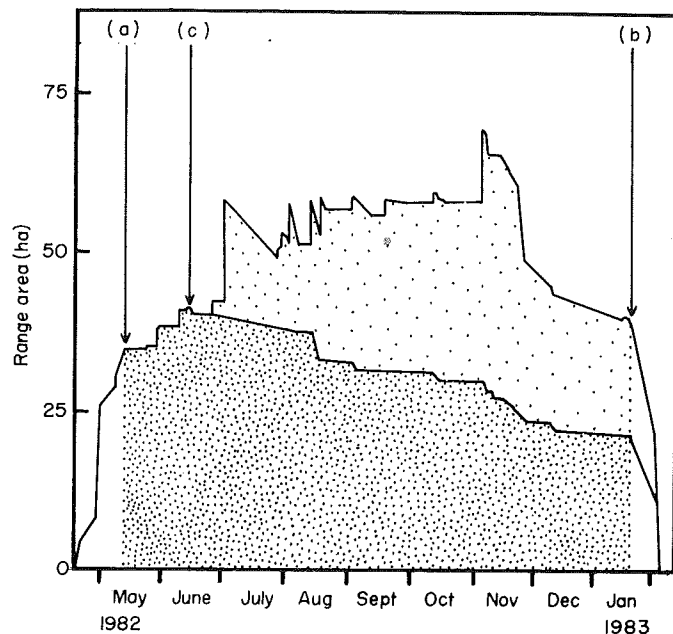
FIG. 3. Changes in size and position between May 1982 (a) and January 1983 (b) for the prevailing range of vixen f2 tracked in Oxford city (1912 fixes). Dense stippling shows the group of 50×50 m grid-cells (including adjoining influence cells) which constituted the prevailing range of this fox on 15 June 1982 (c) at the death of her mate m1, and its gradually diminishing size as the fox drifted away to new districts. Light stippling above shows additions to, and losses from, the range of other grid-cells that came into use only after the death of her mate.

visited on that night, plus areas previously visited that would be returned to on any future night that the fox was followed. The number of grid-cells constituting a prevailing range is conceptually equivalent to an enumeration estimator in capture-mark-recapture studies ["minimum numbers known alive" in Nichols & Pollock (1983), equating numbers of cells with numbers of individuals]. As with the enumeration estimator, prevailing ranges could not be calculated from the first and last periods of tracking, when range size is dependent on the cumulative fix total. The prevailing range in Fig. 3 thus increased in size during the first month of tracking—up to (a)—and decreased during the last month—after (b)—as a function of the rate at which fixes were collected. From May 1982 to January 1983, however, changes in prevailing range size from night to night reflected grid-cells coming into use for the first time or being abandoned definitively from the range. The figure shows that by January 1983, 7 months after the death of her mate, the prevailing range was the same size as it had been in June 1982, although it had undergone rapid expansions and contractions over the interval and had shifted in position such that only 51% of the cohort of grid-cells making up the original range still remained in use.

An example of static interaction between two ranges in which one is a subset of the other is given by a vixen (f4) and her yearling son (m6), tracked together in

October and November 1981. The range of the yearling lay almost entirely (99%) within the range of his mother, but was smaller, occupying only 36% of her range. The two foxes had an r of $+0.22$, indicating that while the yearling did not have access to all the most utilized parts of the parental range [Fig. 1(c)], nor was he restricted only to the least utilized parts [Fig. 1(d)]. The yearling was killed by road traffic in mid-November 1981, but the vixen continued to be tracked for a further 6 months. During this time she made heavier use of the parts of her range that had been occupied by her son, shown by a higher value of r, at $+0.42$, for the vixen's range over 8 months compared to the range of her son.

A computer program is available from the author on request, for calculating overlap and Spearman's r between two home ranges as defined by the grid-cell method with influences, which uses two data bases of timed co-ordinates in sequential order [written in BBCBASIC(86), M-TEC, Reepham, Norfolk, U.K.].

4. Dynamic Interaction

Dependency in the movements of two individuals (dynamic interaction), within the known limits of their home ranges (static interaction), can be expressed in terms of probability. Are the animals more likely to maintain a certain separation (positive dynamic interaction) or less likely (negative dynamic interaction) than is expected from the configuration and utilization of their ranges? At small separations in particular, does there exist a bond of attraction between them or do they respond to close contact by mutual repulsion? Answers to these questions provide the basis for understanding the driving motivations behind their combined movements.

Macdonald et al. (1980) describe a parametric test of dynamic interaction based on the multivariate normal distribution. Suppose (x_1, y_1) and (x_2, y_2) represent the co-ordinates of two animals at a simultaneous fix. These co-ordinates are assumed to follow bivariate normal distributions. The means, variances and covariances can be estimated, and "probability ellipses" can be constructed showing areas estimated to cover 50%, 95%... of the fixes on each animal (Jennrich & Turner, 1969).

On the null hypothesis of no dynamic interaction, these distributions are independent. Now suppose (x_1, y_1, x_2, y_2) follows a four-variate normal distribution. The 4×4 matrix of estimated variances and covariances, call this A, can be partitioned into four 2×2 matrices:

$$A = \begin{bmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{bmatrix}.$$

Here, A_{11} and A_{22} represent the variances and covariances for each animal, and A_{12} and A_{21} contain the covariances x_1x_2, x_1y_2 etc involving both animals. On the null hypothesis, these will be small. Following Anderson (1958), a measure of the strength of interaction is given by:

$$V = |A|/(|A_{11}| \cdot |A_{22}|).$$

This will be close to 1 if the null hypothesis is true, but smaller if there is dependency (positive or negative) in the simultaneous movements of the two animals. The values of V can be compared for different pairs of animals, although this could be

misleading if the assumptions of bivariate normality and low serial correlation between successive fixes are not valid. Moreover, relative values of V are difficult to interpret, as dynamic interaction arising out of dependency at large separations may not have the same biological meaning as dynamic interaction when the animals are close to, and aware of, each other (see below). An exact significance test (Anderson, 1958) of the null hypothesis of no dynamic interaction is given by:

$$W = (N-4)(1-\sqrt{V})/(2\sqrt{V}).$$

This follows a F distribution with 4 and $2(N-4)$ degrees of freedom, where N is the number of paired fixes.

Another test of dynamic interaction which is based on similar principles and is more sophisticated but also mathematically complex, uses the multivariate Ornstein–Uhlenbeck model in place of the bivariate-normal model (Dunn, 1979).

On the assumption of independent bivariate normal distributions, it is possible to calculate the theoretical distribution of the distances between two animals (Macdonald *et al.*, 1980). This can be compared with the set of separations observed at simultaneous, or nearly simultaneous, fixes. An excess or deficit of small separations will then indicate positive or negative dynamic interaction when the animals are close to each other. Although this method distinguishes interaction at small separations from the biologically less interesting excess or deficit of larger separations, it still depends on the strong, and often unrealistic, assumptions of bivariate normality and elliptical home ranges. It suggests, however, a non-parametric approach which is also based on the differences between observed and theoretical distributions of separation distances.

The non-parametric comparison is made between the empirical distribution functions of the N paired (simultaneous or nearly simultaneous) separations and the complete set of N^2 separations, or the N^2-N unpaired separations. A significance test of the null hypothesis of no dynamic interaction can be calculated from these separations. It is analogous to Knox's (1964) test for space-time clustering, familiar in medical statistics (Armitage & Berry, 1987). A critical separation is chosen within which presence of dynamic interaction is of interest; for example, the furthest separation at which two foxes can sense each other's presence in the city environment is approximately 50 m (Macdonald *et al.*, 1980 and C. P. Doncaster, unpublished thesis). The data can then be placed in a 2×2 contingency table, showing frequencies of paired and unpaired separations, below and above the critical distance. If there was no relationship between the separations of two animals in time (simultaneous or not) and in space (relative to the critical distance), cell frequencies would be expected to be proportional to the marginal totals.

An example is given in Fig. 4(a) for the cumulative probability of distances separating the vixen (f2) described in Fig. 3 and her mate (m1) when they were both active. Observed separations were calculated from a list of 44 pairs of co-ordinates given by fixes that were collected simultaneously on each animal or within a short time interval, and cumulative probabilities were obtained from the fraction of $N = 44$ separations that fell within regular distance increments. The corresponding probabilities for the null hypothesis line of no dynamic interaction were determined
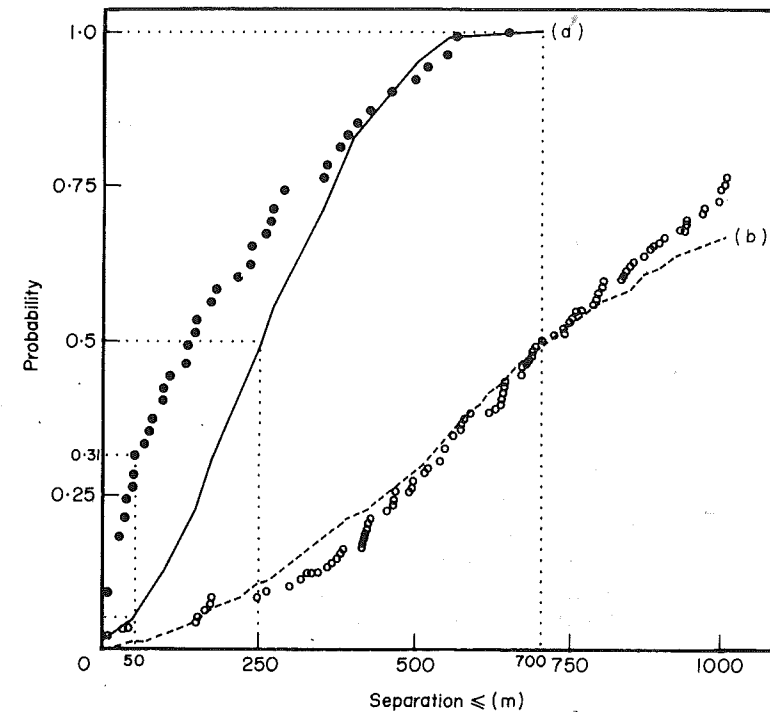
FIG. 4. Two examples of dynamic interaction between pairs of foxes during nightly activity, expressed in terms of the cumulative probability of separation distances. (a) The vixen f2 described in Fig. 3 and her mate m1. Attraction at up to 50 m is given by the excess of observed separations (filled circles) relative to the proportion expected under the null hypothesis of no dynamic interaction (continuous line). (b) A dog-fox (m4) and vixen (f5) occupying adjacent ranges (open circles and dashed line). Observed separations were calculated from fixes on each animal falling within the same 15-min time-block; consecutive fixes were taken at intervals of ≥ 10 min.

from separations given by all possible combinations of fixes on the two animals, no value being attached to the times and dates at which fixes were collected: for each fix on one animal, distances were calculated to all 44 fixes on the other animal, and probabilities were obtained from the fraction of $N^2 = 1936$ separations that fell within the distance increments. The cumulative expected probabilities therefore express static interaction in the absence of a dynamic element.

The cumulative probability of observed separations deviates from the null hypothesis line at separations up to the critical distance of 50 m, indicating positive dynamic interaction up to this distance apart. Of the total of 44 observed separations, 14 (31%) were at least this close. The null hypothesis line gives only 5%, or 97 of 1936 separations, up to 50 m apart (Table 1). Three tests can be performed on this information, all effectively equivalent. The expected number of paired separations ≤ 50 m is $44 \times 97/1936 = 2.20$, and a χ^2 test with correction for continuity gives $\chi_1^2 = 62.3$ ($P < 0.0001$). Alternatively, the probability of 14 or more events can be calculated from a Poisson distribution (Armitage & Berry, 1987) with mean of 2.20,

TABLE 1

The 2×2 contingency table of $N = 44$ paired and $N^2 - N = 1892$ unpaired distances separating vixen f2 and her mate m1, and those below and above the critical distance of 50 m for mutual awareness of the other's presence

Separation	≤ 50 m	> 50 m	Totals
Paired	14	30	44
Not paired	83	1809	1892
Totals	97	1839	1936

or a binomial distribution with an expected proportion of 5%; probabilities are virtually the same, except that the latter can be a one-tailed test.

In the absence of dynamic interaction, therefore, the probability of separations ≤ 50 m occurring at least as often as 14 times in a sample of 44 is small, and it is very unlikely that such a strong deviation from the expected proportion of 5% is caused by random variation. It should be noted that the significance tests depend on successive data points being independent, giving each animal the opportunity to travel to any other part of its range between successive fixes. In addition, they are valid only for fixed ranges. The significance of positive dynamic interaction could have been affected in the above example if the ranges of f2 and m1 had drifted substantially during the period they were tracked together; in this case the N^2 separations could be reduced to those pairs obtained within a shorter period of range stability.

Examples of negative dynamic interaction are less easy to find, as mutual repulsion is generally resolved by the foxes occupying non-overlapping home ranges. A pair suggesting negative dynamic interaction is illustrated in Fig. 4(b). A dog-fox (m4) and a vixen (f5) showed mutual attraction on the rare occasions they met, with 4 of 123 (3%) observed separations ≤ 50 m compared to an expected proportion of 1% ($\chi_1^2 = 4 \cdot 28$, $P = 0 \cdot 038$, binomial test: $P = 0 \cdot 036$). Positive dynamic interaction, however, does not exclude the possibility of agonistic encounters. When it occurs rarely, as here, it may result from one animal seeking out and chasing the other. This may have been the case for these two foxes, which tended to avoid approaching the critical distance: 6 of 123 (5%) observed separations were at 50–250 m compared to an expected proportion of 9%, although this difference may have been due to random variation ($\chi_1^2 = 2 \cdot 09$, $P = 0 \cdot 15$, binomial test: $P = 0 \cdot 15$).

The presence of dynamic interaction does not necessarily imply mutual awareness among the respective animals. At separations beyond the limit at which the two individuals can normally perceive each other, such as those indicating negative interaction in Fig. 4(b), dynamic interaction can result from co-ordinated time-tabling in their movements, which may or may not be intentional. A positive component is likely to arise particularly when the two animals have separate resting sites at which they regularly begin and end their cycles of activity. Where such

information is of little biological interest, it can be removed by considering only the middle portion of the active period.

As foxes in this study were active during the night for 6 hr 52 min on average, regardless of season (C. P. Doncaster, unpublished thesis), Fig. 4(a) indicates that the pair f2-m1 were 50 m apart or closer for an average of 128 min in each night's activity, or 107 min longer than was predicted under the null hypothesis of no dynamic interaction. Two further examples show how analysis of dynamic interaction can be useful to quantify temporal investment in proximity by related individuals. The vixen (f4) and her yearling son (m6) described in the last section were active and ≤ 50 m apart for 32 min longer on an average night than predicted on the basis of their static interaction alone (12 min; $r = +0 \cdot 22$). For a group range that was shared by an adult dog-fox (m3) and two breeding vixens (f3 and f8), an analysis of dynamic interaction on 574 fixed pairs clarified the relations between them. On an average night of 6 hr 52 min activity, one of the vixens (f8) stayed within 50 m of the dog for 64 min longer than was predicted from their static interaction alone (where Spearman's $r = +0 \cdot 62$), while the other vixen (f3) was within 50 m of both these two for 31 min longer than predicted (r with dog m3 $= +0 \cdot 44$ and r with vixen f8 $= +0 \cdot 43$).

In addition to the information on dynamic interaction, this method reveals two key features of the static interaction between concurrently tracked animals. The null hypothesis line in Fig. 4(a) shows that the maximum separation possible, given the lie of their home ranges, was 700 m, confirming a substantial overlap for ranges of

TABLE 2

During 9 hr of continuous activity by a pair of foxes (f2 and m1), the table shows the time-lags by which the vixen followed the dog (positive) or the dog followed the vixen (negative) to arrive at a minimum distance within 50 m of the other's tracks. Only time-lags up to 60 min are considered and data are pooled into time-blocks of 12 min each

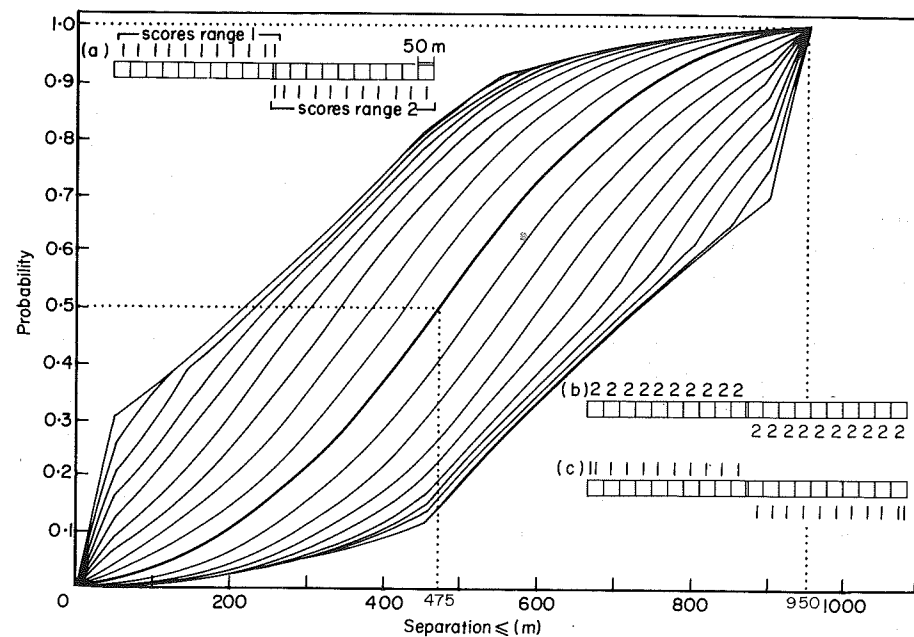| Clock time (hr:min)	Separation distances (m)		Time-lag (min)
	Instantaneous	Lagged	
21:12	85	25	−12
21:24	25	25	0
22:00	185	15	−60
00:00	375	25	+27
01:00	<5	<5	0
01:12	<5	<5	0
01:24	<5	<5	0
03:24	335	25	−45
04:36	220	15	+30
04:48	200	35	+21
05:00	185	45	+33
05:36	5	5	0

FIG. 5. Relationship of concordance in the utilization of two home ranges to the cumulative distribution of N^2 separations under the null hypothesis of no dynamic interaction. The utilizations of two abutting home ranges are given by the numbers of fixes, out of 20 on each animal, in 50×50 m grid-cells arranged along a one-dimensional axis (insets). Each of the 19 cumulative distributions of separation distances was calculated in 50 m increments from the complete set of 400 possible distances between the two animals. Inset (a) shows two home range utilizations skewed towards each other, giving the most concave distribution of N^2 separations. For a step-wise redistribution of fixes away from the congruent border of each range, the distribution of N^2 separations becomes increasingly sinusoidal, towards the middle line (emphasized) corresponding to the unskewed home range utilizations shown in inset (b). For a step-wise increase in utilization of the furthest extremities of each range, the distribution of N^2 separations becomes increasingly convex, with inset (c) giving the most convex distribution.

35–40 ha (circular diameters of 670–710 m). Moreover, the broadly concave shape of the line between minimum and maximum separations reveals that 50% of all combinations of fix pairs were ≤ 250 m apart, or considerably less than half the maximum separation. In other words, the two utilization distributions were skewed towards each other, confirming the high degree of concordance in utilization of shared areas that was suggested by the strong positive value of Spearman's r.

The relationship of concordance in the utilizations of two home ranges to the cumulative distribution of N^2 separations (under the null hypothesis of no dynamic interaction) is determined in Fig. 5 for two abutting, but non-overlapping, ranges. The two hypothetical home ranges undergo step-wise changes between centres of utilization that are skewed towards each other (giving concave distributions of cumulative probability), not skewed (sinusoidal), and skewed apart (convex). The flattened aspect of concavity and convexity was produced by numerous repetitions of fix pairs, which will occur when animals return repeatedly to one or more centres

of activity. These cumulative distributions are independent of both the scale of measurement and sample size, although resolution decreases with smaller samples.

Finally, the relative movements of two animals should be considered as dependent if one animal follows in the tracks of another through the shared parts of their territories. Table 2 illustrates this point for the fox pair f2–m1 described in Fig. 4(a). During 9 hr in a single night of activity, they were ≤ 50 m apart on five occasions, or an estimated 60 min, but they were within 50 m of each other's tracks for 144 min. Dependency such as this can be allowed for in the analysis of dynamic interaction by calculating observed minimum separations within relatively wide time-blocks.

A computer program is available from the author on request, for calculating non-parametric measures of dynamic interaction.

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