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30

Quantity versus quality: programmed collection and analysis of radio-tracking data

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In a review of publications from the first decade of radio-tagging, Lance & Watson (1980) concluded that the technique 'seldom exploited its full potential... due less to drawbacks in the equipment than to how the technique has tended to be used'. A decade later, many studies still fail to achieve their full potential because of problems with the collection and analysis of data, especially location data (Harris *et al.* 1990). A particular problem is the choice of appropriate methods to represent an animal's 'home range', for which there are at least six fundamentally different approaches (Macdonald, *et al.* 1980, Voight & Tinline 1980, Kenward 1987, Worton 1987, White & Garrott 1990, Harris *et al.* 1990). There are also many different ways of using home ranges and other location data to investigate sociality and habitat use. How can a beginner cope with this plethora of analysis possibilities, many of which involve extensive computation?

The wrong strategy is to delay a decision until the end of a study, after the data have been collected. This can at best result in the collection of unnecessary data, and at worst produce inadequate material. A better approach is to start analysis at an early stage, after collection of some representative material in a pilot study, so that subsequent data collection can be modified to give maximum efficiency during the rest of the study (Harris *et al.* 1990). Computer software is now available to aid both preliminary and final analyses. This chapter examines what is needed in an analysis system, and concludes by noting what software was available by 1991 and what may be expected in the future.

REQUIREMENTS OF AN ANALYSIS SYSTEM

Data entry and display

Analysis systems should acquire data with minimum effort. At present they need mainly to handle location data copied from field notebooks, but should also accept files imported from databases, from other popular packages and from automatic recording systems. Lightweight computers with long battery lives make it increasingly practical to key bearings to map displays in the field, with immediate fix accuracy checks (Salz & Alkon 1985, Nams 1989). Much effort is saved if map and habitat data can be input from a digitizer tablet, by tracing round complex habitat shapes instead of keying map coordinates. There should also be facilities for screen display and editing of the data, and for eventual plotting of analysis results, ideally by export of vector files to graphics packages for enhancement and laser printing.

Movement analysis

Location data are usually collected either by continuous monitoring, where each movement of an animal is noted (e.g. each flight made by a bird), or by interval sampling. The data then provide, respectively, either a full record of the distances, headings, times and speeds between successive locations, or a means to produce an index of movement during a particular period. For instance, a 'day-distance' index of activity is estimated by the total distance between just four or five fixes per day. Much effort is saved by an analysis system which can calculate and combine these interfix values.

Calculation of speeds between locations requires that a time be recorded with each fix, and it may be desirable to record other data which qualify each record, such as a behaviour code, height above ground, habitat or physiological measurement (e.g. heart rate, temperature). An analysis system should therefore be able to record a number of parameters with each set of location coordinates. If subsequent analyses permit the selection of fixes with particular qualifiers, they can, for example, separate movements made by day from those at night, or foraging in trees from that on the ground.

The analysis software should be able to produce a number of summary statistics for each monitoring session with a particular animal (e.g. average or median speeds or flight distances) as well as proportions of fixes in particular categories. In this way, the collection of fixes from each separate session provides a single record for comparisons within and between individuals, which avoids the awkward question of whether consecutive records from the same animal are statistically independent. The number of records can be maximized by keeping sessions as short as gives a reliable representation of a particular behaviour (i.e. longer sessions for rarer events), noting the need to sample each animal at different times of day.

Continuous monitoring is sometimes the only practical approach for collecting behavioural data, or to track animals at all if terrain makes them difficult to reach. However, temporal autocorrelation makes consecutive fixes redundant in analyses of home range, sociality and habitat use, and breaches assumptions in parametric range analysis models. In the absence of an automatic location system, it is often most efficient to track animals at intervals which are too long for fixes to be linked by rates of animal movement, using each interval to sample many different animals before the first individual is located again. Even so, a few days of continuous monitoring during a pilot study (or 'trial run' *sensu* Harris *et al.* 1990) will enable an autocorrelation analysis (Swihart & Slade 1985) to indicate a sampling interval at which there is little temporal correlation between consecutive fixes. This should minimize data redundancy, but fixes will still lack statistical independence if an animal's experience leads it to favour particular foraging areas, travel routes and dens. Any tests which assume that fixes are independent should be used with great caution.

Home range estimation

What is the point of collecting home range data? There can be value in recording an average home range *size* of secretive or very mobile species, for example when planning the dimensions of nature reserves. However, many studies are also interested in home range *shape*, for instance to define the habitat available to an animal, or to identify other individuals with which it may interact. Home range *structure* is another consideration, for example to define whether dens coincide with foraging centres, and whether there are one or many such centres, or to separate excursive areas which may overlap between individuals, from cores which may be defended. Provided that fixes are a representative sample of animal locations along a time-base, the area with the densest fixes is also the area where the animal spent most of its time. Even if the only requirement is to measure an average home range size, it is well worth collecting data which are

suitable for analysis of range shape and structure too, if there is no extra cost. Home range analyses should therefore be able to define not only size, but also shape and structure.

In more sophisticated studies, home range parameters, habitat use and sociality may be compared under different conditions, such as between different sexes at different reproductive states in different areas. This requires larger samples of animals than for merely recording an average range size. Even more home range records may be required if experiments (e.g. artificial feeding) are designed to test hypotheses resulting from initial observations. In this case the analysis system should be able to handle large numbers of animals with minimum effort. Moreover, unless an automatic location system collects the fixes, as few as possible should be needed for each home range record, so that time in the field can be devoted to sampling as many animals as possible. Table 1 indicates how the six main home range analysis types meet this and other study requirements.

Table 1. How different home range analysis methods meet a number of study requirements

| | Grid cells | Normal ellipsoids | Concave polygons | Convex polygons | Contour methods | Cluster analysis |
|--|------------|-------------------|------------------|-----------------|-----------------|------------------|
| Home range outlines conform well to all recorded fixes | Yes | No | Yes | Yes | No | Yes |
| Home range outlines conform well to multinuclear cores | Yes | No | No | No | Yes | Yes |
| A single home range centre is estimated | No | Yes | No | Yes | Yes | No |
| Home range structure statistics (patchiness or fix dispersion) | Yes | Yes | No | No | Yes | Yes |
| Home range size stabilizes with fewer than 100 fixes | No | Yes | ? | Yes | Yes | Yes |

If analysis is to define size, shape and structure of a home range from as few fixes as possible, the first three methods in Table 1 are less suitable than the others. Although the grid cell approach (Siniff & Tester 1965, Voight & Tinline 1980) meets most criteria, it typically requires more than 150 fixes, and sometimes 200-300, to obtain a record of home range size which increases little if more fixes are added (e.g. Doncaster & Macdonald 1991). Areas estimated with the last three methods typically reach asymptotes with 25-50 fixes (Kenward 1987, Jaremovic & Croft 1987, Harris *et al.* 1990). With mobile tracking, on foot or in vehicles, collecting fixes requires at least three times as much effort for grid cell analyses as for the other techniques. Although this presents less of a problem with automatic location systems, fixed systems often cover too small an area to meet the aim of sampling large numbers of animals,

The earliest home range models (for trap data) assumed that animal locations conformed to circular normal or bivariate normal distributions, and could therefore be represented by circles or ellipses with axes set to include a chosen percentage of the distribution (Calhoun & Casby 1958, Harrison 1958, Jennrich & Turner 1969, Koepl *et al.* 1975). Although areas of these ellipsoidal home range models can reach asymptotes with only 25-35 fixes (Jaremovic & Croft 1987), animal locations tend not to be normally distributed (White & Garrott 1990). For this reason, and because animals often have more than one activity nucleus, home range outlines modelled as ellipsoids tend to conform poorly to the fixes (Macdonald *et al.* 1980), which is a serious disadvantage if home range outlines are used to assess either habitat use or the degree of overlap between neighbouring individuals. Lack of readily available software has prevented evaluation of the multinuclear parametric model from Don & Rennolls (1983), but it too is unsuitable for strongly skewed fix distributions. There seem to be no studies of the number of fixes required for concave (minimum area) polygons, based on the sorted polygon or restricted edge-length

techniques (Voight & Tinline 1980, Clutton-Brock *et al.* 1982), but their lack of core outlines or structure statistics are a disadvantage compared with the other approaches.

Convex polygons, including versions which estimate a core by excluding fixes furthest from an activity centre (peeled polygons), are the least satisfactory of the three remaining analysis techniques. However, minimum convex polygons which contain all the fixes provide comparability with previous studies, because they have been widely used (Harris *et al.* 1990). They also define a limit to the area which may be visited by an animal, and thus of the habitat types and neighbours it can encounter. In contrast, isolines (contours) which include all fixes often 'balloon' into areas not visited by the animal (Spencer & Barrett 1984), and the outermost isolines from Fourier analysis (Anderson 1982) may even be discontinuous (Jaremovic & Croft 1987). Peeled polygons provide a passable single territory outline for studying overlaps of home ranges which are not strongly multinuclear, but are not suitable for multinuclear fix distributions, and also conform poorly to fixes in crescent-shaped home ranges (White & Garrott 1990). The mathematics of contouring techniques aim to define fix density distributions (Neft 1966, Worton 1989), and provide an ideal approach for identifying an *activity centre*, where fix density is maximum. This centre is unique if density is estimated at each fix (Spencer & Barrett 1984), and tends to be the same if the inverse reciprocal function (Dixon & Chapman 1980) or other density estimators (Worton 1989) are used. Spencer & Barrett (1984) also provide indices of fix dispersion (skew, kurtosis) about the activity centre, and of spread among all the fixes. However, contouring depends on density estimation at intersections of an arbitrary grid imposed on the fixes, so that isoline positions are influenced by size and origin of the grid. Although grid dependence is minimized by avoiding inverse reciprocal functions (Worton 1989), density estimation is a smoothing process, so that even the core isolines do not always conform well to the fixes.

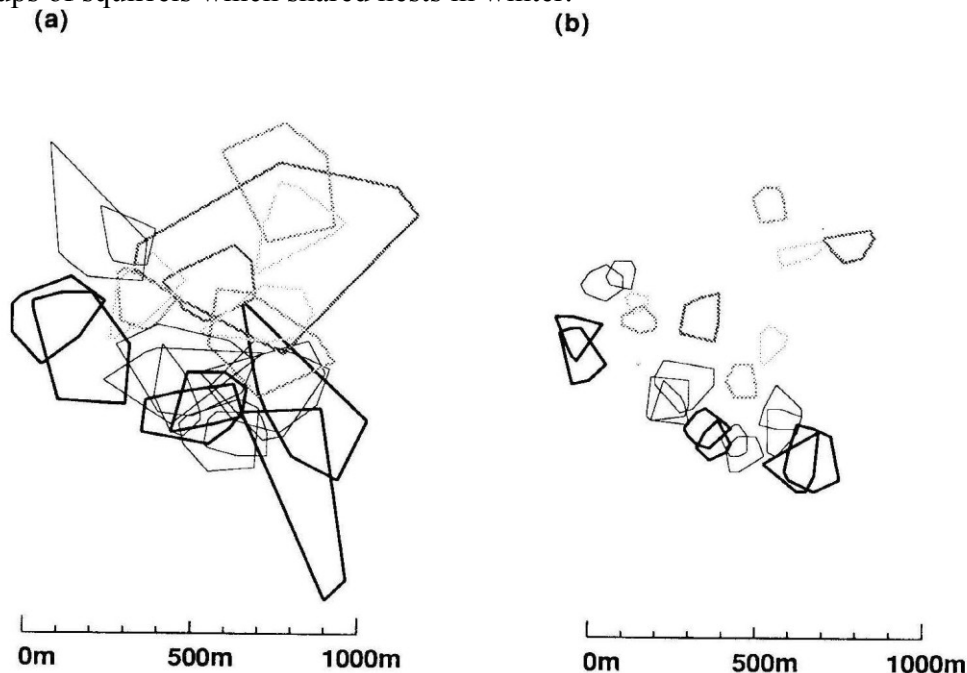
The maths of hierarchical incremental cluster analysis are aimed at forming groups and separating outliers (Anderberg 1973, Everett 1980). The approach in home range analysis, of starting by identifying the densest cluster, and then either adding fixes to it or starting a new cluster depending on distances between neighbouring fixes (Kenward 1987, 1990), is therefore very suitable for identifying much-used patches. A convex polygon gives a tight-fitting outline round each cluster without its shape being influenced either by other fixes or by an arbitrary grid. The only way to vary the outlines, for a given percentage of fixes, is to change the analysis algorithm (e.g. the minimum number of fixes per cluster), which is equivalent to changing the density-generating function in a contour analysis. Although cluster analysis provides no unique activity centre, exclusion of outliers by the hierarchical incremental approach is particularly good for distinguishing range cores from excursive areas, and provides indices of patchiness and fix dispersion (diversity of fix numbers and density) as well as the number of activity nuclei for each core (Kenward 1990).

Multi-animal routines

Displays

Fig. 1 illustrates another requirement of an analysis system: that it should be able to combine data from numbers of separate home ranges. Plotting the data together can alert the researcher to effects which were not noticeable during the hustle of fieldwork. In this case it showed that although grey squirrels home ranges overlapped extensively if all the fixes were included, core ranges were group territories.

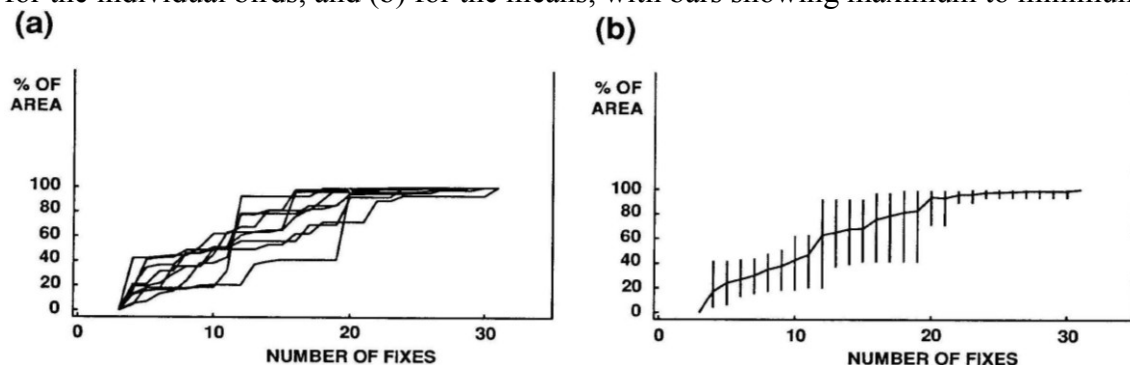
Fig. 1. Home ranges of 23 grey squirrels in autumn 1982, shown (a) as a minimum convex polygon round all the fixes and (b) as 60% cores obtained by peeling towards the harmonic mean fix. Examining the multirange file on screen showed that although outer ranges overlapped extensively, cores were either separate (stippled lines) or remained overlapping (solid lines) for small groups of squirrels which shared nests in winter.



Developing a data collection protocol

Combining records from many animals (or from the same animal at different times) is useful not only for displaying location data, but also for plotting analysis results. Fig. 2 shows that minimum polygon ranges of common buzzards (*Buteo buteo*) increased little in size after the first 20 fixes were added (three per day). Software which automates incremental analyses and provides multirange plots is a great help for deciding how many fixes are needed for a standard range record, because there is no point in collecting 150 fixes for each home range if 30 suffice. Appropriate software can make it easy to decide just how few fixes are needed, and thus not only how many individuals can be tracked at one time, but also how frequently consecutive ranges can be recorded for the same individual, for instance to investigate trends during a breeding season. Such software should if possible be obtained before starting fieldwork because, as noted by Harris *et al.* (1990), 'it is important to test the radio-tracking regime before launching into the detailed study'.

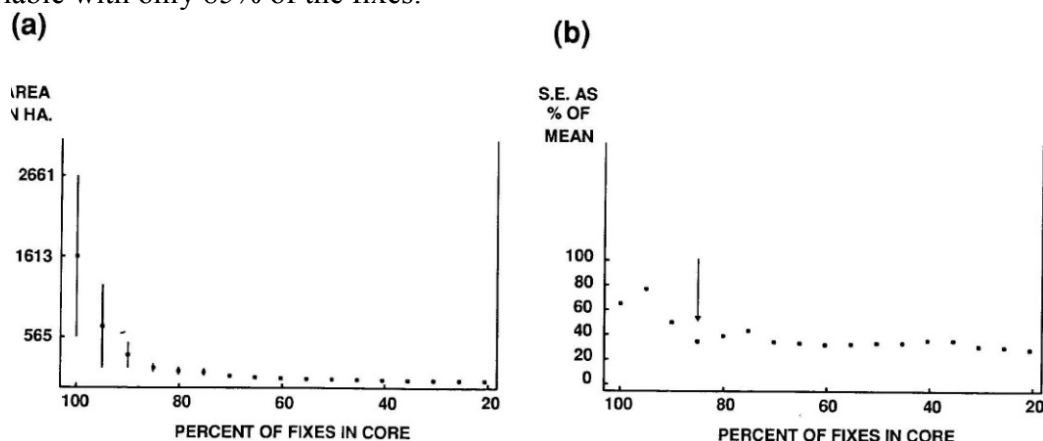
Fig. 2. Convex polygons round all the fixes increased little in size after the first 20 fixes were collected for 11 buzzards in October 1990. RANGES *N* plotted the incremental area analyses (a) for the individual birds, and (b) for the means, with bars showing maximum to minimum values.



If there is no time for a pilot study, however, it is worth noting that 30-35 fixes taken over 10-15 days have provided similar sampling saturation for a variety of mammal and bird species, including badger (*Meles meles*), grey squirrel *Sciurus carolinensis*, goshawk (*Accipiter gentilis*), pheasant (*Phasianus colchicus*) and red squirrel (*S. vulgaris*) (Holm 1990, Kenward 1982 and unpublished, Parish & Kruuk 1980, P. A. Robertson, pers. comm.). Recording 40 fixes, for possible subsequent reduction to a 30- fix range after incremental analysis, is a reasonable strategy for short studies using polygon techniques, although around 60 fixes may be needed to obtain areal asymptotes with harmonic mean contouring (Jaremovic & Croft 1987, Harris *et al.* 1990). If there is no sampling standard, summary statistics will have different uncertainty estimates, which can cause problems in subsequent analyses (Batschelet 1981).

Multirange displays can also be used to define range cores. In single ranges, cores may be identified by plotting a core area as a function of number (or expected number) of fixes in the core, and then inspecting for a discontinuity in the slope which occurs if area increases sharply as outlying fixes are added (Clutton-Brock *et al.* 1982, Harris *et al.* 1990). A test for divergence from an expected distribution can be used to identify the core objectively, but care must be taken with inspections or tests, because there are often ranges which are small and lack slope discontinuities, suggesting that they lack excursive areas and are all core. If data are available for many home ranges, there is also the question of whether to use the average core size, the minimum core size, or perhaps to use the specific core value of each separate range (Holm 1990). The most reasonable approach may be to use the maximum value which includes 95% of the ranges. Alternatively, if cores of similar size occur in many ranges at a similar percentage of fixes, whereas excursive areas are more variable, then variance in range size tends to drop at that point and can be detected as a minimum in a plot of variance ratios (Fig. 3). Whereas plots of slope discontinuities or variance ratios tend to indicate cores at 50-60% for essentially mononuclear ranges (Clutton-Brock *et al.* 1982, Kenward 1985, Harris *et al.* 1990), cluster analysis tends to produce sharp discontinuities and cores at 85-90% for buzzards, grey squirrels, goshawks and red squirrels (Holm 1990, Kenward unpublished, Fig. 3).

Fig. 3. Multirange utilization plots, of area within cluster polygons against proportion of fixes, for 27 female goshawks tracked in a Swedish study area during winter. Plots of mean area with 95% confidence limits (a) show that range size was large and highly variable when all fixes were included, but a minimum in the coefficient of variation (b) showed that core areas became much less variable with only 85% of the fixes.



Long analysis runs

Combining records of individual ranges into one long file is also convenient for prolonged analyses, especially when much calculation is needed to process each record. Much 'number-crunching' is required in clustering and contouring analyses of home ranges, and a multi-animal

file may need to be left to process overnight on slow computers. RANGES IV runs on Acorn RISC machines, which operate at 4-15 million instructions per second (MIPS) for as little as £600, as well as on MS-DOS systems, which only approach 5 MIPS with relatively expensive 486 computers. It is therefore worth considering an Acorn machine just for running location analyses if there are data from many animals, let alone for the speed advantages which these multitasking machines offer in diagram and document processing.

Multirange files are of particular value for quantitative examination of how well different home range analyses answer a biological question, which is the ultimate test of their value as a research tool. Table 2 shows how three analyses compare for producing correlations between the mean grey squirrel range size each year and the density of acorns in their woods. Each column represents data from one analysis run of a file containing 138 home ranges, with at least four 10-day records from different animals in each of 11 years. The longest analyses, harmonic mean contouring, took about 130 min per run of the file on an Acorn R410 with ARM3 processor. The least significant results were obtained with RAc peeled polygons (peeled by excluding fixes furthest from the recalculated arithmetic mean activity centre), although the minimum convex polygon which contained all the fixes (the 100% RAc polygon) correlated slightly better than the 100% harmonic mean isoline. The most significant results were for the 85-90% cores from cluster analysis.

Interaction routines

Combining records from different sources is a convenience for visual interpretation, for analyses to define sample sizes and for lengthy analyses. However, for the study of interactions between animals, or between animals and habitats, combining records is a necessity.

Table 2 . Correlation coefficients for the relationship between acorn density under oak canopy and the area of grey squirrel home range estimates in autumn at 11 sites.

| % of fixes | Peeled polygons (RAc-based) | Contouring (harmonic mean) | Cluster analysis |
|------------|--------------------------------|-------------------------------|---------------------|
| 100 | -0.53 | -0.48 | -0.61 |
| 95 | -0.53 | -0.51 | -0.55 |
| 90 | -0.58 | -0.59 | -0.76** |
| 85 | -0.55 | -0.67* | -0.79** |
| 80 | -0.60 | -0.61 * | -0.71*† |
| 75 | -0.61* | -0.63* | -0.65* |
| 70 | -0.61* | -0.62* | -0.65* |
| 65 | -0.63* | -0.66* | -0.71*† |
| 60 | -0.62* | -0.66* | -0.69*† |
| 55 | -0.66* | -0.65* | -0.64* |
| 50 | -0.64* | -0.52 | -0.60 |

Significance levels (with 9 d.f.) are * $p < 0.05$, *† $p < 0.02$ and ** $p < 0.01$.

Sociality

Macdonald *et al.* (1980) noted that relationships between movements of different animals could be investigated as static interactions or dynamic interactions. Overlaps between home range outlines are static interactions, with each home range measured as a record along a time axis, whereas dynamic interactions are measured across a time axis, being a function of distances between animals at the same point in time. Fig. 1 provides an example of static interactions, and data from it could be used to show that squirrels whose 60% core ranges overlapped showed more interaction than expected ($p < 0.02$). The principle was to compare the observed overlap distribution with an expected distribution, which was generated by randomizing core placement

100 times within the fixed envelopes of the 100% polygon outlines. A median test was used to compare the two distributions.

Since static interactions can conceal the fact that, although ranges overlapped, the animals avoided being in the same place at the same time, dynamic interactions are the more subtle measure of animal relationships. This is illustrated by analysing data from goshawk broods in the post-fledging period. The information from measuring static interaction is that range outlines of siblings round the same nest show almost complete overlap. However, each range represented a collection of n pairs of fix coordinates $(x_{1j}, y_{1j}, x_{2j}, y_{2j})$ for each pair of siblings. This gave an observed mean distance between siblings

$$D_O = \frac{1}{n} \sum_{j=1}^n \sqrt{(x_{1j} - x_{2j})^2 + (y_{1j} - y_{2j})^2}$$

which could be compared with the mean distance:

$$D_E = \frac{1}{n^2} \sum_{j=1}^n \sum_{k=1}^n \sqrt{(x_{1j} - x_{2k})^2 + (y_{1j} - y_{2k})^2}$$

obtained by considering all possible pairs of locations at which the young hawks were detected. After calculating observed and expected distances between siblings for a number of nests, a sign test was used across all the pairs of sibs to test whether D_O was significantly smaller than D_E , indicating that they tended to aggregate, or if D_O was larger than D_E , indicating that they avoided each other. Fixes with one bird at the nest were omitted, because the nest was a known attraction point, but there was still a tendency for young hawks to aggregate, whether they were of the same or different sexes (Kenward, Marcstrom & Karlbom, unpublished). If greater sensitivity were justified by the data set, and a symmetrical index were prepared from D_O and D_E (see below), a Wilcoxon matched-pair test could have replaced the sign test. Note that these tests use only one pair of values (D_O and D_E) from each pair of birds, with no assumption that observations within D_O are statistically independent. Nor was it necessary to assume that fix distributions conformed to an elliptical or Orstein-Uhlenbeck model (Dunn 1979, Macdonald *et al.* 1980).

For analysing sociality, software should be able to generate matrices of overlaps for large numbers of range outlines, and time will be saved if there are also routines to extract overlap distributions from these matrices. If an interval-sampling protocol aims at taking fixes from many animals in rapid succession, such that animals cannot move far before their neighbours are located too, then the data will also be suitable for dynamic interaction analysis routines when these become more widely available.

Habitat analyses

In habitat analyses it is necessary not only to determine what is available (A) in an area, but also what is used (U) by each animal, where U is defined as (observations in habitat i)/(observations in all habitats), and A is defined as (area of habitat i)/(area of all habitats). This requires analysis routines which can estimate habitat contents of maps as a measure of habitat available throughout an area, as well as estimating the habitat content within home range outlines and the habitat at fixes (if this was not recorded in the field). It is then possible (1) to compare habitat within home range outlines with that available on the map, to see whether animals settled in particular parts of the countryside, (2) to compare habitat at fixes with that in home range outlines, to see whether animals preferred particular parts of their ranges, and (3) to compare habitat at certain fixes with that at all fixes, to see whether animals preferred to perform certain activities in particular habitats. It may also be desirable for the analysis routines to estimate numbers of point features, such as individual trees or scent marks, within home range or core

outlines, and to estimate habitat proportions within circles of chosen radius from single fixes or centres of activity.

A robust way of testing analysis results, avoiding assumptions of fix independence which typically underpin the use of χ^2 tests, is to base non-parametric tests on a selectivity index for each animal in each habitat. A test for extreme reactions (e.g. Moses 1952) can then be used to see whether there is evidence of divergent strategies between animals, with some favouring habitat *i* whereas others do not, before applying rankbased tests for differences in the use of habitats and to show preference or avoidance of individual habitats. It is important to use a symmetrical selectivity index, such as Ivlev's index, $(U - A)/(U + A)$, so that results are not biased towards preference or avoidance. The procedure is illustrated in Table 3 with data from seven Swedish goshawks tracked during the winter.

Table 3. Habitat use, availability and Ivlev's index for goshawks in a Swedish study area

| | JM4 | AM6 | AM8 | AM9 | JFIO | AFII | AF14 | Availability (A) |
|------------------------|------|------|------|------|------|------|------|------------------|
| <i>Fixes in</i> | | | | | | | | |
| Open country | 58 | 32 | 38 | 14 | 22 | 4 | 5 | |
| Woodland edge | 203 | 92 | 162 | 139 | 70 | 70 | 81 | |
| Deep woodland | 4 | 2 | 3 | 13 | 1 | 1 | 12 | |
| <i>Utilization (U)</i> | | | | | | | | |
| Open country | 0.22 | 0.25 | 0.19 | 0.08 | 0.24 | 0.06 | 0.05 | 0.46 |
| Woodland edge | 0.76 | 0.73 | 0.80 | 0.84 | 0.75 | 0.93 | 0.83 | 0.26 |
| Deep woodland | 0.02 | 0.02 | 0.01 | 0.08 | 0.01 | 0.01 | 0.12 | 0.28 |
| <i>(U-A)/(U + A)</i> | | | | | | | | |
| Open country | -0.4 | -0.3 | -0.4 | -0.7 | -0.3 | -0.8 | -0.8 | |
| Woodland edge | +0.5 | +0.5 | +0.5 | +0.5 | +0.5 | +0.6 | +0.5 | |
| Deep woodland | -0.9 | -0.9 | -0.9 | -0.6 | -0.9 | -0.9 | -0.4 | |

In this case there was no sign of a divergence in habitat preferences, although this might have arisen if there had been tracking during breeding, in which case some adults would probably have shown a strong preference for nest areas deep in the woods. As it was, woodland within 200 m of an edge ranked most preferred by each bird, and open country ranked less preferred than deep woodland for only two of them (AM9, AF15). Comparing selectivity scores between pairs of habits, woodland edge is preferred significantly more than deep woodland or open country (Wilcoxon signed-rank matched-pair tests, two-tailed, $p = 0.018$ in each case), but there was no significant tendency to avoid deep woodland more than open country in winter ($p = 0.107$). A Friedman test also shows highly significant differences in preference between habitats ($p = 0.0012$), but lack of independence between habitats (whose proportions add to 1) breach the assumption in this test that ranked values are independent. Nevertheless, comparable results are obtained by compositional analysis, which avoids this assumption (Aebischer *et al.* pers. comm.; Chapter 34 this volume).

CONCLUSIONS

If the aim is to produce quantitative results, by minimizing numbers of fixes per record and thus maximizing the numbers of movement statistic or home range records, it is almost essential to have analysis software available at the start of the study. Processing to assess how many fixes are needed per record, and at what intervals, can then start within the first few days of a pilot study,

leading to efficient fieldwork and adequate samples of animals in subsequent stages. In the concluding analysis, the software will need to handle data from large numbers of animals, to produce a single record from each collection of fixes for use in robust statistical tests.

Before the advent of microcomputers, it was not easy to analyse data from large numbers of radio-tagged animals. Home range areas were estimated from polygons round all the fixes, or by counting grid cells, but few field-workers were prepared to calculate circle and ellipse models. By the early 1980s, biologists were not only writing mainframe computer programs for more sophisticated analyses, but also sometimes making them available for general use (Dunn 1978, Kroll & Johnson 1980, Samuel *et al.* 1985). Nowadays, most biologists either own or have access to microcomputers, and programs for many of the tasks reviewed here are readily available on disc. Thus LOCATE II (addresses in Appendix 1) plots bearings and error ellipses on habitat maps for fix filing and editing, TELEM-PC (Lewis & Haithcoat 1986) and HOME RANGE (Samuel *et al.* 1985) estimate outer polygons, ellipses and harmonic mean contours, MCPAAL (Stuwe & Blohowiak 1985) provides these plus Fourier series contouring, and HOMER (White & Garrott 1990) lacks contouring but includes grid cell counts. There are also listings for peeling polygons, cluster analysis and harmonic mean contouring in Kenward (1987). White and Garrott (1990) provide SAS listings for polygons and ellipses, stressing the need for analysis systems which can provide many operations on each data set. The SEAS suite from John Cary also provides useful routines for handling and displaying fix and map data, with estimation of polygons, ellipses and harmonic mean contouring. However, although individual fix files can be queued in SEAS, processing has on the whole remained limited to one set of fixes at a time. By 1991, RANGES IV was the only system to use multirange files in analyses of movements, home ranges (outer polygons, peeled polygons, clustering, harmonic mean and kernel contouring) sociality and habitat use, although this suite still requires the addition of routines for field entry of data, for autocorrelation analyses and for assessment of dynamic interactions.

Looking ahead, analysis systems can be expected to contain all the facilities outlined in this review, to run on all common computer systems, to interact with other GIS systems (e.g. to accept data mapped by satellites), and to accept data from automated systems as easily as from field-workers in vehicles or on foot. Improved access to flexible software systems will lead to further conclusions about which analyses and tests are most appropriate in different situations, and including this knowledge as an expert system will produce software to automate analyses and the testing of results. Radio-tracking will then be a truly mature technology.

Looking back, lack of processing facilities must take quite a large share of the blame for complaints that radio-tracking tended to produce essentially qualitative results from small handfuls of animals. Nevertheless, the time is fast approaching when lack of suitable software will no longer provide an excuse for radio-tracking which fails to produce quantitative results.

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APPENDIX

Addresses of suppliers of software for analysing location data from radio-tracking.

HOME RANGE: Fish and Wildlife Department, University of Idaho, Moscow, ID 83843, USA.

HOMER: Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA.

LOCATE II: Pacer, PO Box 1767, Truro, Nova Scotia, Canada B2N 5Z5. MCPAAL: Smithsonian Institution, Front Royal, VA 22630, USA.

RANGES IV: Chitech, Institute of Terrestrial Ecology, Purzebrook, Wareham BH20 5AS, UK.

SEAS/DC80: Department of Wildlife Ecology, University of Wisconsin, Madison, WI 53706, USA.

TELEM PC: Department of Fisheries and Wildlife Science, Virginia Polytechnic. Blacksburg, VA 24061, USA.