Home range analysis using radio-tracking data ? A review of problems and techniques particularly as applied to the study of mammals

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Home-range analysis using radio-tracking data—a review of problems and techniques particularly as applied to the study of mammals

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ABSTRACT

Ninety-three papers on home-range analysis using radio-tracking data were reviewed; these papers were found in a literature search of 18 of the major journals likely to include such papers, published in the 5-year period to the end of 1988. The review showed that even 25 years after the first radio-tracking studies, in the majority of papers there was still insufficient attention given to accurate and sufficient data collection, and to using appropriate and sophisticated analytical techniques to assess home-range size and configuration. This paper is designed to help people undertaking a radio-tracking study to avoid some of the most common pitfalls. It is based on some of the problems we have experienced studying several species of larger mammals. We use our collective experience to produce a guide on how to plan a radio-tracking study, to highlight some of the potential problems in designing the study and collecting the data, and to identify some of the difficulties that may be encountered during the analytical stages. The advantages and disadvantages of the most frequently used methods of home-range analysis are discussed and methods for determining the minimum number of radio-fixes and techniques for adjusting inadequate sample sizes are described, as are the problems that may be caused by autocorrelated data.

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INTRODUCTION

The concept of a home range has been defined and refined by several authors (Burt, 1943; Mohr, 1947; Jewell, 1966; Baker, 1978). A home range consists of a more or less restricted area within which an animal moves when performing its normal activities. Stating the time period over which a home range is measured, and the status (e.g. sex, age or class) of the individuals involved, should be fundamental to the definition of a home range (Morris, 1988). Measuring an animal's home-range size, shape and pattern of utilization is important for most ecological and/or behavioural studies, particularly those concerned with, for example, population density, foraging behaviour, habitat selection and distribution of resources, spacing of individuals and their interactions.

A variety of analytical techniques exist to evaluate home-range size and to determine patterns of home-range utilization, based on sampling an animal's position along a time-base. This brings a new fundamental issue in to the concept of a quantified home range; that one is sampling from a statistical population of fixes when measuring a home range. The resultant home-range analysis should bear this in mind.

Radio-tracking is a technique that is used frequently to provide data on location, movement and behaviour of a species, from which home-range size and patterns of utilization can be determined. Following the introduction of the technique in the early 1960s (e.g. Cochran & Lord, 1963), there have been many papers on home-range analysis from radio-tracking data. Amlaner & Macdonald (1980) and Cheeseman & Mitson (1982) have both produced review volumes on the subject, and Kenward (1987) has provided a comprehensive account on how to radio-track animals. Because of its wide application, radio-tracking was described by Macdonald & Amlaner (1981) as a technique that 'transformed field studies, and promises to provide answers to a host of biological questions', although Lance & Watson (1980) had concluded that radio-tracking was seldom exploited to its full potential in ecological research. As we will show, this conclusion still appears to be valid.

In this paper we review some of the recent literature on home-range analysis using radio-tracking data, particularly to see how the data were collected and subsequently analysed. We then use the results of this review and our own work on Foxes *Vulpes vulpes*, Badgers *Meles meles*, Muntjac *Muntiacus reevesi*, Roe Deer *Capreolus capreolus* and Brown Hares *Lepus europaeus* (Harris, 1980, 1982; Cheeseman *et al.*, 1988; Cresswell & Harris, 1988; Forde, 1989; Woollard & Harris, 1990) as the basis for the rest of the paper. Firstly, we deal with the collection of radio-tracking data, since the method of collection affects its subsequent use. We then sumarize how such data may be used in the various methods of home-range analysis. Finally, we discuss some of the problems that are likely to be encountered during the analytical stages of a radio-tracking study.

This review cannot be fully comprehensive and discuss all the problems associated with radio-tracking and home-range analysis; rather, it seeks to highlight the most important points and to provide a source of references for further details. Radio-tracking data may be collected in order to answer a variety of questions in addition to those relating to home-range analysis (e.g. studying activity patterns, foraging behaviour and habitat selection, dispersal movements, etc.). However, these uses are largely beyond the scope of this paper, although the section on data collection will still be relevant. There are also methods of locational data collection other than radio-tracking which can be used for home-range analysis; these alternative techniques are also beyond the scope of this review. Nevertheless, the points concerning the methods of home-range analysis, and their associated problems, are still relevant to studies using methods

Table 1
Journals from January 1984 to December 1988 covered in the literature review

General animal ecology journals	Volumes
**Australian Journal of Ecology*	9–13
Ecological Monographs	54–58
Ecology	65–69
Journal of Animal Ecology	53–57
Journal of Applied Ecology	21–25
Journal of Wildlife Management	48–52
Oecologia	61–77
Oikos	42–53
General zoological journals	
**American Naturalist*	123–132
**American Zoologist*	24–28
Canadian Journal of Zoology	62–66
Journal of Zoology	202–216
Mammal journals	
Journal of Mammalogy	65–69
Mammal Review	14–18
Bird journals	
The Auk	101–105
Condor	86–90
Ornis Scandinavica	15–19
Reptile journals	
**Journal of Herpetology*	18–22

*No relevant references found in these journals.

other than radio-tracking. Finally, although we concentrate on radio-tracking studies on mammals, the conclusions apply equally to a range of vertebrate species.

REVIEW OF RECENT LITERATURE

Eighteen major scientific journals were searched for papers using radio-tracking data for home-range analysis, to determine the different approaches and the analytical techniques currently used and to assess by subjective criteria the results presented. The literature search covered the period January 1984 to December 1988, in journals dealing with both general zoological and ecological topics, and also those specifically catering for mammal, bird and reptile interests; details are given in Table 1. Of these 18 journals, 13 provided one or more suitable references, and a total of 93 papers was included in the review. Of these, 82 were on mammals, nine on birds and two on reptiles. Any paper that dealt partly or totally with home-range analysis by means of radio-tracking was investigated. For each paper, information was collated on the species studied, the area in which the work was undertaken, and the methods of data collection. Information was also collated on the methods of home-range analysis and various technical features and assumptions relating to the analysis that may or may not have been carried out. These results are summarized in Table 2.

The review shows that home ranges are determined for a variety of reasons, ranging from providing information on an animal's ecology or behaviour to investigating management implications due to its spatial distribution. For this review, we felt that whatever the reason for the study, authors should have used appropriate methods of

Table 2

Summary of the data presented in the papers included in the review. The category 'uncertain' includes those papers in which the point was not clear in that paper, although it might have been discussed in a previous paper by the same authors; for this review we did not cross-check earlier papers

Data collection and handling			
Assessment of accuracy of fix given		Yes	30
		No	57
		Uncertain	6
Time period over which home range measured given		Yes	77
		No	15
		Uncertain	1
Method of radio tracking	Discontinuous fixes		77
	Continuous fixes (≤15 min)		9
	Both		1
	Uncertain		4
	Not given		2
Autocorrelation considered		Yes	9
		No	79
		Uncertain	5
Asymptote in home-range calculation considered		Yes	22
		No	70
		Uncertain	1
Number of fixes for asymptote or for home-range analysis given		Yes	30
		No	62
		Uncertain	1
Corrections applied to home-range calculations		Yes	2
		No	89
		Uncertain	2
Home-range analysis			
Method(s) of analysis used	Minimum convex polygon (unmodified 59, modified 22)		81
	Harmonic mean		15
	Probability ellipse		12
	Grid square		6
	Other		3
	Not given		5
Number of analytical methods used		One	69
		More than one	19
		Not given	5
Justification of method used		Yes	20
		No	72
		Uncertain	1
Core area estimated		Yes	24
		No	69
Method of core area estimation	Harmonic mean		10
	Observed vs. expected number of fixes per cell		4
	Subjective assessment		1
	Not given		3
	Uncertain		6
Reasons for determining home range			
Management implications			10
Comparison of techniques			7
Not stated			2
Ecological/behavioural study			74
spatial or temporal use of home range			25
habitat use			18
part of a demographic study			9
study of effect of one factor on home-range size			9
comparison of range size between species			5
part of manipulative experiments			5
evaluation of home-range size			3

data collection, analysis and presentation, without violating assumptions inherent in the technique or failing to carry out essential parts of the analysis. We also felt that papers should include some justification for the techniques chosen. The summary shows that, on the subjective criteria we applied, less than one-third of the papers included an assessment of the accuracy of the radio fixes, less than 10% considered whether or not locational fixes were autocorrelated, less than a quarter considered whether or not sufficient fixes had been obtained for the home-range estimation to reach an asymptote, and less than a third stated how many fixes were used to calculate the home-range size. It would appear that there was also a low level of sophistication in the analysis of the subsequent data, since the majority of the papers used only one method of home-range analysis, principally the minimum convex polygon, and did not justify why this method was used. There is, to some extent, an understandable time delay in using new methods of analysis. This is shown by the date of publication of the 15 papers that use a harmonic mean method of range analysis; respectively, one, two, four, three and five papers from 1984 to 1988. However, there still appears a reluctance by authors to utilize the advantages offered by the availability of different techniques for home-range analysis.

It is not intended that this summary should be taken as a critique of the value of the results presented in these papers. It is simply used to show that radio-tracking data are often collected or analysed inadequately and hence under-utilized. From our review, it appears that the limiting factor is not what the data were used for, but how accurately they were gathered and whether or not they were used correctly in a variety of different methods of home-range analysis. The following sections of this paper are designed to help people undertaking a radio-tracking study to obtain the maximum benefit from their data.

PLANNING A RADIO-TRACKING STUDY

Before deciding to use radio-tracking in a study, it is worth bearing in mind that other methods can be used for obtaining locational fixes suitable for home-range analysis, and it may be that radio-tracking is not the most appropriate technique. In some bird species, for instance, home ranges have been calculated from visual observations of tagged individuals (Metcalfe, 1986; Porter & Labisky, 1986; Ridley & Hill, 1987), and visual observation is often more appropriate when studying the behaviour of individuals in herds (Lawrence & Wood-Gush, 1988), flocks (Metcalfe, 1986) or colonies (Davis & Murie, 1985). Mills & Gorman (1987) calculated home ranges of Spotted Hyaenas *Crocuta crocuta* from spotlighting marked individuals at night, and also used the method to study scent-marking behaviour. Home-range size may also be calculated on the basis of recapture data (Dice & Clark, 1953), by the use of fluorescent dyes (Mullican, 1988) or by bait-markers (Sowls & Minnamon, 1963; Randolph, 1973; Kruuk, 1978). Radio-tracking may also be used to supplement other techniques such as visual observations (Hanski & Haila, 1988), to improve estimates of relative abundance and home-range size obtained by other less accurate techniques such as track-counts (Servin, Rau & Delibes, 1987) and grid trapping methods (Trevor-Deutsch & Hackett, 1980), or to supplement other estimates of habitat use such as pellet counts (Loft & Kie, 1988).

Objectives

All radio-tracking studies should begin with a precise set of objectives. It is important to decide at the outset exactly which questions are to be answered and which hypotheses are being tested, since these will dictate how the study is undertaken. It is essential to take into account the constraints concerning the study animal and its habitat, and the resources available. Amlaner & Macdonald (1980) and Kenward (1987) provide information on how to organize a radio-tracking study.

It is useful to have at least some idea of the type of movements likely to be made by the study animal as this dictates the type of data that can be collected. For instance, if the species is fast-moving and liable to travel long distances, continuous radio-tracking (see below) may not be feasible. In addition for small mammals, the constraints of a short battery life (in the order of a few days) mean that continuous or short interval discontinuous tracking are the only options, since longer time intervals would yield too few locational fixes.

The type of habitat will affect the goals of the study. It may be difficult, in a highly heterogeneous habitat, to pin-point an animal using radio-telemetry with sufficient precision to identify the particular habitat type it occupies. Furthermore, the accuracy of a radio fix varies with the habitat type (White & Garrott, 1986), and this may result in a bias in observed habitat preference.

Since radio-tracking is a study of the behaviour of individual animals, it is ideally suited to the study of differences between individuals. Individual differences in performance have often been neglected by ecologists, and radio-tracking offers one of the best means available for studying them; some of the analytical problems posed by individual variation are discussed by Caro & Bateson (1986) and Martin & Kraemer (1987). However, if the goal is to look at population parameters, then an adequate sample size will be needed to ensure that seasonal/monthly, etc. differences are not masked by individual variation.

The importance of evaluating the cost of undertaking a radio-tracking study in terms of time and money has been noted by numerous workers (e.g. Macdonald & Amlaner, 1980; Mech, 1980; Morris, 1980; Sargeant, 1980), and we would also emphasize that the cost:benefit ratio is considered carefully in relation to the questions that are to be answered. It is clear that enough manpower and equipment must be available to catch and collar at least the minimum number of animals that will be needed to attain the objectives. In planning the project, the number of animals to collar, the age and sex classes that need to be caught, and the time period over which the animals have to be tracked to provide enough fixes (see below) should all be considered. In particular, when deciding how many animals to collar, allowance should be made for early deaths, transmitter failure and dispersal off the study area. Although these will vary from species to species, and with the quality of the transmitters, as an approximate estimate an allowance of one-third extra animals should be made.

Defining the home range

The time period over which a home range is measured is one of the most important parameters needed to fully define home range (Morris, 1988). The age, sex, dominance, breeding status, etc., of the animal should also be specified, along with the method of data analysis (see below).

For species that show marked seasonal changes in behaviour, a seasonal/quarterly home range may be the most appropriate time period. Table 3 illustrates a seasonal change in mean range size for a population of Badgers. It is important to use seasonal divisions that reflect real aspects of the animal's ecology, rather than any arbitrary division of the time period which may obscure important changes of behaviour. Using an example of sympatric Muntjac and Roe Deer (Forde, 1989), bimonthly ranges were calculated (Table 4). For Muntjac, home ranges were of a similar size throughout all six

Table 3

Average group range size for Badger Meles meles *social groups in each quarter of the year. The ranges were calculated by 95% harmonic mean isopleths, and the figures are hectares ± SE. From Cresswell & Harris (1988)*

Spring (March–May) $n=8$	Summer (June–August) $n=6$	Autumn (September–November) $n=9$	Winter (December–February) $n=9$
50·8 ± 10·1	30·1 ± 13·8	33·9 ± 4·2	10·3 ± 5·1

Table 4

Bimonthly and yearly 95% isopleth harmonic mean ranges of adult Muntjac Muntiacus reevesi *and Roe Deer* Capreolus capreolus *to show seasonal and annual changes in range size. The figures are hectares ± SE, sample sizes are in parentheses*

	Muntjac		Roe Deer	
	Bucks	Does	Bucks	Does
J/F	17·6 ± 1·9 (14)	11·1 ± 0·9 (33)	51·0 ± 10·9 (3)	60·2 ± 8·8 (7)
M/A	14·4 ± 1·3 (15)	11·9 ± 0·9 (35)	36·2 ± 9·5 (3)	32·5 ± 4·3 (7)
M/J	15·0 ± 1·8 (16)	9·6 ± 0·6 (32)	20·2 ± 7·3 (3)	21·3 ± 3·6 (7)
J/A	17·9 ± 3·0 (14)	10·5 ± 0·8 (36)	20·5 ± 6·5 (3)	27·4 ± 2·0 (6)
S/O	15·7 ± 2·4 (14)	11·1 ± 1·2 (39)	16·1 ± 3·8 (3)	25·7 ± 2·4 (6)
N/D	14·6 ± 1·8 (18)	10·8 ± 0·9 (45)	25·4 ± 5·3 (3)	42·0 ± 6·7 (6)
Annual	45·5 ± 9·7 (9)	20·1 ± 2·3 (29)	82·8 ± 42·7 (3)	94·2 ± 14·7 (6)

sampling periods, whereas for Roe Deer there were marked bimonthly differences. However, for both species, the home-range site changed during the course of the year resulting in significantly larger (and less meaningful) annual ranges. The use of bimonthly ranges illustrated these changes in the annual cycle; monthly ranges would have provided little additional information but would have required approximately twice as much data to produce asymptotic range estimates.

Ranges calculated over a shorter period may be required for a variety of reasons, particularly where specific behaviour patterns are being examined. These include an assessment of daily/nightly foraging patterns, or a temporary range expansion associated with mating behaviour. In particular, short-term home ranges are necessary for studying dispersing or itinerant animals, where a daily distance travelled, using continuous radio-tracking data, may be the only meaningful measure that can be obtained. Short-term ranges are also useful when monitoring change in range use over time; for example, Barrett (1984) examined the expansion in range size of Pronghorn Antelopes *Antilocapra americana* fawns as they developed.

For some social species, it is often desirable to calculate a group home range as well as individual ranges, e.g. Brown (1982) and Rylands (1986) working on Marmosets *Callithrix humeralifer*, Stacey (1986) working on Yellow Baboons *Papio cynocephalus* and Johnson (1989) working on Red-Necked Wallabies *Macropus rufogriseus banksianus*.

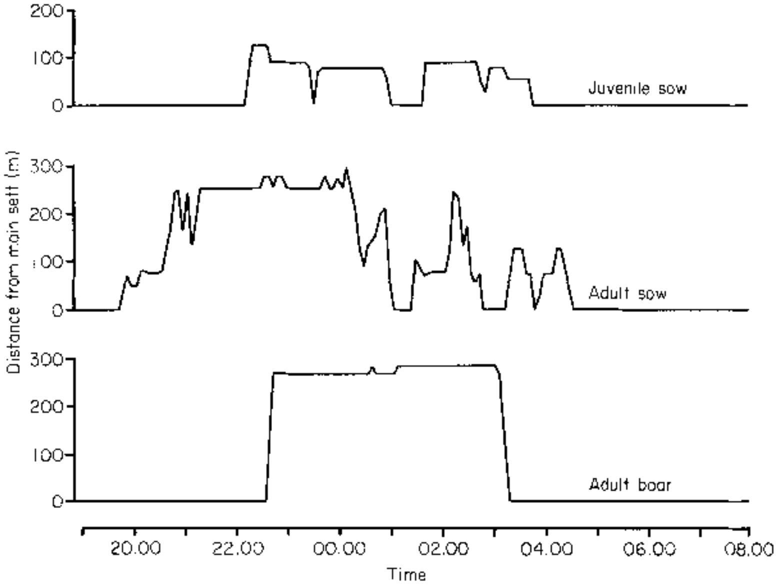

Fig. 1. Nightly tracer plots comparing the distances typically moved away from the main sett by different age and sex classes of Badgers *Meles meles*. All animals were radio-tracked continuously; above, a juvenile female at the start of its second year (tracer for the night of 13–14 April); middle, an adult sow (tracer for the night of 27–28 March); and below, an adult boar (tracer for the night of 15–16 April). From Cresswell & Harris (1988).

For this to be valid, it is important to determine whether or not the animals in question form a socially cohesive unit, since socially unstable groups without long-term affiliations should not be studied in this manner. Even species such as the Badger, which may normally live in well-defined social groups (Kruuk, 1978), may in certain circumstances form temporary, unstable groups whose ranging behaviour differs from that of more permanent groups (Cheeseman *et al.*, 1988).

When combining data for social groups, it is important to ensure that the animals included in the study are representative of the social group being studied. Animals of different age and sex may have different movements and patterns of range use; that this is the case for Badgers is shown in Fig. 1. Therefore, the animals included in the analysis must be representative of the age, sex and dominance classes of the whole group. For comparative purposes, those same proportions should as near as possible be used in all the groups studied. This presupposes a certain level of understanding of the population parameters and social organization of the study species.

For any study of home range, a number of constraints may act to restrict the sample of animals available or the time period over which they may be studied. Battery life of a transmitter may preclude the long-term study of individual small mammals, or for rare or 'trap-shy' mammals a spread of age and sex classes may be difficult to obtain. In such cases it is important to realize that the data obtained are not necessarily representative of the whole population.

The type of radio-tracking

One of the first decisions that has to be made is what radio-tracking regime is most suited to the project. There are two main options; continuous and discontinuous radio-tracking.

Continuous radio-tracking involves radio fixes being taken at very short intervals, usually between 5 and 15 min, over a set time period. This technique produces a series of fixes which provides at the very least a rough approximation of an animal's travel route. The technique is particularly useful for showing the intensity with which an individual uses its home range, the study of dispersing individuals, for the study of movement and activity patterns, interactions between individuals or the effects of parameters such as weather on an animal's movement patterns or behaviour. It is also particularly useful for detailed studies on habitat selection, especially when the habitat patches are small. The technique can only really be used successfully where the chance of losing the study animal due to sudden fast movements or unsuitable terrain is slight, and where it is possible to determine an animal's position quickly and easily.

Discontinuous radio-tracking involves locating an animal at either discrete or random time intervals throughout the study period. If these time intervals are selected to avoid or minimize the problems of autocorrelation (see below), it facilitates the analysis. The technique is useful for determining home-range size, and can be used for the assessment of habitat selection, providing a sufficient number of animals is being studied. Discontinuous data collection allows the concurrent study of a larger number of animals. This is valuable in studies of social groups, discrete populations or sympatric species. For discontinuous data it is important to structure the radio-tracking programme to ensure that the data are a true sample of the animal's behaviour. For instance, comparing sympatric Roe Deer and Muntjac (Forde, 1989), the former had distinct diurnal and nocturnal range shifts, whereas the latter did not (Fig. 2). For home-range calculations, it was important that data collection for Roe Deer was structured to sample equally throughout a 24-h period, whereas this was less critical for the Muntjac. In some radio-tracking studies, animals have been relocated once daily at 24-h intervals, and the distance between consecutive fixes used as an index of the total daily movement for an individual. Laundré *et al.* (1987) have investigated the validity of determining actual distance travelled from 24-h relocations and found serious problems with this approach.

One other approach to radio-tracking is radio-assisted surveillance; radio-tracking is used simply to locate an animal so that its behaviour can then be observed directly without further use of radio-tracking. It has also been called predictive radio-tracking (Macdonald, 1978). The technique is most useful for diurnal species, or nocturnal species such as Badgers or Foxes that may spend considerable periods of time in open habitats where they can be observed with the aid of night-viewing equipment (Kruuk, 1978; Macdonald, 1978). It is not particularly useful for diurnal or nocturnal species that live in closed habitats.

Accuracy of radio fixes

Heezen & Tester (1967) and Springer (1979) discuss the problems and methods for assessing the accuracy of radio fixes. As Springer (1979) pointed out, bearings determined by radio-tracking are only estimates, not exact locations. Heezen & Tester (1967) introduced the concept of an 'error polygon' to represent the confidence area associated with a point locational fix obtained by triangulation.

Accuracy of fixes can be determined in the field by placing test transmitters in various habitats and taking fixes on these. Litvaitis, Sherburne & Bissonette (1986) did this for Bobcats *Felis rufus*, measuring the error polygon 1 km from the trial transmitter, as this was the distance from which they were usually tracked. Estimates of error parameters should be included with any radio-tracking study (Saltz & Alkon, 1985). Estimating and defining these errors allows the formulation of a threshold error value,

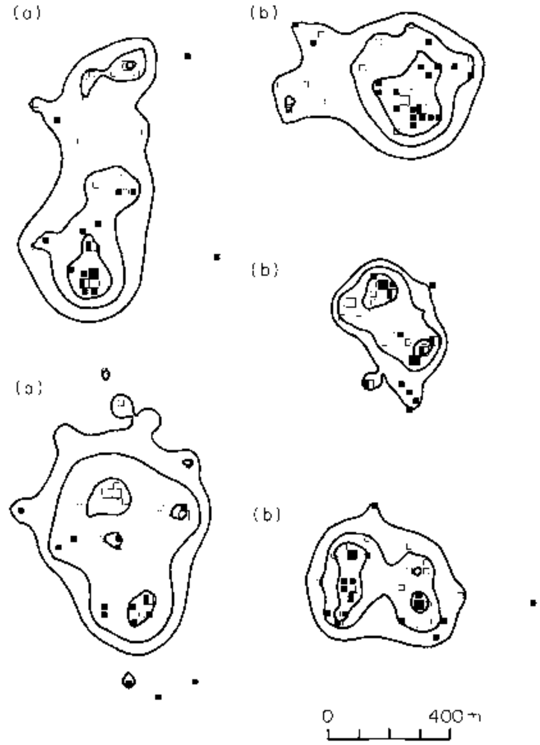

Fig. 2. (a) Diurnal and nocturnal distribution of radio fixes within two adult Roe Deer *Capreolus capreolus* doe home ranges; there are distinct areas for diurnal and nocturnal fixes. The contours are 95%, 80% and 50% harmonic mean isopleths: (■) 25-m squares that contained night-time fixes (beginning of dusk until the end of dawn); (□) 25-m squares that contained daytime fixes (end of dawn until the beginning of dusk); (◧) 25-m squares that contained both daytime and night-time fixes. Larger symbols denote 25-m squares with more than one radio fix. Both ranges based on 42 locations from Roe Deer does tracked discontinuously during March and April. (b) Diurnal and nocturnal distribution of radio fixes within three adult Muntjac *Muntiacus reevesi* doe home ranges; diurnal and nocturnal fixes are scattered throughout the range. Legend as for Roe Deer. Upper range based on 39 locations, middle one on 36 locations and lower one on 40 locations, all from Muntjac does tracked discontinuously during March and April.

so that radio locations with errors exceeding this value can be excluded from subsequent analyses (Saltz & Alkon, 1985). For example, Tidemann *et al.* (1985), following Australian Ghost Bats *Macroderma gigas*, excluded all fixes where the error polygon was greater than 2 km^2. Where subsequent home-range analysis relies on a grid cell, or where locational fixes are related to habitat data, it is important that the grid cell size used reflects the accuracy of the fixes obtained by radio-tracking.

Factors that increase the size of the error polygon include the distance away from the animal, the nature of the terrain, particularly how hilly, wooded and discontinuous it is, the atmospheric conditions and the time taken between cross-bearings. If an animal is moving fairly fast, and several minutes elapse between cross-fixes, the accuracy of the final position is questionable. To compensate for these problems, during the trial run (see below) fixes should be taken on radio transmitters placed in different and unknown positions and habitats in the study area. This will identify areas of poor signal reception, and enable a quantified estimate of fix accuracy to be obtained. It also means that the best positions from which to take radio fixes, the minimum distance between locations needed to get an accurate cross-bearing, and the travel time between locations can be established before the onset of data collection. All these variables may require that the aims of the study are modified, depending on how realistic it is to obtain accurate radio fixes.

Collection of ancillary data

Catching animals to radio-collar them is a time-consuming business; it is usually also traumatic for the animal. Having caught an animal, it is important to maximize the return by collecting as many background data as possible, since these are vital in helping with the radio-tracking analysis. Sex, breeding condition, age or age category and weight are obvious. If a precise age is required for the analysis, removal of a tooth for counting incremental lines in the cementum is a useful technique for many species, e.g. Sea Otters *Enhydra lutris* (Garshelis, 1984). For some species an approximate age category such as juvenile or adult may be sufficient. However, adults of different ages may behave differently (e.g. Badgers; Cresswell & Harris, 1988), and an accurate age allows variation between age classes to be eliminated in the analysis. Collection of blood samples for DNA-fingerprinting may be useful to determine the interrelationships of the study animals (Burke & Bruford, 1987), particularly in studies of a social species, and this may greatly facilitate understanding of the animal's behaviour. In addition, the collection of samples of blood or body fluids can help assess the reproductive state or health of the animal; diseased animals may behave abnormally (e.g. Badgers; Cheeseman & Mallinson, 1981) and their data should be analysed separately. In Britain, many of the above procedures require a Home Office licence under the 1986 Animals (Scientific Procedures) Act.

For many (usually longer-term) studies it is often useful to add other information (e.g. habitat or climatic data) to the radio-tracking data for a more detailed analysis. For such analyses it will be necessary to record whether or not the animal is active or lying up and, if active, what type of behaviour is occurring (moving, foraging, etc.). At the outset it is important to consider which ancillary data may be needed, and how best they can be integrated with the radio-tracking data. Failure to do this at the start of the study can cause considerable problems in the analytical stages.

A trial run

It is important to test the radio-tracking regime before launching into the detailed study. Ideally the work should be split into three separate stages. The first is a trial sampling period during which radio-tracking data should be collected from a few animals of representative sex and age classes. This sampling period should be used to check that the equipment works satisfactorily, and to experiment with different radio-tracking regimes. It will also provide an opportunity to decide whether or not the study objectives and work regime are achievable, and what additional data may need to be collected. The second stage should be a preliminary analysis of the data obtained during the trial sampling period. This will ensure that the data are being collected in the correct fashion, and if discontinuous data are being collected they can be tested to check that the fixes are not autocorrelated. If the data are autocorrelated, the minimum time interval between fixes to achieve independence can be calculated (see below) and the tracking regime altered if necessary. Finally, the number of fixes needed from each individual to determine home-range size and obtain an asymptote (see below), the size of the core area(s), and any habitat preferences can be established. At the outset it is important to consider any seasonal variation likely to be encountered. Although the selected number of fixes may be adequate to calculate a home-range size during months of limited activity, it may not be sufficient when the animal is particularly active. A preliminary analysis of the data will ensure that any problems with the data will be discovered early enough to be rectified. Stage three is when the majority of the field work will be undertaken, using a work regime that has been tested already, and which will lend itself to proper analysis to fulfil the objectives of the study.

METHODS OF HOME-RANGE ANALYSIS

With the advent of radio-tracking techniques, there has been a considerable increase in the amount of data that can be collected and used to analyse home-range size, shape and internal configuration. As a result, in addition to a purely spatial representation of home range, it has become possible to define it in statistical terms. The various analytical techniques have been reviewed by Macdonald, Ball & Hough (1980), and more recently by Jaremovic & Croft (1987) and Worton (1987). As the various techniques available become increasingly sophisticated, their methodology and assumptions further modify the concept of home range itself. Here we comment on the advantages and disadvantages of the most commonly used methods of home-range analysis. The list is not exhaustive, and other techniques may be better suited where, for instance, there are few locational fixes and/or a restricted time period. In such cases simple indices of space use, such as observed range length (Stickel, 1954; Abramsky & Tracy, 1980; Gaines & Johnson, 1982), which make no attempt to measure home-range area, may be more appropriate.

Minimum convex polygons

Although one of the earliest and simplest techniques for home-range calculation, the minimum convex polygon (Mohr, 1947; Southwood, 1966) is still the most frequently used (Table 2). An advantage of the minimum convex polygon is that it is the only technique that is strictly comparable between studies, and its inclusion as one of two or more methods of range calculation is therefore valuable. It is also one of the few methods to give comparable results between grid trapping and telemetry data (Jones, 1983). Although it is more robust than other techniques when the number of fixes is low, it does have a number of disadvantages. The range boundary encompasses all the fixes, including occasional fixes well beyond the main area of activity. This means that the range size is strongly influenced by peripheral fixes, and the range area can include large areas which are never visited. In addition, there is no indication of the intensity of range use. Some of these disadvantages can be reduced by using concave polygons, e.g. Clutton-Brock, Guinness & Albon (1982) and Kenward (1987), or by correcting minimum convex polygon ranges by manipulative adjustments such as restricted polygons (Wolton, 1982; Mills & Gorman, 1987). Such approaches may be useful in certain situations, but the assumptions are seldom valid in others, and the techniques are thus not comparable between studies.

Grid cells

Another 'non-statistical' technique is the overlaying of grid cells (Siniff & Tester, 1965). This technique is useful for a representation of habitat usage (Lawrence & Wood-Gush, 1988) or conspecific interactions (Adams & Davis, 1967), and is the best methodological basis for a simple three-dimensional contouring of ranges for graphical presentation. However, it is not so useful for calculating home-range areas, where an 'outline' technique is more suitable.

Probabilistic methods

The probabilistic methods of home-range analysis attempt to assess an animal's probability of occurrence at each point in space—the 'utilization distribution' (UD) (Van Winkle, 1975)—and these methods can be divided into two groups. The first assumes that an individual's pattern of space use conforms to a particular probability distribution, e.g. bivariate or circular normal. The second, and more recent group of analytical techniques, do not require this assumption and seek to characterize a variety of UDs accurately.

The former group evolved from a statistical concept of home range first defined by Hayne (1949). For these methods home ranges are analysed as probabilistic circles or ellipses; see Van Winkle (1975) for a review of such techniques and also Koeppl, Slade & Hoffmann (1975) and Koeppl *et al.* (1977). The ellipse boundary can be used to define home-range size and more restricted ellipses used to represent something of the internal range structure. However, they suffer from several major drawbacks. Firstly, there is the assumption that an animal's use of space will be normally distributed around a centre of activity, and this is seldom likely to hold true (Macdonald, Ball & Hough, 1980). Secondly, they assume that the fixes are independent, which is often not the case (see below) and dependence within the sample will cause a reduction in the variance of each sample of locations (Swihart & Slade, 1985). Thirdly, the techniques assume that there is always only one centre of activity, and that this is placed centrally. Both these last two assumptions are often unwarranted in mammal studies (see section on core areas below). In the probabilistic techniques, the 'centre of activity' is derived from an arithmetic mean which may not have any biological significance, and in fact certain home-range configurations could cause this to lie outside the animal's actual range. Also, the arithmetic mean centre calculation is affected greatly by extreme locations and any movement within the ranges will cause some change in its location (Dixon & Chapman, 1980). Despite these problems, this approach has been used widely to study home-range size and internal structure, and many of these studies seem not to have taken full account of the likely effects of violating these three basic assumptions.

More recently, attempts have been made to improve the applicability of probabilistic techniques. Don & Rennolls (1983) developed a method which assumes a circular normal distribution of activity about several 'nuclei of activity' within a home range, thus overcoming one of the problems. Ford & Krumme (1979) developed a technique to calculate the UD without making *a priori* assumptions as to the shape of that distribution. In addition, they derived an index which enabled an area to be calculated relating the UD to home-range size. However, a realistic estimate of the UD by their method 'required much more extensive individual records than are usually available'. Hence their technique directly combined locational records of a numbr of individuals into what was termed a 'population utilization distribution' (PUD), assumed to be an average for that population. Anderson (1982) developed the fourier transformation method as a technique directly combined locational records of a number of individuals into what was tion of a normally distributed UD. The kernel methods proposed by Worton (1989) were a further development of probability density functions, versatile with respect to how they represent the UD. Similar (but more complex) in calculation to the harmonic mean method of Dixon & Chapman (1980) (see below), this technique appears sophisticated in its representation of the internal structure of an animal's home range. However, relatively minor changes to the smoothing parameters have a large effect on overall range size, and in general each of the more sophisticated probabilistic methods may be more suited to an analysis of range use than to a calculation of range size. One principal

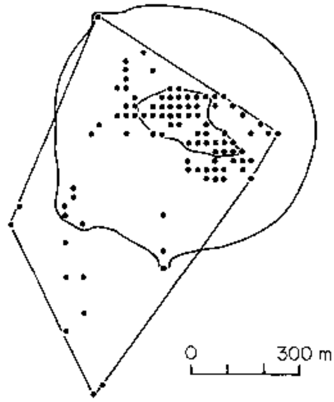

Fig. 3. Home-range plots for a subadult male Fox *Vulpes vulpes* radio-tracked continuously for seven nights (231 locations) in November. The polygonal line is a minimum convex polygon range (area 40 ha), the outer contour is a 95% harmonic mean isopleth (area 41 ha), and the inner contour is a 60% isopleth. The symbols denote 25-m squares with one or more radio fixes. Because of the skewed distribution of the radio fixes, the 95% harmonic mean isopleth is not appropriate for illustrating this home range.

drawback also remains, and that is the assumption of independence: if there is autocorrelation within the sample of locations used to construct the UD, then an important assumption is violated.

Harmonic mean method

Dixon & Chapman (1980) developed an elegant technique by which one or more centres of activity, home-range size and home-range configuration could be determined. This method calculates a harmonic mean centre of activity based on areal moments. These moments can be used to develop measures of central tendency, a measure of 'average position' (Neft, 1966) and dispersion, and are calculated from a grid superimposed upon the distribution of fixes. The values calculated at each grid intersection form a matrix upon which to draw isopleths relating to contours in range use. Although movements of the grid can cause shifts in the position of the harmonic mean centre, Spencer & Barrett (1984) showed that this problem can be avoided by calculating the harmonic mean independent of the grid, and by calculating isopleths after translocating the animal loci to grid cell centres. This method thus provides a technique for the accurate calculation of centres of activity, representation of range use and, by calculating isopleths within which a proportion—e.g. 75% (Windberg & Knowlton, 1988) or 95% (Cresswell & Harris, 1988)—of all fixes lie, a method of estimating home-range areas.

The harmonic mean method produces range configurations that relate well to the actual distribution of fixes. However, it will also include areas that are not visited by the animal. Although the technique is less sensitive to departures from a normal distribution of fixes, highly skewed or leptokurtic distributions will result in inaccurate home-range representations (see Fig. 3). For this reason, it is desirable during the analysis to produce a print-out of each range calculation to compare the distribution of fixes and the harmonic mean range, to ensure that skewness is not causing a misrepresentation of the range. This is a particular problem when the number of fixes is low, and may be most pronounced when using a 95% isopleth, in which case using a lower isopleth (e.g. 80%) will usually give a more accurate range representation.

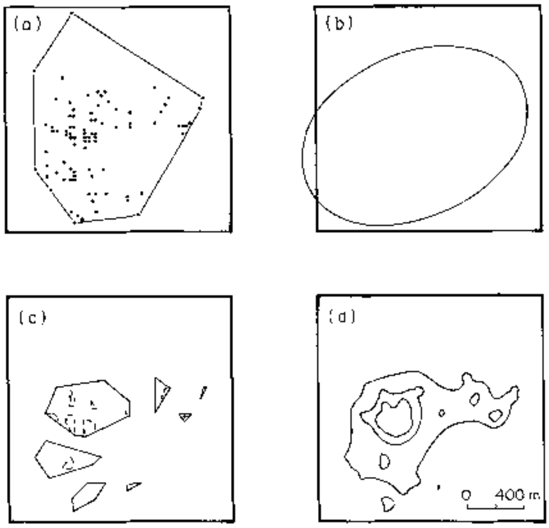

Fig. 4. A comparison of different home-range analysis techniques, using the same data set for an adult male Brown Hare *Lepus europaeus* radio-tracked discontinuously in May and June (123 locations). (a) Minimum convex polygon (116 ha); the symbols denote 25-m squares with one or more radio fixes. (b) 95% probability ellipse (153 ha). (c) Cluster analysis; the solid line denotes the 95% cluster (28 ha) and the broken line the 60% cluster. (d) Harmonic mean; the outer line is the 95% isopleth (56 ha), the others the 60% and 30% isopleths.

Because of the method of calculation, it is possible to have more than one centre of activity, and the technique is particularly useful for calculating 'core areas', when the contour lines are used for defining areas of high and low usage within the home range. A disadvantage of the technique is that it is difficult to compare harmonic mean ranges between studies, since each computer program may use a different set of algorithms and a different grid cell size.

Two-dimensional cluster analysis

As with the harmonic mean, this technique may be used to investigate the pattern of range use, but the methodological basis is different (Kenward, 1987). The technique begins by locating the three fixes with the smallest mean distance between them. The next cluster is built up only if the mean distance within it is less than the distance to the first cluster's nearest neighbour. Thus, as the analysis progresses, many of the initial clusters merge. As with the harmonic mean method, 'contours' can be drawn at any stage, and these relate to the percentage of fixes enclosed by the clusters present at that time. The main difference between the two approaches is that each cluster is treated separately, whilst isopleths drawn from the harmonic mean centre matrix relate to all the other fixes. One drawback of the technique, as with the harmonic mean method, is the lack of comparability between studies because of the different cluster algorithms.

From the above resumé of the various analytical techniques currently used most frequently, it can be seen that no one technique is 'perfect', and each has a number of disadvantages. It is particularly important to ensure that none of the implicit assumptions in each technique is violated, and that the technique being used is suitable to each individual range calculation. Different methods can give different results even when

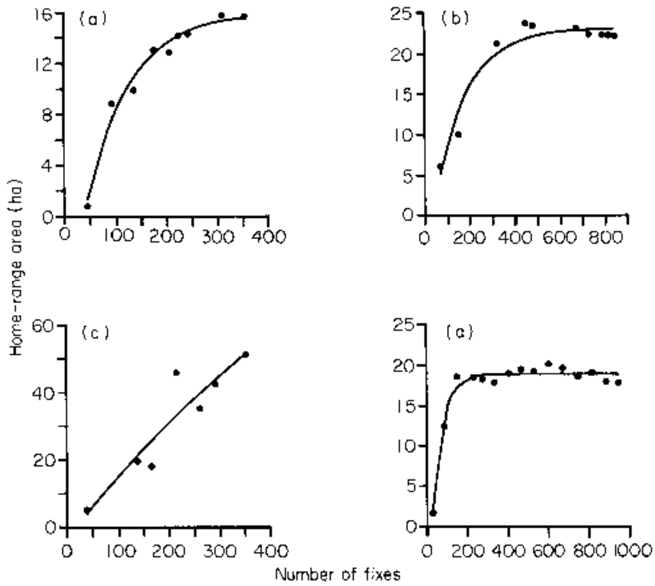

Fig. 5. Graphs showing the number of radio fixes needed to obtain asymptotic home-range estimates for subadult male Foxes *Vulpes vulpes* radio-tracked continuously in (a) January, (b) November, (c) October and (d) January. For the animal shown in (c) an asymptotic range size could not be obtained.

analysing identical data (see Fig. 4) and it is extremely difficult to transform home-range estimates made with different methods to a common basis for comparison (Worton, 1989). Finally, since no one method is likely to be entirely satisfactory, at least two techniques should be used with the data set, and if one of these is a minimum convex polygon then the problems of comparability are lessened. Voigt & Tinline (1980) also emphasized the importance of using a variety of analytical techniques to get the most out of radio-tracking data, and drew attention to the fact that most studies, to their detriment, use radio-tracking simply to determine the size and shape of the home range.

HOME-RANGE ESTIMATION—PROBLEMS WITH ANALYSIS

Home-range asymptotes and sample size

The number of radio fixes required to calculate a home-range size must be known before the majority of the field work is done. During the trial tracking period it is important to collect a large number of fixes from a range of animals to encompass, wherever possible, variations due to sex and age, and to determine at what point home-range size reaches an asymptote (Stickel, 1954; Hawes, 1977). This is calculated by plotting range size vs. number of locations, and defined as the point after which additional locations result in a minimal increase in range size. Fig. 5 illustrates monthly home-range estimates for urban Foxes, using continuous tracking data. As can be seen, estimates for individual home ranges reach asymptotes at different values and with a variety of curves, depending on the pattern of home-range utilization and range size for that particular animal. In addition, some animals may never reach an asymptote even though a large volume of data might have been collected (Fig. 5c). This may occur when the individual is a transient adult, a dispersing subadult, or when the time interval for calculating the home range is inappropriate, e.g. Bowen (1982), who illustrated these problems for Coyotes *Canis latrans*. If, for instance, the selected time interval covers part of a period of reduced motor activity followed by a period of range shift, or a period covering a

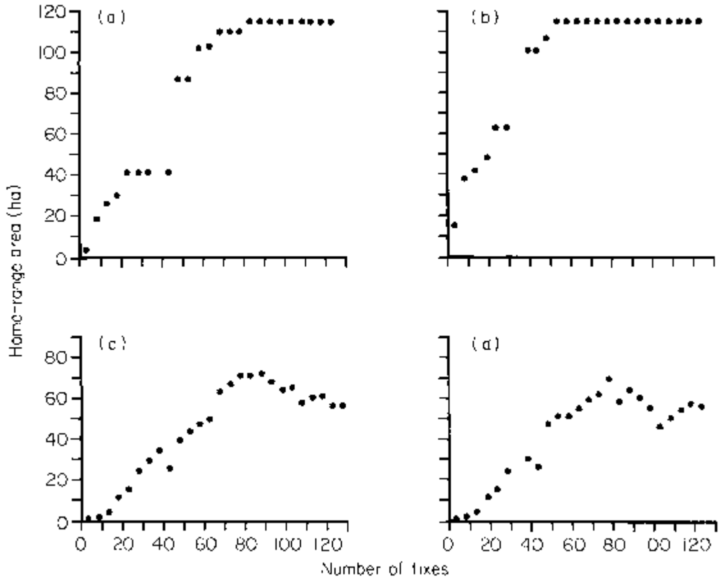

Fig. 6. Methods of calculating home-range asymptotes for an adult male Brown Hare *Lepus europaeus* radio-tracked discontinuously during May and June. (a) Minimum convex polygon range size with fixes removed sequentially; (b) minimum convex polygon range size with fixes removed randomly; (c) harmonic mean 95% isopleth with fixes removed sequentially and (d) harmonic mean 95% isopleth with fixes removed randomly. Minimum convex polygon ranges produce a smoother asymptote than harmonic mean 95% ranges (compare a and b with c and d); fixes should be removed randomly for discontinuous data (compare b and d with a and c), whereas the reverse is true for continuous data.

seasonal range shift, such a result may occur. For this reason, it is important that the selected time interval for the range calculation is based on a sound assessment of the animal's biology. To produce home-range asymptotes, fixes can be removed or added to a database either randomly or sequentially. How this is done depends on how the data have been collected; in general it should be done at random for discontinuous radio-tracking data and sequentially for continuous radio-tracking data. Also, the data should be tested against the different analytical techniques to be used; in general, minimum convex polygons produce smoother home-range asymptotes than, for example, harmonic mean methods. These points are illustrated in Fig. 6.

Once the number of fixes normally needed to calculate an asymptotic home range is known, the details of the study can be planned. For the final analysis, the data for each time interval should be tested to ensure that they reach an asymptote; some data sets may not. If this is because the data are from a transient animal or one undergoing a distinct change in behaviour, as described above, the results should not be combined with those from resident animals. However, it is also possible that some sets of locational data do not reach an asymptote, even though the animal's range has not changed during that period of time. In this case the data can be corrected to produce an asymptotic range estimate, using regression equations calculated from asymptotic home ranges. Illustrations of this for Foxes are given in Fig. 7. The obvious disadvantage with this approach is that it turns a real home-range value into a hypothetical one, although corrected home-range estimates are preferable to uncorrected estimates when the calculated home-range size will be affected by the sample size.

An alternative for home ranges that do not reach an asymptote, and possibly a preferable approach, is to present a home-range estimate based on a standard number of

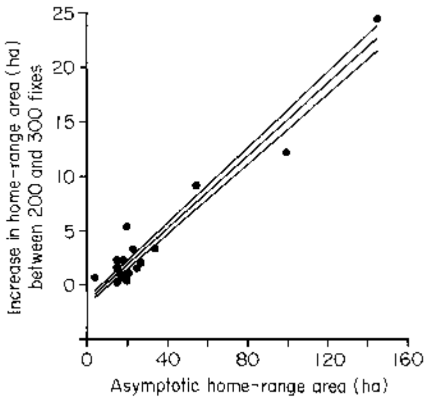

Fig. 7. Correction graph for calculating asymptotic home-range sizes (95% harmonic mean isopleths) for Foxes *Vulpes vulpes* radio-tracked continuously. The line is a best-fit with ±2 SE.

Table 5

Regression equations used to correct Muntjac Muntiacus reevesi *home-range and core areas*

		n	r^2	F	P
Minimum convex polygon	$a = 2{\cdot}58 + 27{\cdot}00b$	31	90·2	279·2	<0·001
95% isopleth harmonic mean range	$a = 2{\cdot}46 + 26{\cdot}81b$	34	88·3	248·8	<0·001
50% isopleth harmonic mean core area	$a = 0{\cdot}69 + 13{\cdot}76b$	36	59·8	53·0	<0·001

Where a is the bimonthly range size at 35 fixes (in hectares) and b is the rate of increase per fix between 10 and 25 fixes.

fixes. For this a number of fixes close to the figure at which most home-range estimates reach an asymptote should be chosen. As an example, for an analysis of bimonthly Muntjac home ranges, a figure of 35 fixes was chosen, and over the range 30–40 fixes, home-range estimates were unaltered. When there were more than 40 fixes, only the first 40 in the time interval were used, and for fewer than 30 fixes correction regressions were used relating the rate of increase between 10 and 25 fixes to the range size obtained with 35 fixes (Table 5). In this study, a lower limit of 25 fixes was set below which a home-range size was not calculated (Forde, 1989).

At the end of the analysis a number of asymptotic, corrected or standardized home ranges will have been calculated for each animal. When combining the results to give, for example, a mean (or group) home range, it is particularly important to avoid pseudoreplication, i.e. having more than one observation from each animal contributing to each pooled data set, since this violates the assumptions of independence within the data set (Hurlbert, 1984; Machlis, Dodd & Fentress, 1985; Martin & Bateson, 1987). Radio-tracking studies are particularly prone to pseudoreplication since most data sets consist of large amounts of data from relatively few animals.

Calculating the size and number of core areas

Very few, if any, species of mammal will use their home range in a uniform manner; most will have preferred areas, from which a high proportion of the locational records

Table 6

Asymptotic minimum convex polygon ranges, 95% isopleth harmonic mean ranges and 60% isopleth core areas of subadult male Foxes Vulpes vulpes *during the main dispersal period. Figures are monthly means in hectares ± SE, sample sizes are in parentheses. Data from Woollard & Harris (1990)*

		October–December	January–February
Non-dispersers	MCP	55·0 ± 13·3 (9)	49·1 ± 16·5 (12)
	95%	35·2 ± 9·5 (9)	34·1 ± 9·2 (12)
	60%	4·5 ± 0·6 (9)	4·9 ± 0·8 (12)
Dispersers			
pre-dispersal	MCP	45·8 ± 16·8 (7)	
	95%	33·3 ± 11·3 (7)	
	60%	4·1 ± 0·5 (7)	
during dispersal	MCP	224·2 ± 37·9 (15)	
	95%	115·3 ± 21·6 (15)	
	60%	6·5 ± 1·5 (15)	
post-dispersal	MCP		24·8 ± 0·7 (4)
	95%		14·8 ± 1·5 (4)
	60%		3·0 ± 0·9 (4)

will be obtained (e.g. Spencer & Barrett, 1984; Samuel, Pierce & Garton, 1985; Windberg & Knowlton, 1988; Jones, 1989). A number of ways have been used to define these preferred areas, but the use of many of these definitions can be imprecise. 'Focus of activity' is a term in frequent use, but is rarely defined so that it can be unclear as to what it refers. Also, 'centre of activity' has been the source of some confusion. Dixon & Chapman (1980) reviewed the different methods of defining centres of activity, based on both arithmetic mean and harmonic mean calculations. Harmonic mean isopleths, probability ellipses and cluster boundaries can be drawn to include an arbitrary percentage of fixes; these are usually referred to as 'core areas', which we will discuss here, and show how they can be defined empirically. An alternative method of defining core areas is to use a grid cell method of home-range analysis (Samuel, Pierce & Garton, 1985). In this case, the core area is defined by those grid cells containing a significantly greater proportion of fixes than the mean for all cells. This generates a rather 'coarse-grained' impression of the intensity of range use, with the core area(s) thus defined often comprising a large proportion of the overall range area.

Core areas vary in size and number between species, but are important in that they denote areas of particularly high home-range usage, and often may provide a clearer measure of the changing pattern of range use than total home-range area. For instance, the sizes of the core areas and home ranges of dispersing and non-dispersing sub-adult male Foxes are shown in Table 6; whereas the home-range area varies greatly during the main dispersal period, the number and size of the core areas remain constant for both dispersing and non-dispersing Foxes. Three-dimensional plots sometimes give a useful visual indication of the core areas, but the calculation of core-area size, and seasonal changes in size and position, are probably more useful since this approach allows for comparisons between species or study areas. Also, when calculating a core area, it is important to decide on the aims of the analysis. If, for instance, the aim is to show the differences in the pattern of range utilization throughout a 24-h period, then all fixes may be used, and these should have been collected equally throughout the 24-h period. However, for many species core areas will then be biased towards lying-up areas. Such a

Table 7

Number of core areas (defined as the 50% isopleth) in bimonthly harmonic mean home ranges for Muntjac Muntiacus reevesi *and Roe Deer* Capreolus capreolus. *Figures are means ± SE, sample sizes are in parentheses*

	Muntjac		Roe Deer	
	Bucks	Does	Bucks	Does
J/F	1·8 ± 0·28 (15)	1·7 ± 0·14 (34)	2·3 ± 1·33 (3)	2·7 ± 0·47 (7)
M/A	1·7 ± 0·18 (15)	1·5 ± 0·10 (36)	2·0 ± 0·00 (3)	3·3 ± 0·52 (7)
M/J	2·0 ± 0·26 (17)	1·4 ± 0·12 (34)	3·0 ± 0·58 (3)	2·1 ± 0·40 (7)
J/A	1·5 ± 0·19 (15)	1·4 ± 0·10 (36)	1·7 ± 0·33 (3)	2·0 ± 0·51 (6)
S/O	2·2 ± 0·32 (14)	1·4 ± 0·09 (40)	1·3 ± 0·33 (3)	1·8 ± 0·48 (6)
N/D	1·6 ± 0·25 (18)	1·6 ± 0·11 (45)	2·3 ± 0·88 (3)	1·8 ± 0·40 (6)
Mean	1·8 ± 0·10 (94)	1·5 ± 0·05 (225)	2·1 ± 0·28 (18)	2·3 ± 0·20 (39)

Mean number Muntjac buck and doe core areas significantly different (Mann–Whitney *U*-test, $P < 0·05$); mean number Roe Deer buck and doe core areas not significantly different.

bias causes problems when trying to analyse an animal's movement patterns, or habitat utilization when foraging; in such cases only active fixes should be used in the analysis. It is important to consider such problems from the start, and to ensure that the number of fixes collected in each sampling period is adequate to subsample if required and still provide asymptotic range size estimates.

Core areas are often more useful than the more peripheral isopleths/contours for understanding both intraspecific and interspecific patterns of range use. For example, comparing Roe Deer and Muntjac in the same habitat, the number of core areas differs between the species (Table 7), as does the relative position of the core areas (Fig. 8), but such differences are masked when comparing total home ranges. Similarly, although home ranges as calculated by a 95% isopleth may overlap in some species, core areas may not. For instance, core areas for male and female Muntjac do overlap, and one male covers the core areas of more than one female. However, although male Muntjac ranges may overlap to some extent, their core areas are mutually exclusive.

Figure 9 shows how the core area was defined for Muntjac and Roe Deer on the same study area, using a harmonic mean home-range calculation. By plotting a graph of area against harmonic mean isopleth value, it is possible to identify the point at which the gradient of the slope changes. When the point of inflexion lies between two values, the lower one should be used to define the core area. For Muntjac and Roe Deer, the 50% isopleth was used, and the 50% or 60% isopleth has been found to be suitable to define the core area for several species, e.g. Red Deer (Clutton-Brock, Guinness & Albon, 1982) and Foxes (Woollard & Harris, 1990). However, not all species will show distinct core areas. Hares on the same study area as the Muntjac and Roe Deer had less obvious core areas. This is probably because Hares do not regularly use a single lying-up site, but will move short distances between a number of forms in daylight hours. Inactive radio fixes may thus be centred on a preferred habitat type rather than a specific point, thereby causing patterns of space utilization to be less distinct.

The calculation of the appropriate proportion of fixes, by which a core area is defined, will vary depending on the analytical technique employed. A method which is multi-nucleate in conception (e.g. cluster analysis) will tend to produce a number of core areas,

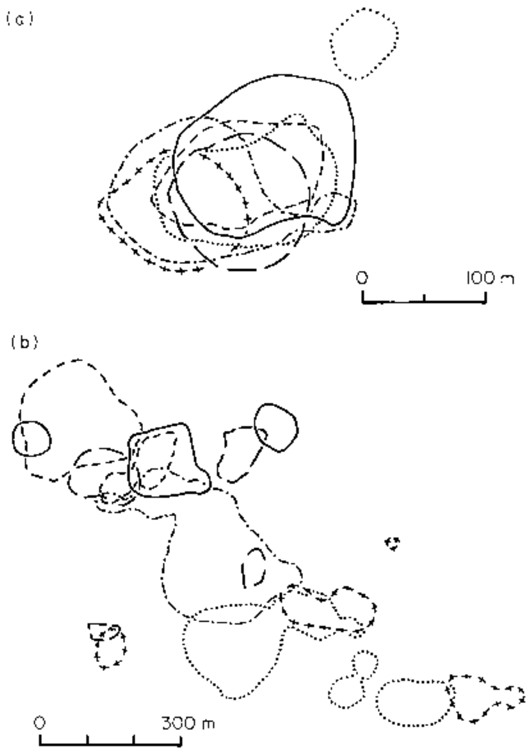

Fig. 8. The position of successive bimonthly 50% isopleth core areas for (a) an adult Muntjac *Muntiacus reevesi* doe radio-tracked discontinuously during 1987 and (b) an adult Roe Deer doe *Capreolus capreolus* radio-tracked discontinuously during 1987. For Muntjac there is no positional change in core areas, whereas there is for Roe Deer: (————) January–February; (– – –) March–April; (— —) May–June; (–·–) July–August; (+ + +) September–October; (. . . .) November–December.

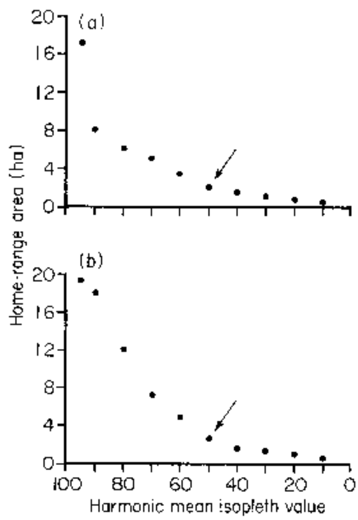

Fig. 9. Harmonic mean isopleth value plotted against home-range area for (a) an adult Muntjac *Muntiacus reevesi* buck radio-tracked discontinuously in January and February (35 locations) and (b) an adult Roe Deer *Capreolus capreolus* doe radio-tracked discontinuously in September and October (50 locations). The inflection point at the 50% isopleth value (arrowed) was used to define the core area.

which together account for a relatively larger percentage of fixes than core areas defined using a method based on one, or few, centres of activity (e.g. harmonic mean analysis).

Autocorrelation of data

Many statistical methods of home-range analysis have as a basic assumption the independence of successive locations. If the data are temporally autocorrelated, these home-range models will tend to under-estimate the true home-range size, and the magnitude of the error is related to the degree of dependence between successive observations (Swihart & Slade, 1985). Since this value may vary considerably from one series of data to another, without an estimate of the level of autocorrelation, the ranges generated by these models are not comparable. 'Non-statistical' methods of home-range analysis, such as minimum area techniques, are not affected in this way.

For most studies summarized in Table 2, autocorrelation and its effects did not appear to have been taken into account when calculating home-range size. Some workers have used a time interval between successive locations large enough to be confident that their data are independent (Eberhardt, Hanson & Cadwell, 1984; Loft, Menke & Burton, 1984; Anderson, 1988; Rolstad, Wegge & Larsen, 1988), although few have tested this assumption. A notable exception is Litvaitis, Major & Sherburne (1987), who calculated that fixes more than 12 h apart were independent on the basis of asymptotes of time–distance curves. Newdick (1983) and Hofer (1986), working on Red Foxes, calculated a 'time to independence' of fixes from a Fox's theoretical speed of travel and its home-range diameter, thereby producing a hypothetical length of time necessary for one positional record to be unaffected by the location of another. However, Foxes tend to move in a much more circumscribed manner than this technique assumes, and the time interval of approximately 30 min calculated in this way almost certainly has a high degree of dependence between successive observations, as will be seen from the calculations on similar Fox data below.

Autocorrelation of locational data is a widespread phenomenon, and can have a significant effect upon the techniques of home-range analysis. It is important to consider how to test properly for it, and how to calculate a valid 'time to independence'. To illustrate the process, tests of independence were applied to a large sample of radio fixes, to assess the increase in the time interval necessary to reach independence. The essence of these calculations is given in Swihart & Slade (1985), who demonstrated a bivariate test of independence using empirically derived critical values for the ratio of mean squared distance between successive observations (t^2) to mean squared distance from the centre of activity (r^2). The data set used was that for a subadult male Fox; 1700 continuous fixes were collected at 5-min intervals from January to April 1984. Asymptotic home ranges of 76 ha (minimum convex polygon) and 47 ha (harmonic mean 95% isopleth) were obtained with approximately 500 fixes. Schoener's (1981) ratio (t^2/r^2) was calculated for a range of intervals from 30 to 240 min, along with the $\alpha_{0\cdot250}$ critical value in each case, this being the upper boundary of significance from Table 1 in Swihart & Slade (1985). The result for each 30-min increment in the time interval is shown in Table 8. The smallest time interval corresponding to a non-significant t^2/r^2 ratio, followed by two successive 'non-significant' time intervals, was 120 min; this was defined as the time to independence between fixes.

If a large time interval between successive locations is possible and/or the calculation of home-range size is the primary aim of the study, then strict adherence to the collection of non-autocorrelated data is worthwhile. However, the goals of most radio-tracking

Table 8
Calculation of the time to independence using continuous radio-tracking fixes for a subadult male Fox Vulpes vulpes *in Bristol; see text for full details of the analytical procedures*

Time interval (min)	t^2/r^2	$\alpha_{0\cdot250}$
30	0·99	1·94
60	1·19	1·90
90	1·33	1·87
120	1·86	1·85
150	1·87	1·82
180	1·90	1·78
210	1·99	1·74
240	2·13	1·69

studies require the collection of data which are dependent to some degree; even with a very large database, it may be difficult to translate autocorrelated data into an independent form and still retain a sample size that is adequate for the home-range size to reach an asymptote. The only recourse is to use the trial tracking period to collect enough data to look at autocorrelation, and then to design a regime to collect locational data in a manner which minimizes its effects as far as possible. It is then the interpretation of the home-range data that is critical, and it is important not to select an analytical technique which is unduly affected by dependence within the sample of locations. This rules out the use of probabilistic techniques. However, harmonic mean isopleths and cluster analysis contours should be less sensitive to the effects of autocorrelation and the simpler polygon techniques unaffected. These points are illustrated by Andersen & Rongstad (1989), who also show that for highly mobile species the 'time to independence' may be an over-estimate of an appropriate sampling interval, and in such cases the biological and logistical considerations that result in autocorrelated data do not necessarily bias estimates of home ranges.

CONCLUSIONS

Home-range analysis is an important method of investigating behavioural and ecological questions. From our review, radio-tracking is obviously widely regarded as a useful technique to provide the type of data suitable for home-range analysis. Radio-tracking has been available as a technique for more than 25 years, so clear and accurate presentation of such data should be established procedure in recent papers. With new, more sophisticated and more useful techniques becoming available to analyse such data, modern studies should be capitalizing on such advances. However, in the 93 papers reviewed over a recent 5-year period, we feel that many failed on one or both of these accounts.

Collecting radio-tracking data is a time-consuming procedure, and it is important to collect data by the most appropriate method. Only by having a clear set of objectives at the start of the study, and by attempting a trial run with the data collection, will it be possible to avoid wasting precious time and/or money. Once collected, the data should be presented in a rigorous fashion, and the various points outlined in this review should have been considered. However, resources of time and money may not be available to achieve all such aims. It is then important to be aware of the limitations imposed by the sample that is available. It may be possible to describe accurately the home range of a few select individuals, and infer from those data what other members of the population are doing. Alternatively, there may not be sufficient data to fulfil the justifications of some of the methods of home-range analysis. If this is the case, methods other than home-range analysis may be more appropriate to measure or describe simple space utilization patterns of individuals.

Although home range is a concept, attempts to measure it mean that it also becomes a quantifiable factor with associated statistics. The parameters that are associated with each home-range analysis are important and should be included when home-range sizes are quoted. These parameters include sample size, level of autocorrelation of data, whether or not the data are asymptotic, and the method of analysis used, as well as the time period and status of the animal. Without these, the home-range value quoted may well be meaningless to anyone other than the author of the study. These parameters are particularly important when other researchers are attempting to use published results to draw comparisons with their own investigations. Also, using more than one method of home-range analysis provides information on the pattern of space and time use by an animal, and so it is important to make the best use of the techniques available. Which of the different methods are used depends on the questions that are being asked. As Voigt & Tinline (1980) stated, a multifaceted approach using more than one technique best serves this point; it also helps to overcome the drawbacks inherent in some of the methods of home-range analysis.

This review is designed particularly for people about to undertake a radio-tracking study and discusses many of the problems they are likely to encounter. We do not claim it to be a comprehensive treatment of all the potential problems but a guide to the ideals to aim for. Since radio-tracking is merely a technique for providing data and not an end in itself, considering the points raised here in the planning stage of a project, having clear-cut study objectives, having a trial period of data collection and analysis, understanding the limitations of the data collected, and full data presentation at the end will greatly improve the value of radio-tracking studies. It is only by addressing these points that the full potential of radio-tracking as a scientific study technique will be realized.

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