As published in Ecology 82(2001):1905-1920

DENSITY AND LINKAGE ESTIMATORS OF HOME RANGE: DEFINING MULTI-NUCLEAR CORES BY NEAREST-NEIGHBOR CLUSTERING.

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Abstract. Methods used to estimate home ranges from point locations are based either on densities of locations or on link-distances between locations. The density-based methods estimate ellipses and contours. The other class minimizes sums of link-distances, along edges of polygons or to range centres or between locations. We propose a new linkage method, using nearest-neighbor distances first to exclude outlying locations and then to define a multi-nuclear outlier-exclusive range core (OEC) by cluster analysis. The assumption behind exclusion of outliers, that movements inside and outside range cores involve different activities, was supported by data from radio-tagged buzzards. We compared the new method with other techniques by using location data from each of 28 goshawks, 114 buzzards, 138 grey squirrels and 14 red squirrels. Range structure statistics from OECs showed marked differences between species in numbers and extent of core nuclei. Range analysis displays illustrated relationships of range area with age categories, food supply, population density and body mass within species. The OECs gave highly significant results in three of five within-species tests, perhaps because animal movements in these cases were affected by coarse-grained habitat boundaries. When movements were likely to have been influenced by diffuse social interactions and foraging for scattered prey, the most significant results were from density-based estimators, especially kernel contours that had been optimized by least squares cross validation. We recommend use of both density and linkage estimators of home range until a basis for *a priori* choices has been established.

Key phrases: home range estimation by location density vs minimal distances; cluster analysis by nearest neighbor distances; defining cores objectively by outlier exclusion; comparing estimators along utilization distributions; range size vs age, food supply, population density, body mass.

Key words: home range; cluster analysis; nearest neighbor; outlier exclusion; raptor; squirrel.

INTRODUCTION

During the last three decades, radio-tracking has revolutionized studies of the use of space by terrestrial vertebrates. Locations of radio-tagged animals can be collected systematically, free from the restrictions and bias that may be imposed on visual records by elusive behavior or dense vegetation. The resulting sets of locations often provide a basis for estimating home ranges, which are used in studies of animal density, social behavior, predation and other foraging activities (reviews in Amlaner and Macdonald 1980, Harris et al. 1990, White and Garrott 1990, Samuel and Fuller 1994).

Home range estimators are typically used to provide measures of size, shape and structure. Estimates of home range size may be needed for management purposes, such as planning reserves, or as indices of movement differences between or within species (Schoener 1968, Hulbert et al. 1996). Shape may be important for analysing how home ranges conform to the landscape when meeting resource and security requirements (Covich 1976, Redpath 1995), or how home ranges of conspecifics fit together to indicate territoriality or social cohesion (Macdonald et al. 1980, Ims 1988). Internal structure may differ between home ranges (Adams and Davis 1967), and range cores that are used with different degrees of intensity may vary in habitat content, or in extent of overlap with neighboring animals (Poulle et al. 1994). The widely-used definition of home range as an "area traversed by the individual in its normal activities" (Burt 1943) implies that high-use cores may be separable from peripheral areas that are seldom visited. However, as noted by White and Garrott (1990), how does one define "normal"?

As a result of requirements to measure range size, shape and structure, biologists face a wide choice of methods for estimating home range boundaries and internal cores (Dalke and Sime 1938, Mohr 1947, Hayne 1949, Calhoun and Casby 1958, Stickel 1964, Harvey and Barbour 1965, Siniff and Tester 1965, Jennrich and Turner 1969, Koeppl et al. 1975, Dunn and Gipson 1977, Dixon and Chapman 1980, Voight and Tinline 1980, Schoener 1981, Anderson 1982, Don and Rennolls 1983, Geissler and Fuller 1985, Samuel and Garton 1985, Hartigan 1987, Kenward 1987, Worton 1989, 1995a, Loehle 1990, Wray et al. 1992a). The methods differ in ability to (i) distinguish core areas as well as outer boundaries, (ii) estimate shapes that conform to the observed pattern of locations, which may be multinuclear, (iii) derive statistics that describe the range structure and (iv) achieve stable size and shape estimates with few locations per range, so that analyses can be based on large numbers of individual ranges with minimal field effort (Kenward 1992, Robertson et al. 1998).

In this paper, we describe how the methods estimate home ranges in two main ways: either as isopleths of location density, or as polygons that minimize the sum of link-distances between locations. Early methods estimated density isopleths as circles or ellipses, by assuming that locations were distributed normally about one nucleus of activity (Calhoun and Casby 1958). These mononuclear shapes do not met criterion (ii), so attention has recently focused on methods that estimate an extensive matrix of location density values, and then interpolate contours that can depict multinuclear ranges (Dixon and Chapman 1980, Don and Rennolls 1983, Worton 1989, 1995, Seaman and Powell 1996). An early use of link-distances was to estimate minimum convex polygons (MCPs) from the minimum sum of linkages round the outermost locations; however, such outer MCPs are mononuclear and lack internal structure, thus do not satisfy criteria (i)-(iii). We show how another type of link-distance, between nearest neighbor locations, can be used in cluster analysis to meet all the criteria for estimating size, shape and structure of home ranges. We also show how nearest neighbor distances can be used for objective definition of an outlier-exclusive core (OEC) assumed to contain the "normal activities" of Burt (1943). Finally, we use 294 home ranges from four species to address the question of whether there is a "best" home range estimator, or at least if a choice between estimators may be possible on *a priori* grounds.

STUDY SPECIES AND DATA COLLECTION

The range estimators are tested with data from two raptor and two squirrel species. The species differed greatly in mobility and in patch size of foraging habitats relative to outer MCP areas. Standardized sets of 30 locations per individual were collected for each species, by recording coordinates three times daily in a 10-day period that was either continuous or separated by a weekend. Locations were recorded 3-4 hours apart, to minimize serial spatial correlation (Swihart and Slade 1985). This was enough time for each species to cross an average range at its mean foraging speed. It also matched the 3-3.5 h interval that Cresswell and Smith (1992) found (a) to maximise spatio-temporal independence in sub-sampled field data, and (b) to minimize effects of spatial correlation on home ranges estimated from simulated data. On occasions when raptors remained on a kill or squirrels were recorded more than once in a nest, only the first location at the site was included in the analysis.

Seven adult and 21 juvenile Northern goshawks (*Accipiter gentilis*) were radio-tracked during October-February in 1980-84 on the Swedish island of Gotland. Rabbits (*Oryctolagus cunniculus*) and pheasants (*Phasianus colchicus*) dominated the prey biomass (Marcström et al. 1990, Kenward et al. 1993). Goshawks forage preferentially in the 200 m woodland-edge zones that are used by these prey (Kenward 1982); foraging habitat along the edge of abundant and fragmented woodland was fine-grained and strongly heterogenous through the average 1330 ha (spread of 200-3180 ha) outer MCP ranges of these hawks. In other parts of Sweden, outer MCP areas of goshawks differed between adult and juvenile hawks (Kenward et al. 1981).

The other three species were studied in southern Britain. We recorded 114 ranges for common buzzards (*Buteo buteo*) in Dorset during October 1990-94, shortly after their main autumn dispersal period (Walls and Kenward 1995). Signal modulation by posture sensors on the radio tags was used to record, at the start of checking each individual, whether it was perched, flying, or probably feeding on the ground. For 29 birds, ranges were recorded in their first autumn and at the same time again in their second year. These raptors, with outer MCPs averaging 252 ha (25-2050 ha), were feeding mainly on invertebrate prey in fields averaging 6 ha (1-33 ha). Measured in one dimension (using √[patch-area/range area]), fields averaged 15% the width of buzzard ranges, whereas the arbitrary 200 m woodland edge zones were 5% the width of goshawk ranges.

Location data for 138 grey squirrels (*Sciurus carolinensis*) were collected in September-October and in January during 1980-88 in three woods of 9-157 ha. The woods were dominated by oaks (*Quercus robur*), but species composition and age varied between the 3-10 ha compartments. These habitats were very coarse grained compared to squirrel outer MCPs, which averaged 4.3 ha (0.5-32 ha). Grey squirrel densities were estimated by live-trapping, and winter food supplies by counting fallen acorn cups in spring (Kenward and Holm 1993). We also tracked 14 red squirrels (*Sciurus vulgaris*) during October 1991 and January 1992 in patches of Scots pine (*Pinus sylvestris*) around two oil extraction sites on Furzey Island in Poole Harbour (Kenward et al. 1998). The patches of 0.1-2.5 ha were less than 5 m wide, about a third the width of the 2.7 ha (1.2-6.2 ha) outer MCP ranges on Furzey Island. Outer MCPs of grey squirrels are known to be larger for males than females, and increase in size with decrease in squirrel density and with decrease in acorn abundance (Don 1983, Kenward and Holm 1993); red squirrel ranges have similar relationships between range sizes and food supplies (Wauters and Dhondt 1992).

HOME RANGE ESTIMATORS

Density methods

Early methods of estimating home range from point location data assume that a single area of animal activity can be bounded by an ellipse (Dalke and Sime 1938, Jennrich and Turner 1969, Koeppl et al. 1975, Dunn and Gipson 1977). This approach (Fig. 1a) assumes a bivariate normal distribution of locations about a range center, and fits poorly when locations are biased from the center or in multiple nuclei, but gives stable (albeit biased) estimates of range size with small numbers of locations (Robertson et al. 1998), sometimes for only 10-15 points (Kenward et al. unpublished). We estimated Jennrich-Turner ellipses (method *Ejt*; abbreviations are summarized in Table 1) for the data sets and also derived an asymmetry index (*JTasym*) as the ratio of standard deviations on the major and minor ellipse axes.

Recent methods estimate a mean location density at each intersection of an arbitrary grid imposed on the data, using the harmonic mean or other kernel density functions, and then interpolate contours between the estimated density values (Dixon and Chapman 1980, Worton 1989). The density isopleths that are defined by these contouring methods can depict multinuclear ranges with as few as 30 locations (Harris et al. 1990, Seaman et al. 1999). However, the size and shape of density isopleths varies considerably with the implementation, because of dependence on the scale and position of grids used to estimate harmonic mean densities, or on variation in a smoothing parameter (also called bandwidth) for other kernel techniques (Worton 1989, Seaman and Powell 1996). The resulting implementation-dependence enables deliberate variation of analysis conditions, but also provides scope for subjectivity and is a problem for standardization (Lawson and Rogers 1997).

We plotted isopleths to fit a grid of 40x40 cells. For harmonic mean analyses, locations were not centered in cells (Spencer and Barrett 1984). Isopleths were either "density-inclusive" when they contained a given proportion of the density distribution (method *Hud*, Fig. 1b), or were "location-inclusive" if they contained the equivalent proportion of the locations ranked by their density score (*Hul*). In these cases, the outer boundaries were Hud_{99}, which included 99% of the estimated density distribution, and the Hul_{100} isoline that just included all the locations. In general, for estimations using method Mmm_k, the capital *M* denotes the fundamental technique, the lower-case letters *mm* give details of the implementation (e.g. Harmonic mean, uncentred, density-inclusive); the subscript shows that the core was based on *k*% of the density distribution or locations, as appropriate to the method (see Table 1).

For Gaussian kernel estimators, the reference smoothing parameter (*h*) of Worton (1989) was multiplied by 0.4 (*K4d*), 0.6 (*K6d*), 0.8 (*K8d*), 1.0 (*K10d*, Fig. 1c) and 1.2 (*K12d*). The highest inflection point on a plot of integrated mean square error values against *h* provided a unique choice (by least squares cross validation, LSCV) of an "optimized" smoothing constant (*Kod*), defaulting to *K10d* when there was no inflection (Worton 1989). We also optimized Worton's (1989) adaptive (tail-weighted) estimates, to give plots based on density alone (*Koad*, Fig 1d) or on locations ranked by density (*Koal*). Analogy with definitions for harmonic mean analyses from Spencer and Barrett (1984) provides range structure statistics from kernel analysis estimates of *Kspread* dispersion (*Kdisp*), kurtosis (*Kkurt*) and *Kskew* (all defined in Table 1).

Link-distance methods

The use of link-distances to estimate home ranges is fundamentally less "smoothing" than the density methods, through using single distances to locations instead of mean distances to all the locations. The minimum convex polygon (MCP) of Mohr (1947) has the minimum sum of link-distances between pairs of peripheral locations. This outer MCP fails to distinguish the internal structure of ranges. Moreover, it is highly sensitive to outlying locations (Macdonald et al. 1980) and, although area estimates are often reasonably stable with 30 locations if these are well spaced in time (Kenward 1987, Harris et al. 1990), excursive activity tends to add area continually and create dependence on sample size. We use an X to denote methods based on convex polygons. The concave polygon of Harvey and Barbour (1965) also has a minimum sum of peripheral link-distances, but with no link longer than an arbitrary fraction (i) of the maximum distance between two locations (the range *span*). V_i denotes methods based on concave polygons, which typically have $i = 0.5$ (i.e. $V_{0.5}$). However, progressive reduction from $i = 1$ (i.e. $V_{1.0}$) can produce complex range outlines (Fig. 2a), including separate activity nuclei. Moreover, if a boundary strip is added to these polygons at half the resolution of the tracking technique, to represent assignment uncertainty between adjacent coordinates (Stickel 1964), at $i = 0$ the range is defined by the individual grid cells (Fig. 2b) of Siniff and Tester (1965).

A second family of convex polygon methods is based on ranking distances of locations from a range center, followed by progressive peeling of edges that include the furthest locations (Kenward 1987). This minimizes a mean location-to-center distance. As range centres, we used the tree nest of squirrels (Xn), or the location at which the kernel density estimate was maximized (Xk) or a recalculated arithmetic mean (Xr). Xr was recalculated after excluding each outermost location, such that it tended to move to the area of densest locations (Fig. 2c). Xr thus provides an approximation to a density-maximizing polygon (Hartigan 1987) without the disadvantage that calculation time is an exponential function of location number (Worton 1995a). All these peeled polygons form cores within the outer MCP, which is Xn_{100} ($= Xk_{100} = Xr_{100} = V_{1.0}$). However, the resulting cores are mononuclear and may not conform well to the pattern of locations (White and Garrott 1990).

A third family of polygon methods involves cluster analysis (Anderberg 1973) of nearest-neighbor distances between locations, which enables them to distinguish multinuclear range cores. Our method uses a modification of single linkage cluster analysis (Everett 1980). Locations are linked in clusters that minimize the mean joining distance (Kenward 1987). To reduce fragmentation as a result of serial spatial correlation, the minimum cluster size is three locations. Thus, the three locations with the minimum sum of nearest-neighbor joining distances form the first cluster. This cluster gains a fourth location if the distance to its nearest outlier is less than the mean nearest-neighbor distance in the next potential cluster (Fig. 3). After more than one cluster has formed, clusters fuse if the outlier being assigned to one is already part of another. If more than one cluster has the same distance to its nearest outlier, the cluster gains the outlier with the minimum sum of distances to every location in the cluster (effectively the distance to its centroid). Outlines round the separate clusters are either convex polygons (Cx, Fig. 2d) or concave polygons with $i = 0.5$ (Cv). In this family of polygons, Cx_{100} is the outer MCP and $Cv_{100} = V_{1.0}$ if the range is mononuclear, but also if the distance between two or more separate nuclei is less than from a nucleus to a distant outlier; the shape of Cx_{100} and Cv_{100} is thus, like that of the outer MCP, sensitive to outlying locations.

Locations can be clustered by using other rules, for example by prioritizing a centroid-distance joining rule. We prioritize the nearest-neighbor method on the assumption that animals probably route their initial visits to a new location from one nearby familiar location rather than from many. This approach conveniently encompasses the extension of polygons from their ends along line features, such as field boundaries or woodland edges.

Outlier-exclusive cores from nearest-neighbor distances

Although contours at 95% of the density distribution are sometimes used to describe range cores (Ackerman et al. 1990), there is no biological justification for choosing this arbitrary value along a parametric continuum (White and Garrott 1990). However, if polygons or location-inclusive contours are used to plot a distribution of increasing area against increasing proportion of use (Ford and Krumme 1979), discontinuities often appear. Typically, area increases slowly within a compact core and then rises sharply to include outlying locations. This discontinuity can be used to estimate a high-use core by eye (Clutton-Brock et al. 1982), but the process remains subjective. Similarly, cores defined by the point at which separate isopleths fuse (Wray et al. 1992b) depend on subjective choices of smoothing parameter or of interval size across the matrix used to plot isopleths. Samuel et al. (1985, see also Samuel and Green 1988) provided an objective test for a discontinuity, based on comparing numbers of locations in grid cells; however, χ^2 tests of significance with only 30 locations cannot be based on many grid cells, and thus provide only a very coarse description of range shape.

We base estimation of outlier-exclusive cores (OECs) on the assumption that animals travel at a different rate when they make excursions from these cores, because they are engaging in different activities. For example, they may travel slowly while foraging in the core but move rapidly on excursions to review resources elsewhere (Pyke et al. 1977) or for social purposes. Alternatively, they may tend not to return to the vicinity of outlying locations, so that these remain far apart. If rates or movement or re-visiting differ between excursive and core activities, we expect the distribution of distances between locations in range cores to have a smaller mean than the distribution of distances between excursive locations, such that nearest-neighbor distances of excursive locations tend to become statistical outliers from the main distribution of nearest-neighbor distances.

The Gaussian kernel function introduced for density estimation by Worton (1989) was used to normalize the nearest-neighbor distances (d_i) to r_i where

$$r_i = f(d_i) = \exp(-d_i^2 / 2h^2)/(2\pi h^2) \quad \text{with} \quad h = n^{-1/6}\{\sum_{i=1}^{n}((x_i - \bar{x})^2 + (y_i - \bar{y})^2)/(2(n-1))\}^{0.5} \qquad (1)$$

and $(\bar{x}, \bar{y})$ is the mean of the n locations (x_i,y_i) used to estimate the home range. When tested on data from buzzards, goshawks or squirrels, h was estimated separately for each individual range. However, in tests for departures from normality, the distribution of r_i values was pooled for all ranges of that species. This Gaussian transformation (1) gave a distribution with a smaller (and non-significant, $P > 0.2$) departure from normality than other inverse and logarithmic functions.

Outliers were then defined by determining an "outlier exclusion distance" (OED) in two ways. We first used an analogue of the 95% density-based contour to truncate the distribution of r_i values for each range. If $r_{t05} = \bar{r} - z_{0.05}SD_r$, where $\bar{r}$ and SD_r are the mean and standard deviation of the r_i distribution and z_α is the one-sided α probability value of a cumulative standard normal distribution (i.e. $z_{0.05}$ = 1.645), then the OED is defined as:

$$d_{t05} = f^{-1}(r_{t05}) \qquad \text{where } f^{-1}(r) = \{-2h^2 \log_e(2\pi h^2 r)\}^{0.5} \tag{2}$$

If $r_{t05} < 0$ and hence d_{t05} was infinite, the OED was set to infinity and no locations were considered to be outliers.

The second approach was to exclude the location with the smallest r_i (largest d_i) and re-calculate the mean ($\bar{r}_{(n-1)}$)and standard deviation ($SD_{(n-1)}$) of the distribution, then test if $r_n < \bar{r}_{(n-1)} - z_{0.05}SD_{(n-1)}$, in which case the process was repeated for $r_{(n-1)}$ until $r_{(n-k)} > \bar{r}_{(n-k+1)} - z_{0.05}SD_{(n-k+1)}$ and *k* locations had been excluded. The OED found by this iterative method was the distance $d_{i\alpha}$, where

$$d_{i\alpha} = f^{-1}(\bar{r}_{(n-k+1)} - z_\alpha SD_{(n-k+1)}) \tag{3}$$

The iterative method was tested with α = 0.001 for relatively weak exclusion, eliminating only the most distant outliers, and α = 0.01 for relatively tight cores. If $(\bar{r}_{(n-k+1)} - z_\alpha SD_{(n-k+1)})$ became negative, the OED was again set to infinity and no locations were considered to be outliers. We found that using a continuity correction (d_i + 0.5) for d_i, which was the equivalent of adding a boundary strip at half the tracking resolution, reduced a tendency for the range outline to become grid cells when core locations were closely packed and numerous.

After estimating an OED, heirarchic incremental cluster analysis was used to form clusters representing activity nuclei from all locations with d_i < OED. Convex polygons were drawn round the nuclei, for the OED truncated at the 5% α-level (method *tx05*) and the iterative OEDs with 1% and 0.1% α-levels (methods *ix01* and *ix001*, Table 1). One problem with convex polygon outlines is that clusters with a majority of fixes in a crescent very occasionally create a polygon that overlaps a small cluster. This problem can be solved by using concave polygon outlines. The rescaling of *x* and *y* coordinates to equalise variance (Silverman 1986) was suggested in Worton (1989) for kernel estimation, and could improve OED estimator methods for strongly asymmetric ranges.

The identification of outlier-excluded nuclei provided a number of statistics to describe internal structure of home ranges, including the percentage of locations that comprize the core (*Cloc%*) and the number of separate nuclei (C*nuc*) that these provide. The diversity of use of the different nuclei (*CS-loc*) is indicated by Simpson's index, $1/\sum p_i^2$, where p_i is the proportion of the total *n* locations in nucleus *i*. C*S-loc* is 1 if all the locations form one nucleus, and increases with the number and equitability of the nuclei used. The area of individual nuclei can be treated in the same way to provide an index of area diversity (C*S-area*). The patchiness of the usual area is indicated by expressing the sum of areas of the separate convex polygons (Ax_i) around each nucleus as a fraction of the area(Ax) of a single convex polygon around all of them. This "partial area"

$$C_{part} = \sum_{i=1}^{C_{nuc}} Ax_i / Ax$$

decreases from 1, if all the locations are in one nucleus, to a small fraction if the nuclei are far apart.

COMPARING ESTIMATORS

The nearest-neighbor home range estimators were compared with others that are readily available in software packages (Ackerman et al. 1990, Kie et al. 1994, Camponotus AB and Radio Location Systems AB 1994, Seaman et al. 1998, for others see Larkin and Halkin 1994), in this case using a modified version of Ranges V (Kenward and Hodder 1996). We compared the estimators in terms of ability to detect expected differences between species and age categories, and correlations with food supply, population density and body mass. Differences between species in range structure were expected because of marked differences in mobility and fragmentation of their habitats. When comparing range structure indices between species, we followed up an overall ANOVA with *t*-tests between pairs of species, after arc-sine transformations to normality for *Cpart* and proportions of locations in OECs.

Logarithmic transformations were used for area estimates. Relationships between range areas and age, density or environmental factors, which were expected on the basis of previous studies, are summarised in Range Analysis Displays. These RADs are shaded to highlight significance of test statistics using standard single-test probability levels across a sequence of 15 core sizes (in columns) for a sequence of 17 home-range estimators (in rows), followed by the three OEC estimators placed to indicate the average percentage of locations in the core. Density-based area estimates for cores that contained less than 30% of the distribution sometimes approached 0, so RADs show values from 30% to 95% of the distribution at 5% intervals, and for 99%. Minimum-distance methods (also *Kol*, *Koal* and *Hul*) are shown with 30% to 100% inclusion of locations. For concave polygons, edges were restricted progressively from 30% to 100% of the range *span* (i.e. the maximum distance between two locations) at 5% intervals.

We listed density-based estimators in the top rows of RADs and minimum-distance estimators at the bottom. The least-smoothed kernel contours are towards the top of the displays, becoming smoother towards the middle, before harmonic-mean contours, site-centred mononuclear polygons and then back through density-focusing recalculated polygons to multinuclear cluster polygons at the bottom. There is therefore a sequence of decreasing range detail in density-based methods from top to center of the RAD, and then increasing detail through minimum distance methods towards the bottom, with ellipses falling outside this trend at the top, and a separation at the bottom for concave polygons and OECs.

With test statistics estimated 258 times in each RAD for the same data sets, test results will not be independent and there is a high probability of a Type 1 error over the whole table. However, our aim was not to trawl for significant results, but to assess patterns of test results across range estimators and core inclusion levels, and hence to make recommendations for choice of estimators in future analyses.

RESULTS

Core and excursive activity

The assumption of activity differences between core and excursive areas could be tested with data from buzzards, because their activity was recorded at each location. In order to avoid assumptions about the proportion of locations that might have been excursive, we tested whether activity at the one location with the greatest nearest-neighbor distance was different from that across all other locations. The activity at the outermost of the 30 locations in the 114 range records was 9% in flight, 45% moving but probably not flying and 46% inactive. In contrast, the means from the other 29 locations were 2% in flight, 37% moving and 61% inactive ($\chi^2_2 = 26.54$, $P < 0.001$). Buzzards were more likely to be flying, or otherwise active, when they were at their most extreme locations than at other times. Equivalent activity data were not collected from the other species.

Inter-species comparisons of home-range structure

This section assesses the evidence revealed by different indices for expected differences between species in the structure of home ranges. Intra-species differences in range area are examined in subsequent sections. Range structure indicated by statistics based on location density distributions showed relatively slight differences between species in ANOVAs. Values of *JTasym* show that ellipses were more elongated in shape for red squirrels in the narrow woods of Furzey Island than for grey squirrels ($t_{150} = 4.5$, $P < 0.001$) and buzzards ($t_{70} = 3.7$, $P < 0.001$) in more continuous habitats. Values of *Kdisp* showed that locations in grey squirrel ranges were less dispersed than for the other species ($t \geq 2.0$, $P \leq 0.05$). The density distribution was more leptokurtic for red squirrels than for grey squirrels ($t_{150} = 3.3$, $P = 0.001$).

Among structure statistics derived from outlier-exclusion, those estimated by truncating the nearest-neighbor distribution showed less significant differences between species than those estimated by iterative exclusion. Thus, the proportion of locations contained (*%loc*) within *tx*05 did not vary significantly between species (Table 2). However, cores found by iteration differed strongly between species (P <0.001), both when the α-level was set to be highly exclusive of outliers (i.e. $\alpha = 0.01$ for *ix01*) and for the larger proportion of locations included when the α-level was set to exclude only the most extreme locations (i.e. $\alpha = 0.001$ for *ix001*). In both cases, outlier-exclusive cores of goshawks contained 6-8% fewer locations than those of the other species, with the difference most marked for the strongly exclusive cores ($t \geq 2.6$, $P \leq 0.01$); the proportion of locations in goshawk cores was also more variable than for buzzard or grey squirrel (variance ratio F tests, $P < 0.05$).

The greatest differences in range structure between the species were shown by the fragmentation indices *Cnuc, Cpart, CS-loc* and *CS-area*. All outlier-exclusion methods estimated that goshawks and red squirrels had more activity nuclei (*Cnuc*) than buzzard and grey squirrel ($t \geq 3.2$, $P < 0.01$), and the iterative methods *ix01* and *ix001* also indicated that buzzards had fewer nuclei than each of the other species ($t \geq 3.4$, $P < 0.002$). The effect was again greatest for cores estimated by the weakest outlier exclusion method *ix001* ($t \geq 3.6$, $P \leq 0.001$). Values of other fragmentation indices are constrained by the number of activity nuclei, because partial area (*Cpart*) and diversity index (*CS-loc, CS-area*) values are 1 for mononuclear ranges. These indices would therefore have been highly intercorrelated, with partial areas and diversity indices closest to unity when there was least exclusion of outliers. Although about 1 in 4 buzzard ranges had two activity nuclei (i.e. *Cnuc* = 1.27), the *Cpart* value of 0.98 for buzzards in *ix001* cores shows that there can have been little distance between these nuclei: buzzard ranges were effectively mononuclear.

Age-related home-range area within raptor species

Home-ranges were larger for 7 adult goshawks than for 21 juveniles. Using Gaussian kernels to estimate location densities (Fig 4a), the differences became greater as smoothing relaxed from *K4d* to *K10d*, with a further slight increase using optimisation by least squares cross-validation (*Kod*) and a marked increase in statistical significance when based on LSCV with adaptive kernels (*Koad*). If contours were plotted to include the required proportion of locations (*Koal*), differences were weaker and more erratic, but reached maxima for contours that included 80% of the locations, and again for 55%. Range areas of adults and juveniles only just differed significantly if plotted as density-inclusive harmonic mean contours (*Hud*) that included 75-85% of the location density distribution. However, location-inclusive harmonic mean contours (*Hul* in Fig 4b) gave relatively marked differences when cores contained 45-50% of the locations. Ellipses (*Ejt*) gave a difference that approached significance at the 5% level and did not vary with the percentage inclusion of the density distribution. Among the minimum-distance polygons, age differences based on peeling to maximize fix density (*Xr*) approached significance at the 1% level using 40-55% of the locations. Differences for outer MCPs approached significance at the 5% level.

For goshawks, the range analysis display (RAD) shows that in addition to effects noted in Fig. 4, areas were also greater ($P < 0.05$) for adults than for juveniles in OECs obtained by truncation *tx05* (Fig 5). The age difference was most significant for $Koad_{65}$ ranges, in which the mean area was 260 ha (95% CL 170-380 ha) for juveniles and 670 ha (410-1100 ha) for adults. The areas of these 65% cores were similar to the 290 ha (200-420 ha) and 500 ha (320-780 ha) in the 85% cores that gave the maximum difference in *Hud*, and not significantly different from the 360 ha (220-590 ha) and 850 ha (500-1410 ha) in 85% *Koal* cores. The different estimators thus gave maximum differences for similar home range areas despite including different proportions of the utilization distribution. The greatest difference between the age categories resulted from expressing $Koad_{65}$ as a fraction of the more peripheral $Koad_{95}$ ($t_{26} = 3.82$, $P < 0.005$). Adult goshawks not only had larger ranges than juveniles but also relatively less increase in area as core increased from 65% to 95% of the density distribution.

Average range areas were smaller ($P < 0.05$) when 29 of the buzzards were juvenile than for the same 29 birds a year later when estimated by Huf_{75}, Cx_{100}, Cv_{100}, Cx_{65}, Cx_{70} and Cv_{70}; the difference was most significant when based on outlier-exclusive cores *ix001* ($t_{56} = 2.77$, $P < 0.01$). The increase in area of Cx_{100} with age was improved if the proportion of locations in *ix001* was included in a multiple regression ($t_{55} = 2.19$, $P < 0.05$). This indicates that second-year buzzards, like adult goshawks, had larger ranges than juveniles and relatively less excursive area outside their range cores. However, whereas differences between home ranges of adult and juvenile goshawks were strongest with density-based estimators, for buzzards the polygons showed the largest differences.

Variation of squirrel home range area with food, population density and body mass

Almost all radio-tracked squirrels were in their second autumn, because most were too small to radio-tag for their first autumn, so no age-based comparisons were possible. In view of the known differences in range size of male and female grey squirrels (Don 1983, Kenward 1985), the sexes were analysed separately. Results are presented for the females, because their sample sizes were largest, but males showed the same trends in the analyses.

In autumn (September-October), there were strong relationships between mean range area and the abundance of acorn food for grey squirrels (Fig 6). All correlations were negative: range area decreased with increase in food abundance. There was a strong correlation ($P < 0.002$) for the outlier-exclusive core *ix001*, and also ($P < 0.01$) for harmonic mean contours and polygons that contained 30-75% of the locations. The *ix001* cores averaged 1.42 ha (95%CL 1.25-1.61 ha), which was 60% of the mean outer MCP area of 2.26 ha (1.87-2.74 ha) and an order of magnitude greater than the 0.08 ha (0.07-0.09 ha) average core size of Cv_{35}, the core that gave the strongest correlation of range area with food abundance ($r_9 = 0.85$, $P < 0.001$). Correlations with food supply were therefore strong not only for the weakly exclusive OEC, but also for much smaller areas that were perhaps associated with production of autumn litters when food was especially abundant.

In winter (December-January), home-range area correlated strongly with the density of female squirrels (Fig 7). All correlations were negative: range size decreased with increase in squirrel abundance. In this case, areas within density-inclusive contours correlated most consistently with the environmental variable, the strongest relationship being ($r \leq -0.89$, $P < 0.001$) for all the LSCV-optimized kernel contours ($Kod_{30\text{-}99}$). However, convex polygons from incremental cluster analysis (Cx) and peeled polygons (Xr, Xk, Xn) also showed strong correlations ($P < 0.001$) when 90-100% of the locations were included, as did $V_{0.6}$-$V_{1.0}$ and the core with outlier exclusion by truncation of the link-distance distribution (*tx05*). In contrast to the strong correlations between range areas and squirrel density, range sizes in winter showed only one significant correlation with the size of the acorn crop for that year, in Hud_{99} ($r_{10} = -0.63$, $P < 0.05$).

The 14 red squirrels were tracked and weighed in December 1991, between tracking sessions in October 1991 and January 1992. We compared home-range data with their body mass as a proxy for their individual food supplies. There were negative correlations between red squirrel core areas and body mass for OECs and again at small core sizes. The strongest correlation with body mass was for tx_{05} ($r_{12} = -0.71$, $P < 0.01$), but there were significant correlations ($P < 0.05$) for all other OECs. Squirrels with large body mass had small outlier-exclusive cores. There were also significant correlations ($P < 0.05$) for Xn_{90}, Cx_{95} and $Cv_{85\text{-}95}$, as well as for the smaller core sizes $Xn_{30\text{-}40}$, Xk_{30}, $Cx_{45\text{-}50}$ and Cv_{50}, with a stronger correlations for Xr_{30} ($r_{12} = -0.69$, $P < 0.01$). The only correlations to approach significance among the contouring methods were for the tightest density-inclusive kernel contours ($r_{12} = -0.47$ for $Kd4_{35\text{-}55}$, $P = 0.09$) and for harmonic mean contours plotted around 85% of the locations ($r_{12} = -0.51$ for Hul_{85}, $P = 0.07$).

DISCUSSION

Density-based home range methods create isopleths from density functions derived by averaging distances. They either use one centre, to describe ellipses, or create contours based on local variation in density across a matrix. Increases in the value of a smoothing parameter (bandwidth, *h*) decrease the role of local effects (Worton 1989, Seaman and Powell 1996), until isopleths that may have been multinuclear at small *h* values resemble mononuclear ellipses at large *h* values. The other main class of methods is based on minimising the sum of link-distances to individual locations, either (i) between peripheral locations to create outer MCPs and concave polygons, or (ii) from a range centre for mononuclear peeled polygons, or (iii) between nearest-neighbor locations. Methods based on minimising distances between locations (i and iii) eventually reduce to grid cells (Fig 2), and are therefore sets of sophisticated joining rules for grid cells (Voight and Tinline 1980). As is the case for the density-based methods, the use of increasingly local measures permits multinuclear outlines.

The implications of this similarity between the two classes, whereby estimators increase in ability to describe detailed range structure with increasing dependence on local effects, can be interpreted from analysis of complete movement trajectories in Robertson et al. (1998). These authors examined how variation in the number of locations sampled along animal trajectories affected the ability of ellipses, contours, peeled and cluster polygons to describe shape (in terms of density of trajectory inclusion) and to provide stability (in terms of repeatability of area overlap). Although ellipses were poorer than the other methods for describing shape, they were the most stable with small sample sizes. Polygon methods generally fitted the trajectory more tightly but with less stability than density methods; cluster polygons had the best fit, but least stability at small sample sizes. By analogy with clusters, areas and statistics based on OEC methods are likely to change with sample size, but should become more stable as sample size increases because estimates of range outline become more stable (Robertson et al. 1998). Unlike outer MCPs, these indices should not continue to increase as sample size increases, or to decrease.

This detail/stability gradient in the methods also to some extent reflects parsimony, in that the most parsimonious estimators (ellipses, MCP, ellipses) also provide least detail. However, extension of the linkage-sum approach to nearest-neighbour distances, to give high detail with polygon techniques, is more parsimonious than using a multiplier for the reference smoothing parameter in kernel analyses.

It is likely that the detail/stability gradient would operate similarly for other estimators that can provide detailed shapes but were not tested here. Thus, ranges plotted as grid cells typically require more than 100 locations to reach a maximum area (Harris et al. 1990). Tesselations round locations (Wray et al. 1992a) have areas that are dependent on distance from all adjacent locations, and thus on local density. This tiling process may be better than contouring for detecting density discontinuities, but only when there are enough locations to permit exclusion of edge tiles that extend to infinity.

The assumption behind the use of outlier exclusion to estimate OECs was that activity differences were likely to produce greater nearest-neighbor distances in the excursive areas than in the core. This assumption was suggested by earlier qualitative observations, for example that goshawks made lengthy excursive flights shortly after feeding in their main hunting area (Kenward 1977), and that male grey squirrels expanded outer MCP ranges more than cores (peeled polygons) while they visited females during courtship (Kenward 1985). The assumption of greater mobility in an excursive area was supported by quantitative data on activity of the radio-tracked buzzards. We also found strong size correlations between cores estimated by truncation and those estimated subjectively by inspecting inflexions in utilization distribution plots (Hodder et al. 1998). Moreover, the OECs and their associated statistics, gave highly significant differences ($P < 0.01$) in range structure between species, in range area between buzzard age categories and in all tests with squirrel data.

Outlier-exclusion defines an area that may correspond to that used for "normal activities" *sensu* Burt (1943), which might be called a "usual area" by analogy with the "usual range" territory of Johnstone (1992). The detection of sub-units within home ranges may not stop with outlier exclusion, because there were peaks in the strength of relationships between range size and other factors not only for OECs, but also in much smaller areas that contained only 30-50% of the locations (Figs. 4-7). If these inner "focal areas" represent another discontinuity in behaviour, an objective definition would be useful for them too, as would the definition of a best estimator for the "familiar area" (Hodder et al. 1998) including both usual and excursive areas that defines the habitat available to an animal.

The use of average distances to estimate densities, compared with use of single distances between locations in linkage methods, produces a marked difference between the two classes of estimator in the ability to reflect discontinuities in the spatial distribution of locations. The extension of polygon boundaries into areas not visited by animals can be no greater than the width of a boundary strip, which also creates a single grid cell round outliers or multiple records at a single location. This should be an advantage if the aim is to investigate habitat-linked phenomena for animals foraging in coarse-grained habitats. In contrast, the assumption of a normal distribution in density-based methods either extends contours into unused areas (Fig 1b,c) if defined loosely, or creates rings of variable circumference round individual locations (Fig 1d). Nevertheless, if the aim is to derive area estimates based on general patterns of movements, perhaps around one center of activity, the smoothing of density estimators may be an advantage, especially ellipses if few locations can be sampled.

On this basis, the detection of strong correlations of range area with body mass in red squirrels and food supply in grey squirrels using polygons (Fig 6), but not with contouring methods, probably reflects movements that were influenced by habitat discontinuities. Moreover, structure statistics based on OECs showed that, within squirrels and raptors, the species with the most patchy habitat (goshawk and red squirrel) also had the most multinuclear range structure (Table 2). Strong correlations between range sizes and grey squirrel abundance from the density-based methods may reflect relatively diffuse territorial relations between squirrels in continuous woodland. However, it is not clear why differences in range area between male and female goshawks were more significant when estimated by contours than by polygons (Figs 4,5) whereas polygons gave the strongest discrimination between buzzard age classes. Was this because buzzard habitats were more coarse-grained than for goshawks, or because 30 locations were too few to estimate the strongly multinuclear goshawk ranges adequately with linkage methods?

Until we know why methods differ in their ability to answer particular biological questions, there is a danger in the ready availability of many techniques for describing home ranges. The ability to compile extensive range analysis displays with current software (Figs. 5, 6 and 7) creates much scope for deriving false positive relationships (Type I errors). This may be a particular risk when range outlines are not based purely on density distributions but are vulnerable to chance variation in recording the locations, as is the case both for polygon methods *Xr, Xk, Xn, Cx* and *Cv* and also for location-inclusive isopleths *Koal* and *Hul*.

The solution must be to minimise risk of Type I errors by *a priori* selection of estimators. Our analyses show clearly that no single estimator always produces the strongest results, so how can one choose? The choice will depend partly on which range characteristic is being studied. Outer MCPs have been widely used to estimate range size (Harris et al. 1990) and to assess habitat available in familiar areas (Aebischer et al. 1993), but an alternative would be to use expansive density isopleths such as *Ejt*$_{95\text{-}99}$ or *K10d*$_{95\text{-}99}$ (parsimony favours use of reference *h*, although LSCV gave best results for goshawks). For usual areas, a choice of iterative OECs could be made between weakly exclusive *ix001* and strongly-exclusive *ix01*, perhaps using truncation-based *tx05* by default; it is worth noting that *ix001* and *tx05* gave the strongest results in our studies. There is no easy choice of a density-based equivalent along a continuity of core percentages, but possibilities would be to use contours that either included the same average number of locations or the same average area as the selected OEC. For focal areas, choices among cores of 30% to 50% and between estimators remain unavoidable, although we note that cluster analysis tended to give strong correlations for linkage methods and harmonic means among the density estimators.

There remains the problem of choosing between density and linkage methods. Tests based on simulated locations (Boulanger and White 1990, Glendinning 1992, Worton 1995a,b) might help but results are likely to depend on the way in which data are generated, probably favouring density methods unless simulation models permit abrupt discontinuities. The most appropriate estimator will probably depend on the way the animals are moving, which will depend on their activity priorities at the time. If their priority is foraging in tightly defined patches of discrete habitat, ranges may best be represented by linkage methods, whereas diffuse interactions with social competitors or scattered food may suit density-based models. Until this question is resolved, biologists may choose to use estimators of both types in each analysis, but should note the need to reduce α-levels for acceptance of significant results accordingly. Thus, for the use of one polygon type and one density estimator, a test result with $P < 0.025$ would be necessary for acceptance of significance at the 5% level, or at $P < 0.01$ if five combinations of estimator and core size were to be used.

In conclusion, there is probably no single best estimator of ranging behaviour. Selection of the most appropriate method for answering a particular biological question will probably depend on how the animals are moving, on sample size and on the question being asked. Ready access through software to many range analysis techniques may have opened a Pandora's box of opportunity to trawl for significant results. However it also provides the opportunity for large numbers of tests with large numbers of animals that will help to define rules for a single *a priori* choice in each situation.

ACKNOWLEDGMENTS

We thank M. Karlbom for help tracking goshawks, during work in Sweden organized by V. Marcstöm, and B.H. Cresswell, F.I. Doyle, J.L. Holm, T. Parish, R.J. Rose for help tracking squirrels in Britain. We are grateful to N.J. Aebischer, R.E. Green, J.D. Hardcastle, B. H. Morgan, P.A. Robertson and G.C. White for stimulating discussions, and to N.J. Webb and two anonymous referees for comments that greatly improved the manuscript. Projects that provided data for this work were funded mainly by the British Petroleum Plc, the Natural Environment Research Council and the Swedish Sportsmens Association, with generous provision of S.S.W.'s time and many facilities for the work by Biotrack Ltd.

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TABLE 1. Definitions of abbreviations used for home range outline estimators and structure statistics.

Estimator type	Abbreviation	Description
Density-based		
	Ejt	Ellipse, Jennrich-Taylor type
	Hud	Harmonic mean isopleth, untransformed locations, density-inclusive
	Hul	Harmonic mean isopleth, untransformed locations, location-inclusive
	K4d	Kernel isopleth, 0.4x standard smoothing, density-inclusive
	K12d	Kernel isopleth, 1.2x standard smoothing, density-inclusive
	Kod	Kernel isopleth, LSCV-optimized smoothing, density-inclusive
	Koad	Kernel isopleth, LSCV-optimized smoothing, adaptive, density-inclusive
	Koal	Kernel isopleth, LSCV-optimized smoothing, adaptive, location-inclusive
		LSCV = Least squares cross-validation
Linkage-based		
	MCP	Minimum convex polygon including all locations in a range
	V	Concave (restricted-edge) polygon
	Xn	Convex polygon, peeled by distance from nest or other focal site
	Xk	Convex polygon, peeled by distance from location with peak kernel density
	Xr	Convex polygon, peeled by distance from recalculated arithmetic mean
	Cx	Cluster analysis, convex polygons
	Cv	Cluster analysis, concave polygons with half-span edge-restriction
Outlier-exclusive		
	tx	Truncation outlier exclusion, convex polygons
	ix	Iterative outlier exclusion, convex polygons
Density statistic		
	JTasym	Eccentricity of ellipse (= ratio of minor to major axis standard deviations)
	Kspread	Mean of all kernel-transformed inter-location distances
	Kdisper	Peak mean of kernel-transformed distances from one location to all others/ standard deviation of all kernel transformed inter-location distances
	Kkurt	*Kspread*/peak mean of kernel-transformed distances from one location
	Kskew	Distance of peak density location from arithmetic mean/ standard deviation of all kernel transformed inter-location distances
Distance statistic		
	span	Maximum distance between any two locations
	Cnuc	Number of nuclei defined by cluster analysis
	Cpart	Area of individual cluster polygons as fraction of polygon round clusters
	CS-loc	Simpson's index for diversity of locations across clusters
	CS-area	Simpson's index for diversity of areas across clusters

TABLE 2. Differences between four species in home range structure based on density and link-distance statistics (defined in the text and Appendix I). Mean values are shown for each species with standard errors (in parentheses), together with *F*-values from 1-way ANOVA with 3 and 235 d.f.

Density-based statistics	*N*	*JTasym*	*Kdisp*	*Kskew*	*Kkurt*
Northern Goshawk	28	0.50 (0.02)	1.13 (0.06)	1.53 (0.35)	0.65 (0.01)
Common Buzzard	58	0.57 (0.02)	1.18 (0.07)	1.67 (0.11)	0.65 (0.01)
Grey Squirrel	138	0.58 (0.01)	0.98 (0.03)	1.51 (0.07)	0.64 (0.01)
Red Squirrel	14	0.43 (0.03)	1.14 (0.05)	1.78 (0.21)	0.68 (0.01)
F-value		4.5**	4.3**	0.6	3.0*

Outlier exclusion				Diversity	
by truncation, *a*=0.05	*Cloc%*	*Cnuc*	*Cpart*	*CS-loc*	*CS-area*
Northern Goshawk	89.0 (4.1)	2.67 (0.23)	0.58 (0.33)	1.94 (0.15)	1.75 (0.16)
Common Buzzard	86.7 (3.5)	1.62 (0.11)	0.93 (0.09)	1.34 (0.07)	1.34 (0.07)
Grey Squirrel	87.0 (2.3)	1.83 (0.08)	0.86 (0.08)	1.52 (0.06)	1.40 (0.05)
Red Squirrel	86.2 (8.3)	2.33 (0.27)	0.73 (0.43)	1.81 (0.20)	1.53 (0.18)
F-value	0.8	11.2***	11.9***	7.0**	3.7*

Outlier exclusion				Diversity	
by iteration, *a*=0.01	*Cloc%*	*Cnuc*	*Cpart*	*CS-loc*	*CS-area*
Northern Goshawk	77.6 (9.3)	3.39 (0.22)	0.39 (0.32)	2.55 (0.18)	2.41 (0.17)
Common Buzzard	89.9 (5.0)	1.56 (0.10)	0.94 (0.09)	1.34 (0.06)	1.30 (0.06)
Grey Squirrel	86.3 (3.7)	2.05 (0.08)	0.81 (0.10)	1.70 (0.06)	1.52 (0.05)
Red Squirrel	87.1 (11.8)	2.86 (0.32)	0.59 (0.45)	2.32 (0.28)	2.02 (0.25)
F-value	6.6**	24.2***	19.9***	16.9***	20.3***

Outlier exclusion				Diversity	
by iteration, *a*=0.001	*Cloc%*	*Cnuc*	*Cpart*	*CS-loc*	*CS-area*
Northern Goshawk	88.6 (7.7)	2.89 (0.24)	0.54 (0.34)	2.10 (0.17)	2.05 (0.19)
Common Buzzard	96.6 (3.2)	1.27 (0.07)	0.98 (0.04)	1.14 (0.04)	1.10 (0.03)
Grey Squirrel	94.9 (2.4)	1.63 (0.07)	0.91 (0.07)	1.37 (0.05)	1.27 (0.04)
Red Squirrel	94.4 (9.6)	2.73 (0.35)	0.67 (0.43)	2.18 (0.29)	1.83 (0.25)
F-value	5.8**	27.3***	23.9***	19.7***	21.4***

* $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

Figure legends

FIG. 1. The 30-location (□) range of a red squirrel on Furzey Island described by location density isopleths, based on (a) bivariate normal ellipses (*Ejt*), (b) harmonic mean contours (*Hud*), (c) Gaussian kernel contours with reference smoothing (*K10d*) and (d) kernel contours optimized by least squares cross validation (*Koad*). The squirrel moved on grassland (pale shading) and in woodland (dark shading), avoiding a central oil-production area and the surrounding sea.

FIG. 2. The 30-location (□) range of a red squirrel on Furzey Island shown as minimum-distance polygons with a boundary strip and (a) restriction of edge lengths to 0.35 x *span* (i.e. $V_{0.35}$), (b) restriction of edge lengths to 0 (grid cells), (c) peeling of locations furthest from the nest (*Xr*) and (d) cluster analysis of nearest-neighbor distances with convex polygons around nuclei (*Cx*).

FIG. 3. Defining multinuclear home range polygons by hierarchic incremental cluster analysis of nearest-neighbor distances between locations. Clusters 1, 2 and 3 have formed, with next nearest-neighbor distances d_1 ($=d_2$) and d_3 respectively. Locations 4-9 are unassigned. The mean joining distance will be minimized by next assigning location 4 to cluster 3, to add the smallest nearest-neighbor distance (d_3). Fusion of clusters 1 and 2 will follow, because $d_1 < (d_8+d_9)/2$. Only then will addition of $(d_8+d_9)/2$, to form a new cluster of locations (7-9), be the distance-minimizing option.

FIG. 4. Patterns of Student's *t* values for age-related differences (adult-juvenile mean) of goshawk home range areas in relation to the percentage of either the utilization distribution or locations, shown for areas based on various (a) density-based estimators and (b) adding link-distance polygon methods.

FIG. 5. Range Analysis Display (RAD) showing the pattern of Student's *t* values for range area differences between (n=21) juvenile and (n=7) adult goshawks. Single test statistical significance is highlighted for $P < 0.05$ (bold text) and $P < 0.01$ (light shading). See Table 1 for abbreviations.

FIG. 6. Range Analysis Display (RAD) showing the pattern of correlations between mean range areas of female squirrels in autumn (September-October) and acorn abundance during n=11 site-years. Single test statistical significance is highlighted for $P < 0.05$ (bold text), $P < 0.01$ (light shading) and $P < 0.001$ (bold text and dark shading). See Table 1 for abbreviations.

FIG. 7. Range Analysis Display (RAD) showing the pattern of correlations between mean range areas of female squirrels in winter (January-February) and density of squirrels during n=12 site-years. Single test statistical significance is highlighted for $P < 0.05$ (bold text), $P < 0.01$ (light shading) and $P < 0.001$ (bold text and dark shading). See Table 1 for abbreviations.

FIG. 1.

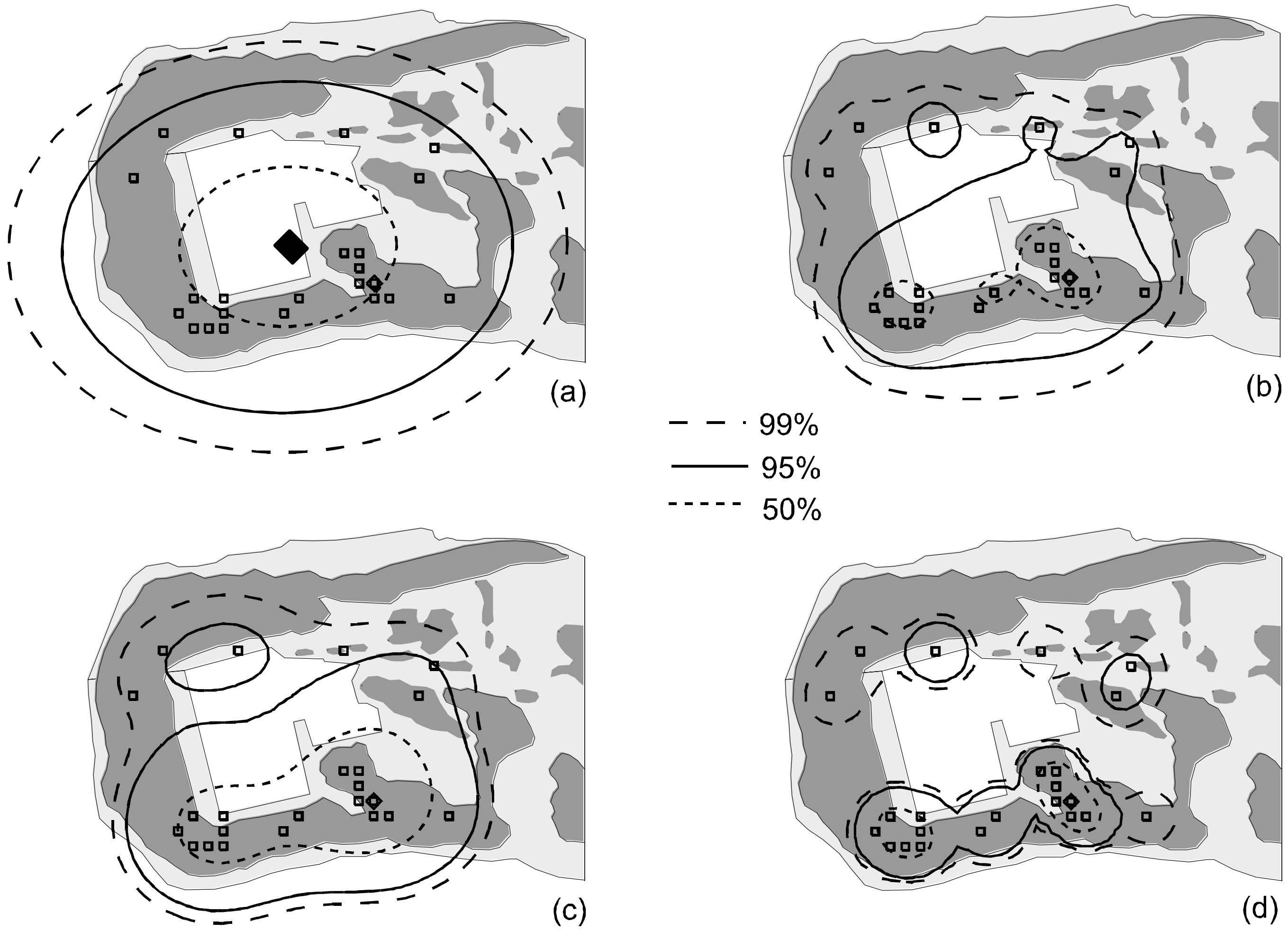


FIG. 2.

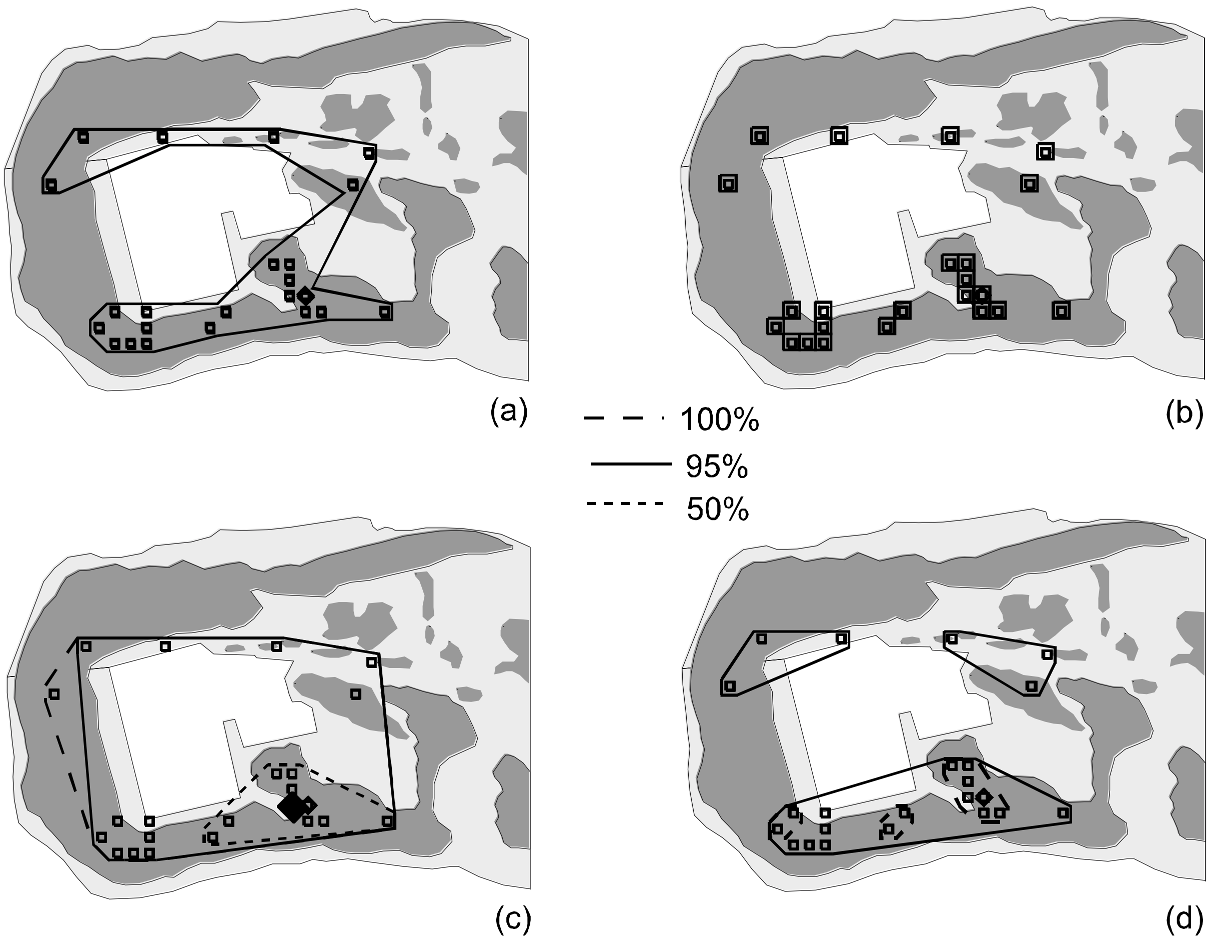


FIG. 3.

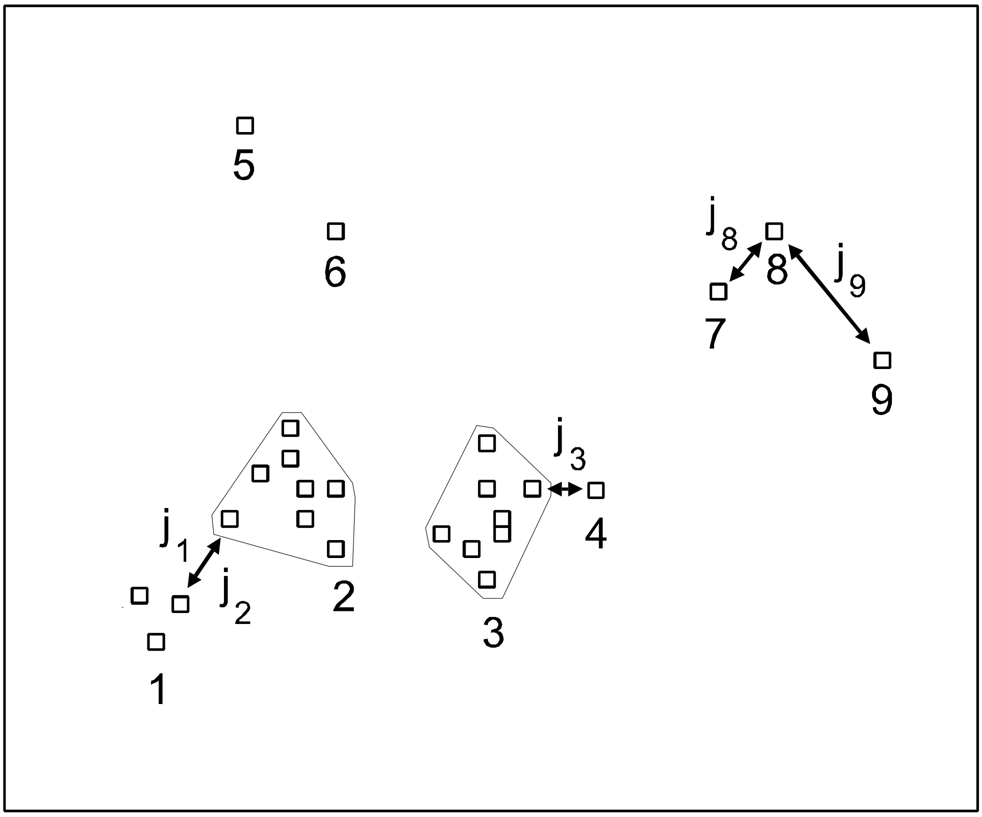


FIG. 4.

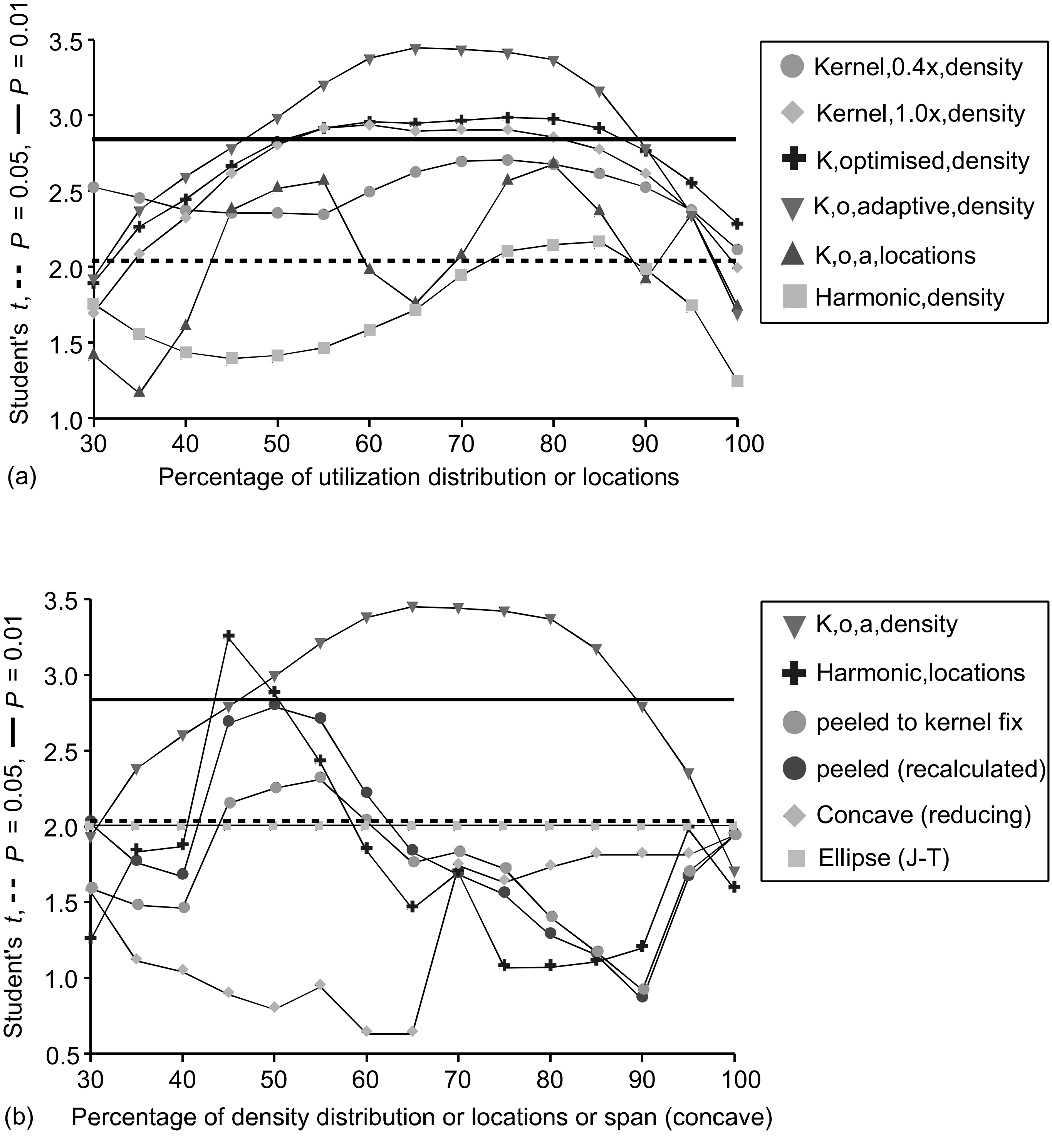
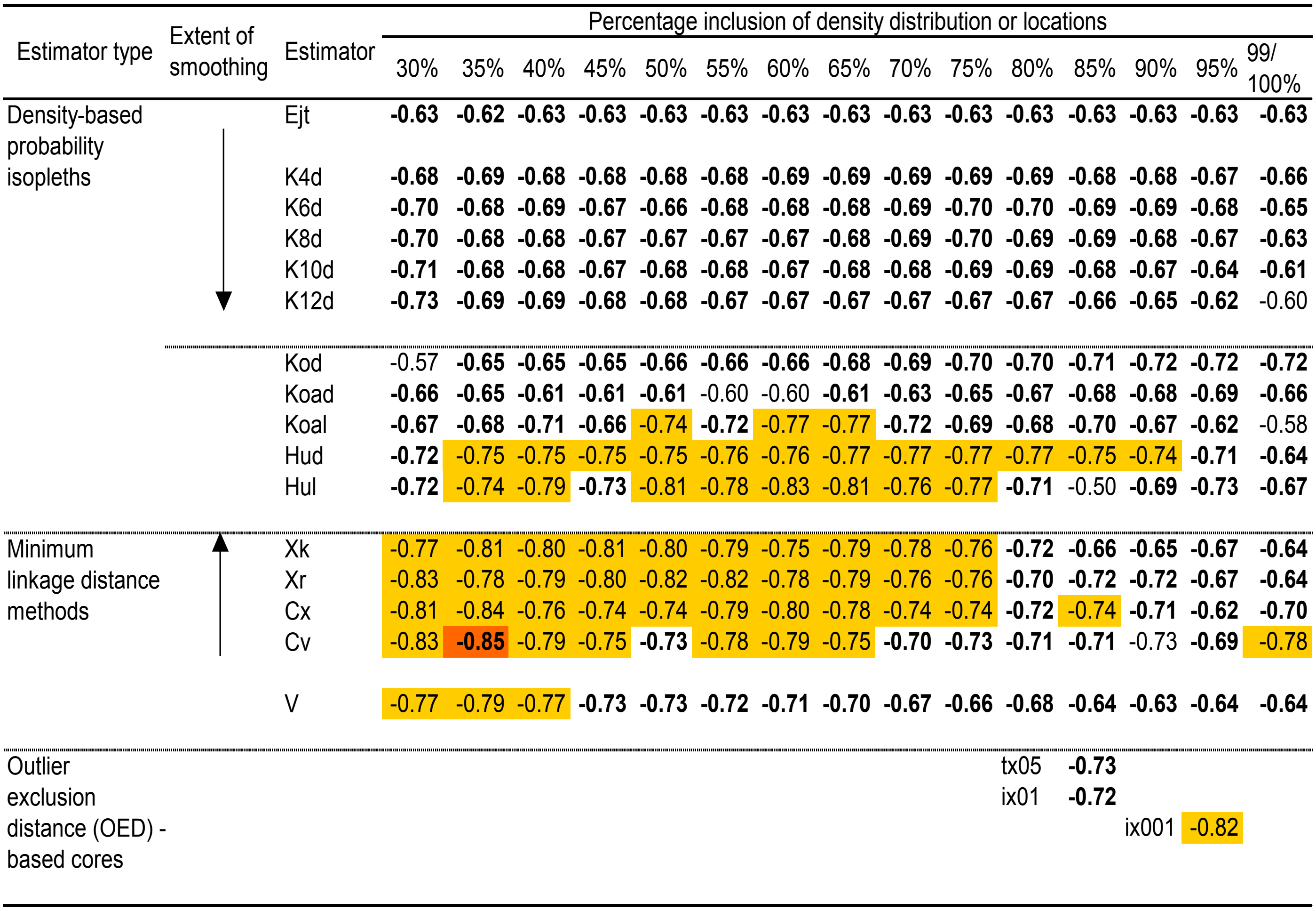

3.5
3.0
2.5
2.0
1.5
1.0
Student's t, - - P = 0.05, — P = 0.01
30
40
50
60
70
80
90
100
(a)
Percentage of utilization distribution or locations
Kernel,0.4x,density
Kernel,1.0x,density
K,optimised,density
K,o,adaptive,density
K,o,a,locations
Harmonic,density
3.5
3.0
2.5
2.0
1.5
1.0
0.5
Student's t, - - P = 0.05, — P = 0.01
30
40
50
60
70
80
90
100
(b)
Percentage of density distribution or locations or span (concave)
K,o,a,density
Harmonic,locations
peeled to kernel fix
peeled (recalculated)
Concave (reducing)
Ellipse (J-T)

FIG. 5.

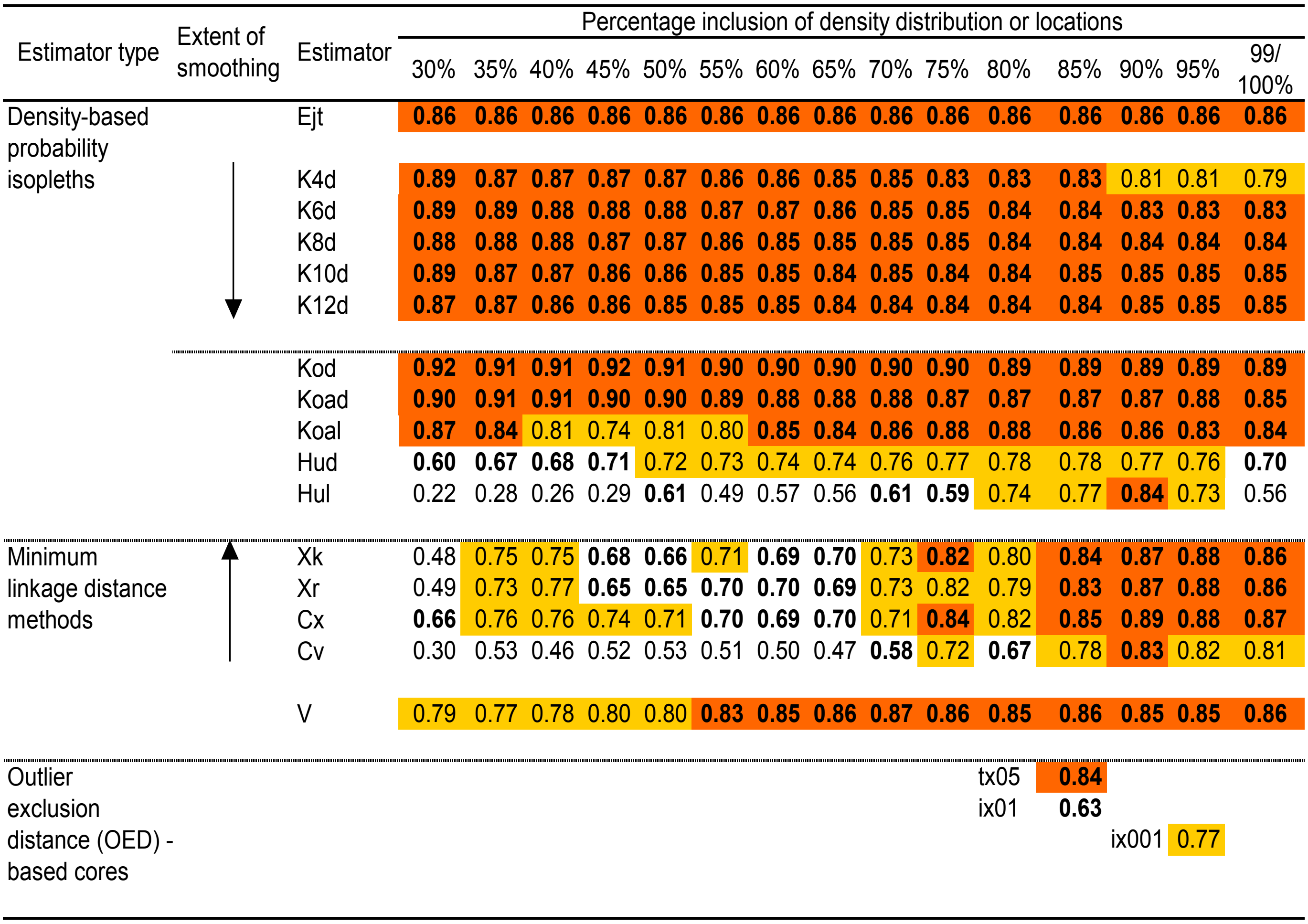
Estimator type	Extent of smoothing	Estimator	Percentage inclusion of density distribution or locations														
			30%	35%	40%	45%	50%	55%	60%	65%	70%	75%	80%	85%	90%	95%	99/ 100%
Density-based probability isopleths		Ejt	2.03	2.03	2.03	2.03	2.03	2.03	2.03	2.03	2.03	2.03	2.03	2.03	2.03	2.03	2.03
	↓	K4d	**2.53**	**2.46**	**2.38**	**2.36**	**2.36**	**2.35**	**2.50**	**2.63**	**2.70**	**2.71**	**2.68**	**2.62**	**2.53**	**2.38**	**2.12**
		K6d	**2.31**	**2.32**	**2.31**	**2.31**	**2.41**	**2.50**	**2.59**	**2.62**	**2.59**	**2.65**	**2.73**	**2.70**	**2.61**	**2.45**	**2.12**
		K8d	1.96	**2.16**	**2.28**	**2.40**	**2.55**	**2.64**	**2.76**	2.80	2.85	2.86	2.84	**2.76**	**2.62**	**2.45**	**2.06**
		K10d	1.70	**2.09**	**2.33**	**2.62**	2.81	2.92	2.94	2.90	2.91	2.91	2.86	**2.78**	**2.62**	**2.37**	2.00
		K12d	1.47	**2.15**	**2.61**	2.81	2.88	2.90	2.89	2.88	2.87	2.88	2.84	**2.73**	**2.56**	**2.30**	1.98
		Kod	1.90	**2.27**	**2.45**	**2.67**	2.83	2.92	2.96	2.95	2.97	2.99	2.98	2.92	**2.77**	**2.56**	**2.29**
		Koad	1.93	**2.38**	**2.60**	2.79	2.99	3.21	3.38	3.45	3.44	3.42	3.37	3.17	2.79	**2.35**	1.70
		Koal	1.92	**2.37**	**2.68**	**2.57**	**2.08**	1.76	1.98	**2.57**	**2.52**	**2.38**	1.61	1.17	1.42	1.73	1.98
		Hud	1.77	1.57	1.45	1.41	1.43	1.48	1.60	1.73	1.96	**2.12**	**2.16**	**2.18**	2.00	1.76	1.26
		Hul	1.25	1.83	1.87	3.24	2.87	**2.42**	1.84	1.46	1.70	1.07	1.07	1.10	1.20	1.98	1.59
Minimum linkage distance methods	↑	Xk	1.59	1.48	1.46	**2.15**	**2.25**	**2.31**	2.03	1.76	1.83	1.72	1.40	1.17	0.92	1.70	1.94
		Xr	2.02	1.76	1.67	**2.68**	2.79	**2.70**	**2.21**	1.83	1.68	1.55	1.28	1.15	0.86	1.66	1.94
		Cx	1.29	0.96	1.48	1.48	1.93	1.70	1.79	1.75	1.59	1.15	1.21	1.64	1.32	1.17	0.46
		Cv	1.34	0.89	1.45	1.42	1.86	1.61	1.65	1.58	1.33	1.00	1.34	1.67	1.34	1.16	0.78
		V	1.57	1.11	1.04	0.89	0.79	0.94	0.63	0.63	1.74	1.63	1.73	1.81	1.81	1.81	1.94
Outlier exclusion distance (OED) - based cores														ix001	0.34		
														tx05	**2.18**		
												ix01	1.39				

FIG. 6.



Estimator type	Extent of smoothing	Estimator	Percentage inclusion of density distribution or locations														
			30%	35%	40%	45%	50%	55%	60%	65%	70%	75%	80%	85%	90%	95%	99/ 100%
Density-based probability isopleths		Ejt	**-0.63**	**-0.62**	**-0.63**	**-0.63**	**-0.63**	**-0.63**	**-0.63**	**-0.63**	**-0.63**	**-0.63**	**-0.63**	**-0.63**	**-0.63**	**-0.63**	**-0.63**
		K4d	**-0.68**	**-0.69**	**-0.68**	**-0.68**	**-0.68**	**-0.68**	**-0.69**	**-0.69**	**-0.69**	**-0.69**	**-0.69**	**-0.68**	**-0.68**	**-0.67**	**-0.66**
		K6d	**-0.70**	**-0.68**	**-0.69**	**-0.67**	**-0.66**	**-0.68**	**-0.68**	**-0.68**	**-0.69**	**-0.70**	**-0.70**	**-0.69**	**-0.69**	**-0.68**	**-0.65**
		K8d	**-0.70**	**-0.68**	**-0.68**	**-0.67**	**-0.67**	**-0.67**	**-0.67**	**-0.68**	**-0.69**	**-0.70**	**-0.69**	**-0.69**	**-0.68**	**-0.67**	**-0.63**
		K10d	**-0.71**	**-0.68**	**-0.68**	**-0.67**	**-0.68**	**-0.68**	**-0.67**	**-0.68**	**-0.68**	**-0.69**	**-0.69**	**-0.68**	**-0.67**	**-0.64**	**-0.61**
		K12d	**-0.73**	**-0.69**	**-0.69**	**-0.68**	**-0.68**	**-0.67**	**-0.67**	**-0.67**	**-0.67**	**-0.67**	**-0.67**	**-0.66**	**-0.65**	**-0.62**	-0.60
		Kod	-0.57	**-0.65**	**-0.65**	**-0.65**	**-0.66**	**-0.66**	**-0.66**	**-0.68**	**-0.69**	**-0.70**	**-0.70**	**-0.71**	**-0.72**	**-0.72**	**-0.72**
		Koad	**-0.66**	**-0.65**	**-0.61**	**-0.61**	**-0.61**	-0.60	-0.60	**-0.61**	**-0.63**	**-0.65**	**-0.67**	**-0.68**	**-0.68**	**-0.69**	**-0.66**
		Koal	**-0.67**	**-0.68**	**-0.71**	**-0.66**	-0.74	**-0.72**	-0.77	-0.77	**-0.72**	**-0.69**	**-0.68**	**-0.70**	**-0.67**	**-0.62**	-0.58
		Hud	**-0.72**	-0.75	-0.75	-0.75	-0.75	-0.76	-0.76	-0.77	-0.77	-0.77	-0.77	-0.75	-0.74	**-0.71**	**-0.64**
		Hul	**-0.72**	-0.74	-0.79	**-0.73**	-0.81	-0.78	-0.83	-0.81	-0.76	-0.77	**-0.71**	-0.50	**-0.69**	**-0.73**	**-0.67**
Minimum linkage distance methods		Xk	-0.77	-0.81	-0.80	-0.81	-0.80	-0.79	-0.75	-0.79	-0.78	-0.76	**-0.72**	**-0.66**	**-0.65**	**-0.67**	**-0.64**
		Xr	-0.83	-0.78	-0.79	-0.80	-0.82	-0.82	-0.78	-0.79	-0.76	-0.76	**-0.70**	**-0.72**	**-0.72**	**-0.67**	**-0.64**
		Cx	-0.81	-0.84	-0.76	-0.74	-0.74	-0.79	-0.80	-0.78	-0.74	-0.74	**-0.72**	-0.74	**-0.71**	**-0.62**	**-0.70**
		Cv	-0.83	**-0.85**	-0.79	-0.75	**-0.73**	-0.78	-0.79	-0.75	**-0.70**	**-0.73**	**-0.71**	**-0.71**	-0.73	**-0.69**	-0.78
		V	-0.77	-0.79	-0.77	**-0.73**	**-0.73**	**-0.72**	**-0.71**	**-0.70**	**-0.67**	**-0.66**	**-0.68**	**-0.64**	**-0.63**	**-0.64**	**-0.64**
Outlier exclusion distance (OED) - based cores											tx05	**-0.73**			
											ix01	**-0.72**			
													ix001	-0.82	

FIG. 7.



Estimator type	Extent of smoothing	Estimator	30%	35%	40%	45%	50%	55%	60%	65%	70%	75%	80%	85%	90%	95%	99/ 100%
Density-based probability isopleths		Ejt	**0.86**	**0.86**	**0.86**	**0.86**	**0.86**	**0.86**	**0.86**	**0.86**	**0.86**	**0.86**	**0.86**	**0.86**	**0.86**	**0.86**	**0.86**
		K4d	**0.89**	**0.87**	**0.87**	**0.87**	**0.87**	**0.86**	**0.86**	**0.85**	**0.85**	**0.83**	**0.83**	**0.83**	0.81	0.81	0.79
		K6d	**0.89**	**0.89**	**0.88**	**0.88**	**0.88**	**0.87**	**0.87**	**0.86**	**0.85**	**0.85**	**0.84**	**0.84**	**0.83**	**0.83**	**0.83**
		K8d	**0.88**	**0.88**	**0.88**	**0.87**	**0.87**	**0.86**	**0.85**	**0.85**	**0.85**	**0.85**	**0.84**	**0.84**	**0.84**	**0.84**	**0.84**
		K10d	**0.89**	**0.87**	**0.87**	**0.86**	**0.86**	**0.85**	**0.85**	**0.84**	**0.85**	**0.84**	**0.84**	**0.85**	**0.85**	**0.85**	**0.85**
		K12d	**0.87**	**0.87**	**0.86**	**0.86**	**0.85**	**0.85**	**0.85**	**0.84**	**0.84**	**0.84**	**0.84**	**0.84**	**0.85**	**0.85**	**0.85**
		Kod	**0.92**	**0.91**	**0.91**	**0.92**	**0.91**	**0.90**	**0.90**	**0.90**	**0.90**	**0.90**	**0.89**	**0.89**	**0.89**	**0.89**	**0.89**
		Koad	**0.90**	**0.91**	**0.91**	**0.90**	**0.90**	**0.89**	**0.88**	**0.88**	**0.88**	**0.87**	**0.87**	**0.87**	**0.87**	**0.88**	**0.85**
		Koal	**0.87**	**0.84**	0.81	0.74	0.81	0.80	**0.85**	**0.84**	**0.86**	**0.88**	**0.88**	**0.86**	**0.86**	**0.83**	**0.84**
		Hud	**0.60**	**0.67**	**0.68**	**0.71**	0.72	0.73	0.74	0.74	0.76	0.77	0.78	0.78	0.77	0.76	**0.70**
		Hul	0.22	0.28	0.26	0.29	**0.61**	0.49	0.57	0.56	**0.61**	**0.59**	0.74	0.77	**0.84**	0.73	0.56
Minimum linkage distance methods		Xk	0.48	0.75	0.75	**0.68**	**0.66**	0.71	**0.69**	**0.70**	0.73	**0.82**	0.80	**0.84**	**0.87**	**0.88**	**0.86**
		Xr	0.49	0.73	0.77	**0.65**	**0.65**	**0.70**	**0.70**	**0.69**	0.73	0.82	0.79	**0.83**	**0.87**	**0.88**	**0.86**
		Cx	**0.66**	0.76	0.76	0.74	0.71	**0.70**	**0.69**	**0.70**	0.71	**0.84**	0.82	**0.85**	**0.89**	**0.88**	**0.87**
		Cv	0.30	0.53	0.46	0.52	0.53	0.51	0.50	0.47	**0.58**	0.72	**0.67**	0.78	**0.83**	0.82	0.81
		V	0.79	0.77	0.78	0.80	0.80	**0.83**	**0.85**	**0.86**	**0.87**	**0.86**	**0.85**	**0.86**	**0.85**	**0.85**	**0.86**
Outlier exclusion distance (OED) - based cores													tx05	**0.84**			
													ix01	**0.63**			
															ix001	0.77	