# Comparison of two sampling protocols and four home-range estimators using radio-tracking data from urban badgers Meles meles

Authors: Huck, Maren, Davison, John, and Roper, Timothy J.

# Comparison of two sampling protocols and four home-range estimators using radio-tracking data from urban badgers *Meles meles*

**Maren Huck, John Davison & Timothy J. Roper**

Radio-telemetry is often the method of choice for studies of species whose behaviour is difficult to observe directly. However, considerable debate has ensued about the best way of deriving home-range estimates. In recent years, kernel estimators have become the most widely used method, together with the oldest and simplest method, the minimum convex polygon (MCP). More recently, it has been suggested that the local convex hull (LCH) might be more appropriate than kernel methods in cases where an animal's home range includes *a priori* inaccessible areas. Yet another method, the Brownian bridge (BB), explicitly uses autocorrelated data to determine movement paths and, ultimately, home ranges or migration routes of animals. Whereas several studies have used simulation techniques to compare these different methods, few have used data from real animals. We used radio-telemetric data from urban badgers *Meles meles* to compare two sampling protocols (10-minute vs at least 30-minute inter-fix intervals) and four home-range estimators (MCP, fixed kernels (FK), LCH and BB). We used a multi-response permutation procedure and randomisation tests to compare overall patterns of fixes and degree of overlap of home ranges estimated using data from different sampling protocols, and a general linear model to compare the influence of sampling protocols and home-range estimator on the size of habitat patches. The shape of the estimated home ranges was influenced by sampling protocol in some cases. By contrast, the sizes and proportions of different habitats within home ranges were influenced by estimator type but not by sampling protocol. LCH performed consistently better than FK, and is especially appropriate for patchy study areas containing frequent no-go zones. However, we recommend using LCH in combination with other methods to estimate total range size, because LCH tended to produce smaller estimates than any other method. Results relating to BB are preliminary but suggest that this method is unsuitable for species in which range size is small compared to average travel speed.

*Key words: Brownian bridge, local convex hull, Eurasian badger, fixed kernel, MCP, Meles meles, radio-telemetry*

*Maren Huck\*, John Davison\*\* & Timothy J. Roper, Department of Biology and Environmental Sciences, John Maynard Smith Building, University of Sussex, Brighton BN1 9QG, UK - e-mail addresses: maren_huck@hotmail. com (Maren Huck); johndavison77@googlemail.com (John Davison); t.j. roper@sussex.ac.uk (Timothy J. Roper)*

*Present addresses:*
\*Mammal Research Institute, Polish Academy of Sciences, Waszkiewicza 1, 17-230 Białowieża, Poland
\*\*Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, Tartu, 51014 Estonia

*Corresponding author: Maren Huck*

Since its first application in ecological research nearly half a century ago (LeMunyan et al. 1959), radio-telemetry has consistently been the method of choice for behavioural studies of species that are difficult to observe directly (Harris et al. 1990). Radio-tracking studies most frequently address questions concerning habitat utilisation or the size and configuration of home ranges (e.g. Marzluff et al. 2004, Jiménez 2007, Safi et al. 2007, Davison 2007). However, there has been considerable debate as to how best to calculate attributes of home ranges such as their size, shape and pattern of use (e.g. Worton 1989, Harris et al. 1990, Worton 1995a, Seaman & Powell 1996).

A number of different methods have been proposed for the estimation of home-range size and shape. The oldest method, which is still widely used, is the minimum convex polygon (MCP; Mohr 1947 cited in Harris et al. 1990). The MCP (a polygon containing all location estimates, i.e. 'fixes', where all vertices are convex) has the advantage of being simple to construct and, because its use has a long history, it often enables comparisons to be made with previous work (Harris et al. 1990). However, several studies have concluded that this method tends to overestimate the area that animals normally use and is also strongly influenced by outliers (i.e. fixes reflecting 'atypical' excursions; e.g. Worton 1995a).

In recent years, kernel estimators have become increasingly popular (Worton 1989, Seaman & Powell 1996, Marzluff et al. 2004). Kernel analysis produces home-range estimates in the form of probability distributions (known as 'utilisation distributions') calculated from the fixes within a home range. Each fix is assumed to have an area of influence in the form of a bivariate normal kernel, the extent of which is controlled by a smoothing parameter (h). However, the value of h can have a profound effect on the resultant range estimates and there has been considerable discussion as to how best to determine this value. Seaman & Powell (1996) argued that using a fixed value of h throughout an animal's range is preferable to using variable (or 'adaptive') kernels, as variable kernels tend to overestimate home-range sizes. Common approaches to selecting a fixed value of h are to use the reference bandwidth $h_{ref}$ (derived from variance in the coordinates of fixes), or a least squares cross validated (LSCV) multiplier of $h_{ref}$ (Worton 1995b). However, further investigation has provided only limited support for either of these methods and has produced some contradictory findings. One study (Seaman & Powell 1996) found that LSCV smoothing provided the most accurate estimates, except with small sample sizes ($N < 50$ fixes) where it performed poorly. By contrast, Blundell et al. (2001) found that $h_{ref}$ performed better than LSCV at estimating the 95% home ranges of river otters *Lontra canadensis*, whereas LSCV was better at estimating 50% core areas. These ambiguities have led some researchers to use a value of h assessed by eye (Silverman 1986, Pope et al. 2004).

More recently, Getz and his co-workers (Getz & Wilmers 2004, Getz et al. 2007) have suggested that a modification of the convex hull method introduced by Worton (1995a), the 'local convex hull' (LCH), might be more appropriate than kernel methods in cases where an animal's home range includes inaccessible areas such as lakes, steep cliffs or motorways. The same may also be true in species whose movements are geographically constrained, such as shoreline birds or river-dwelling mammals. The LCH is a generalisation of the MCP method and is also essentially a non-parametric kernel method. For LCH, a utilisation distribution is produced by constructing a set of local convex polygons for each data point, using a given number of nearest neighbours. Getz et al. (2007) suggest using an adaptive sphere of influence, a, where the sum of the distances between these points and each data point is less than or equal to a. They further show that this method is robust to deviations from the optimal value of a, and

that using the maximal distance of any two data points is a sufficient approximation.

In contrast to all the aforementioned methods, the Brownian bridge (BB) approach, developed by Bullard (1991), explicitly makes use of autocorrelated data (i.e. data in which the time, and hence the distance travelled, between successive points is minimised) to determine movement paths and, hence, home ranges or migration routes of animals. Brownian bridges depend on two smoothing parameters, one dependent on the error due to mobility of the animal and one due to location error. To date, only one published study has used this approach, and this study developed a maximum likelihood approach for estimating the Brownian motion variance (Horne et al. 2007). Thus, the choice of objective and suitable smoothing parameters requires further investigation.

While the BB approach explicitly requires autocorrelated data, several studies have stressed the need to avoid autocorrelation when using the other methods described above, on the grounds that autocorrelation can bias home range and habitat-use estimates (Marzluff et al. 2004). However, other authors (De Solla et al. 1999, Otis & White 1999, Blundell et al. 2001) have argued that autocorrelation conveys useful biological information, and that home-range size, time partitioning and total distance travelled are therefore better represented by autocorrelated observations. As Horne et al. (2007) point out, it is perhaps most important that data points are collected sufficiently often to obtain a representative sample of points through time to cover all modes of behaviour, regardless of whether or not the resultant data are autocorrelated.

Attempts to compare the merits of different methodological or analytical techniques for generating home-range estimates have generally used simulated data rather than data collected from real animals. However, as Börger et al. (2006) state, estimators might simply reflect the parametric distribution function that generated the data. Hence simulations, performing well with artificial data, might not accurately represent the space use of real animals. For example, animals often do not walk randomly within their home ranges, a common assumption in simulations (Blundell et al. 2001). Furthermore, some approaches that are well established and have been shown to be suitable for a variety of species might be less suitable for animals that have unusual movement patterns or that use unusual habitat types (e.g. highly fragmented or urban habitats). In addition, radio-tracking studies often require decisions to be made about the optimum data collection protocol, owing to a trade-off between the number and frequency of fixes per individual and the number of individuals that can be studied (Otis & White 1999). Here, we use data on the ranging behaviour of urban Eurasian badgers *Meles meles* (Davison et al. 2008) to compare two sampling protocols (fixes determined either every 10 minutes on a single focal animal in any one session, or at > 30-minute intervals, following a rotational scheme, on several animals in the same session) and four home-ranges estimators (MCP, fixed kernels (FK), LCH and BB). We aimed to assess differences in the size and configuration of home ranges produced by different combinations of sampling protocol and estimators, as well as determining which combinations best reflect true habitat use.

## Material and methods

### Study area and trapping

Radio-telemetric data were collected on eight urban badgers belonging to five different social groups. The total area including all fixes on all badgers comprised 77 ha in the city of Brighton, UK, consisting of 38.5% streets and other concreted areas, 19.5% buildings, 10.5% private gardens, 14.2% grass, 7.6% allotments and 9.8% scrub (for details on the study area and trapping procedures see Davison 2007).

### Data collection

Animals were radio-tracked on foot and located using standard techniques, including triangulation if it was not possible to approach a study animal sufficiently. Data collection was carried out in 'early' and 'late' sessions ('half nights'), between approximately 20:00-01:00 GMT and 01:00-05:00 GMT (or when badgers finally returned to their sett), respectively. On any given night, only an early or a late session was carried out, and these were alternated throughout the data collection period. We only considered 'active' fixes (i.e. when animals were not inside a sett).

Two sampling protocols were used during the study. Between February 2005 and April 2007, study animals were radio tracked under a rotational scheme, meaning that data were collected from multiple study animals within each study session. A minimum period of 30 minutes (average = 44.5

Table 1. Number of radio-tracking nights, total number of active fixes and sampling periods for eight urban badgers under the two different sampling protocols, i.e. rotational and continuous.

| Animal | Rotational sampling | | | Continuous sampling | | |
|--------|--------|-------|-----------------|--------|-------|-----------------|
|        | Nights | Fixes | Sampling period | Nights | Fixes | Sampling period |
| Flora  | 10 | 47  | 05/2007-06/2007 | 9  | 168 | 05/2007-08/2007 |
| Helen  | 11 | 50  | 05/2007-07/2007 | 11 | 163 | 05/2007-07/2007 |
| Helga  | 9  | 41  | 05/2007-07/2007 | 11 | 168 | 05/2007-07/2007 |
| Hugh   | 34 | 144 | 11/2006-07/2007 | 10 | 181 | 08/2006-08/2007 |
| Kate   | 47 | 125 | 05/2006-04/2007 | 10 | 105 | 05/2006-06/2007 |
| Stacey | 63 | 208 | 11/2005-01/2007 | 7  | 147 | 02/2006-12/2006 |
| Steve  | 31 | 121 | 11/2006-07/2007 | 8  | 168 | 11/2006-08/2007 |
| Wayne  | 85 | 237 | 06/2005-07/2007 | 9  | 103 | 03/2006-12/2006 |
|        |    | 973 |                 |    | 1203 |                |

minutes) intervened between successive fixes on any one animal. In the second sampling protocol, between January 2006 and August 2007, a single focal animal was tracked continuously during any one half-night session and fixes were, wherever possible, recorded every 10 minutes. For three individuals (Florence, Helen and Helga) the two sampling periods overlapped almost completely, whereas for the other animals the continuous sampling period either started much later than the continuous period (Stacey and Wayne) or missed at least one complete season (Stacey, Steve and Wayne; Table 1).

We compared the two sampling protocols with one another rather than comparing the continuous-sampling data set with a subset of, for example, every third fix from the same data set, because subsampling has been shown to underestimate range sizes (Blundell et al. 2001) and because sample sizes of subsets would have been too small for some individuals. Furthermore, since sampling periods using the two protocols did not always overlap completely (see above), our approach is conservative insofar as it will tend to overestimate differences between sampling protocols. Similar range parameter estimates, therefore, would show that home-range estimation is robust with respect to the sample protocol.

## Autocorrelation

We tested for independence of fixes (autocorrelation) in the continuous-sampling data set using the R package adehabitat 1.7 (functions 'testang.ltraj' and 'testdist.ltraj'; Calenge 2006), which randomises the order of increments in a trajectory. For these tests, we used sequences of data containing at least five successive fixes at precisely 10-minute intervals.

## Home-range estimators

We calculated individual home ranges using all possible combinations of the two sampling protocols and four estimation methods. This resulted in seven ranges per badger, since the BB approach could only be applied using data from the continuous-sampling protocol. The four home-range estimation methods were: 100% MCP, 90% FK isopleth (Worton 1989), adaptive 90% LCH isopleth (Worton 1995a, Getz et al. 2007), and 40% BB isopleth (Bullard 1991, Horne et al. 2007). We calculated 90% isopleths for FK and LCH analyses because recent work by Börger et al. (2006) suggests use of 90% rather than 95% isopleths on the grounds that larger isopleths tend to be less accurate. MCPs were calculated in Arc-View 3.3 (ESRI, California, USA), while FK, LCH and BB ranges were calculated using the adehabitat 1.7 package (Calenge 2006) and then imported to ArcView.

FK and BB analyses were calculated using a $200 \times 200$ grid. FK estimators depend crucially on the chosen smoothing factor or bandwidth (Worton 1989, Worton 1995b, Seaman & Powell 1996). In a previous study (Davison 2007), based on a larger database that included the data used here, we tested a variety of approaches to selecting an appropriate bandwidth (h) by running a set of preliminary analyses using: 1) $h_{ref}$ (Worton 1995b), 2) a unique least squares cross validated (LSCV) multiplier applied to each analysis (Worton 1995b), 3) the median of LSCV multipliers applied uniformly to every analysis (Kenward et al. 2003), and 4) the median value of h assessed by eye and applied uniformly to every analysis (Pope et al. 2004). In common with other studies (e.g. Worton 1989, Worton 1995b, Horne & Garton 2006), we found that LSCV tended to under-smooth home ranges, leading to multiple "centres of activity" around many single fixes, while $h_{ref}$ often over-smoothed ranges (see Davison 2007). Overall, approach 4) provided the most consistent levels of smoothing between data sets and, after

470

testing a variety of values for h, a constant bandwidth of 15 m was used for all kernel analyses (Davison 2007).

For the LCH estimators we used the adaptive rather than a fixed LCH, as suggested by Getz et al. (2007). The adaptive LCH chooses the number of neighbours within an adaptive sphere of influence ('a'), rather than the original fixed number of neighbours ('k'). Simulation studies suggest that adaptive LCHs are robust against deviations from the optimal parameter-value of a and that, as a rule of thumb, the maximal distances between any two points in the data set provide a good approximation of a. We used different values of a for each individual badger, chosen according to this rule.

In the available program to calculate BB, only regular trajectories can be used (in our case, trajectories based on fixes at exactly 10-minute intervals). Due to occasional inability to obtain a fix on a given animal at exactly the required time, for example owing to equipment failure or because the focal animal was moving very rapidly, the data set used for the calculation of BB is somewhat smaller than for the other home-range estimators. We calculated the value of $\sigma1$ for each individual using the algorithm suggested by Horne et al. (2007), which is implemented in the package adehabitat for R (Calenge 2006). $\sigma1$ ranged within 1.03-2.38, with an average of 1.69. The value of $\sigma2$ was fixed at 10.26, determined empirically as the average location error in a trial experiment. This value is likely to overestimate the average location error, since during real data collection about 10% of fixes were verified by direct sightings of animals. Primary results using these smoothing factors at the 90% levels led to nonsensical results (e.g. squares that extended well beyond any areas in which animals had ever been located). Choosing smaller smoothing factors still gave no useful results. Finally, we chose a much lower level (40%) that resulted, for four individuals, in home-range estimates that were (by eye) comparable to those obtained with other methods. For the remaining animals it was not possible to obtain sensible home ranges using the BB approach.

### Location of home ranges

We compared the location of home ranges determined with different sampling protocols by calculating the mean of all fixes for each individual (i.e. the centre of the individual home range), using each sampling protocol. We then calculated the distance between these two mean locations. We also compared the overall distribution of fixes using the multi-response permutation procedure in the program Blossom W2007.09.21 (Cade & Richards 2005, 2007). This program calculates first the average distance between all points (fixes) within a data set and then randomises the points. The assumption is that intra-group average distances should be similar to the overall distance under the null hypothesis, whereas they should be small if fixes are clustered. P-values were evaluated as Pearson type III distributions (Cade & Richards 2005). Additionally, we calculated the overlap of home ranges (as proportion of the smaller of the two ranges) and then calculated 500 randomised areas of overlap. A script for these procedures (written mainly by John Davison) is available from the authors. We used the false discovery rate method, assuming independence of tests (Miller et al. 2001, Verhoeven et al. 2005), to account for multiple testing within each home-range estimation method (i.e. eight tests per method). P-values for the randomisation procedures were one-sided because only significantly greater distances of mean locations and significantly smaller overlap between home ranges indicate systematic differences between sampling protocols.

### Habitat composition and statistical analysis

Within each range, we calculated the proportions covered by the following habitat types: 'street' (roads and other hard-surfaced areas), 'buildings', 'grass' (areas of regularly mown grass, either accessible to the public or belonging to schools), 'allotment', 'garden' (private gardens) and 'scrub' (bushes, bracken, brambles and other types of untended wasteland).

Habitat types were assigned using maps obtained from Digimap (Digimap®, ©Crown Copyright 2006) with the help of field surveys and aerial photographs (see Huck et al. 2008 for more details).

FK, LCH and BB estimators represent utilisation distributions, and as such the observed proportions of different habitat types should be identical to the proportions of time that animals spend in each habitat type. This true (expected) habitat use can in turn be estimated from the numbers of fixes taken in the respective habitat types. For each of these three estimators, we compared the proportion of each habitat type present in each home range ('observed' values) with the percentage of fixes recorded in each habitat type ('expected' values).

For purposes of statistical comparison we compared, for each combination of home-range estimator and sampling protocol, the mean (across

badgers) total amount of each habitat type contained within the home-range estimates. We then used a General Linear Model (GLM) to assess the effect of method and sampling protocol on these mean habitat areas, with habitat included as a blocking factor. We also used Linear Mixed Effect Models (LME), with badger included as a random factor, to compare the influence of method and sampling protocol on the arcsine transformed proportional size of each habitat type. Because the BB home ranges could only be estimated using the continuous sampling protocol, and then using a much lower percentage level (see above), we did not include BB in the GLM. We used adjusted ("type III") sums of squares to determine the significance of fixed effects and Tukey's Honest Significant Differences (Tukey HSD) to determine post hoc significant differences between pairs of methods.

Although we did not aim to statistically analyse habitat preferences by badgers (since this was done by Davison 2007), we nevertheless calculated the difference between the proportions of observed and expected habitat types in order to relate the magnitude of possible methodological differences to the relative strengths of habitat preferences by badgers. For visual inspection of methodological differences we calculated the average value for eight study animals of observed minus expected habitat coverage (in ha) using different home-range estimators and sampling protocols. Expected values (E) were calculated in the following way: for habitat h and estimator/protocol combination ep, expected habitat coverage equalled the product of the total home-range size using ep and the number of fixes in habitat h, divided by the total number of fixes using ep. Thus, values close to zero indicate an accurate representation of habitat use. For the calculation of

habitat preferences, we calculated the average use by all study animals of different habitats in relation to their availability within the entire study area (i.e. the MCP containing all fixes of all badgers, combining both sampling protocols). Here, for each badger, observed values (O) were the proportion of fixes in habitat h, while expected values were the product of the proportion of the study area covered by habitat h and the total number of fixes. Since these values have a different unit from those representing methodological differences (i.e. 'number of fixes' rather than ha) we standardised the value by dividing them by the average number of fixes per ha in the MCP ranges of each badger. Thus, positive values of O-E represent habitat preference, and negative values habitat avoidance.

## Results

We collected 973 active fixes (range: 41-237/animal) under the rotational protocol and 1,203 (range: 103-181/animal) under the continuous protocol (see Table 1). For the test of independence of fixes we obtained 77 bursts for the eight badgers (6-13 bursts/individual). After correcting for multiple testing none of the bursts showed significant dependence in terms of either angles or distances between successive fixes.

### Home-range locations
The central points of home ranges calculated either from the rotational sampling database or from the continuous sampling database were on average 19 m apart (Table 2). Fixes contributing to these home ranges, recorded using each sampling protocol, were clustered significantly differently in three animals

Table 2. Distance (in m) between average centres of home ranges using data from continuous and rotational sampling protocols, respectively, and percentage overlap of home ranges determined with the same two sampling protocols, using either 90% FK, 90% LCH or 100% MCP estimators. P-values for the distances between home-range centres were calculated using the multiresponse permutation procedure (Cade & Richards 2005, Cade & Richards 2007), and P-values for home-range overlap were calculated using randomisation tests. P-values in italics are significant and P-values shown in brackets are not significant after correcting for multiple testing.

| Method | Flora | Helen | Helga | Hugh | Kate | Stacey | Steve | Wayne | Average |
|---|---|---|---|---|---|---|---|---|---|
| Distance | 21.9 | 4.0 | 19.2 | 29.7 | 31.8 | 6.9 | 15.1 | 24.0 | 19.1 |
| P | 0.3510 | 0.5970 | 0.4240 | 0.1290 | *0.0002* | 0.0740 | *0.0010* | *0.0040* | |
| FK | 69.2 | 86.3 | 83.1 | 62.6 | 70.0 | 77.4 | 76.1 | 74.3 | 74.9 |
| P | 0.260 | 0.852 | 0.850 | 0.072 | *<0.002* | *<0.002* | *<0.002* | 0.650 | |
| LCH | 53.9 | 62.6 | 82.9 | 62.2 | 41.7 | 81.7 | 73.0 | 65.4 | 65.4 |
| P | 0.308 | (0.040) | 0.878 | 0.228 | (0.020) | 0.352 | 0.128 | 0.682 | |
| MCP | 100.0 | 99.9 | 100.0 | 98.2 | 72.0 | 70.4 | 89.0 | 85.1 | 89.3 |
| P | 0.898 | 0.848 | 0.830 | 0.778 | 0.220 | *0.004* | 0.620 | *0.004* | |

Table 3. Total home-range sizes (in ha) for the eight individual badgers using two sampling protocols (r: rotational, c: continuous) and four home-range estimators (FK: 90% fixed kernel, LCH: 90% adaptive local convex hull, MCP: 100% minimum convex polygon, BB: 40% Brownian bridge). The outer right-hand column shows the average proportion of *a priori* unsuitable habitat (e.g. buildings and open water). n.a. indicates that data were not available.

| Method | Flora | Helen | Helga | Hugh | Kate | Stacey | Steve | Wayne | Unsuitable |
|--------|-------|-------|-------|------|------|--------|-------|-------|------------|
| FK r   | 3.8   | 2.6   | 3.3   | 6.2  | 2.6  | 2.9    | 2.5   | 4.7   | 0.08       |
| FK c   | 4.1   | 3.4   | 4.2   | 6.2  | 2.0  | 2.8    | 2.5   | 3.8   | 0.07       |
| LCH r  | 2.0   | 1.3   | 0.8   | 3.6  | 0.9  | 1.2    | 1.0   | 1.9   | 0.04       |
| LCH c  | 2.0   | 1.6   | 1.5   | 3.7  | 0.5  | 1.1    | 1.0   | 1.4   | 0.05       |
| MCP r  | 7.0   | 2.9   | 4.1   | 12.5 | 6.4  | 5.0    | 3.5   | 7.1   | 0.10       |
| MCP c  | 10.6  | 5.0   | 5.8   | 13.8 | 5.9  | 4.8    | 3.9   | 6.6   | 0.10       |
| BB c   | n.a.  | 3.1   | 3.4   | n.a. | n.a. | n.a.   | 2.4   | 5.8   | 0.07       |

(Kate, Steve and Wayne; see Table 2). Home ranges estimated using the different sampling protocols overlapped on average by 75, 65, and 89% for FK, LCH and MCP estimators, respectively (see Table 2). After correcting for multiple testing, three of the eight individual home ranges overlapped significantly less than expected by chance using FK, none using LCH and two using the MCP estimator (see Table 2). In similar analyses using data collected under the continuous sampling protocol and a subset of these data using only fixes at least 30 minutes apart, home ranges never overlapped less and were never further apart than expected by chance (data not shown).

## Home-range sizes and utilisation

Home-range sizes differed between badgers (GLM: $F = 10.9$, $P \ll 0.001$; Table 3). The largest ranges were produced by MCP, followed by BB & FK and finally LCH (Fig. 1). Both the total amount of each

habitat type contained within home ranges, and the total home range size, differed according to type of estimator (GLM: $F = 39.8$, $P \ll 0.001$; Figs. 2 and 3) but not according to sampling protocol (GLM: $F = 0.26$, $P = 0.61$; see Fig. 2). All three home-range estimators differed significantly from each other, with LCH producing the smallest values (Tukey HSD: FK-LCH: $P = 0.012$; FK-MCP: $P < 0.001$; LCH-MCP: $P \ll 0.001$). Unsurprisingly, the blocking factor habitat also had a significant influence (GLM: $F = 7.4$, $P < 0.001$), though it explained less of the variation than did estimator type. The arcsine transformed proportions of habitat patches in home ranges calculated with the different estimators and sampling protocols, with individual badger being accounted for as random factor, differed significantly (after correcting for multiple testing) for all habitat types according to estimator (LME: allotment: $F = 4.2$, $P = 0.022$; building: $F = 10.2$, $P < 0.001$; garden: $F = 4.5$, $P = 0.018$; grass: $F = 4.5$, $P = 0.018$; scrub: $F = 26.8$, $P < 0.001$; street: $F = 10.6$, $P < 0.001$), but never according to sampling protocol (LME: all $P > 0.1$). LCH habitat sizes deviated less from expected values than those calculated using FK or MCP (see Fig. 2). The difference between the observed number of fixes in certain habitat types and the expected number, given the availability of habitat types in the study area (values written over or under corresponding columns in Fig. 2) indicates that badgers could be found disproportionately often in scrub and gardens, and rarely on open grass, streets and buildings (not tested statistically, but see similar results of compositional analysis
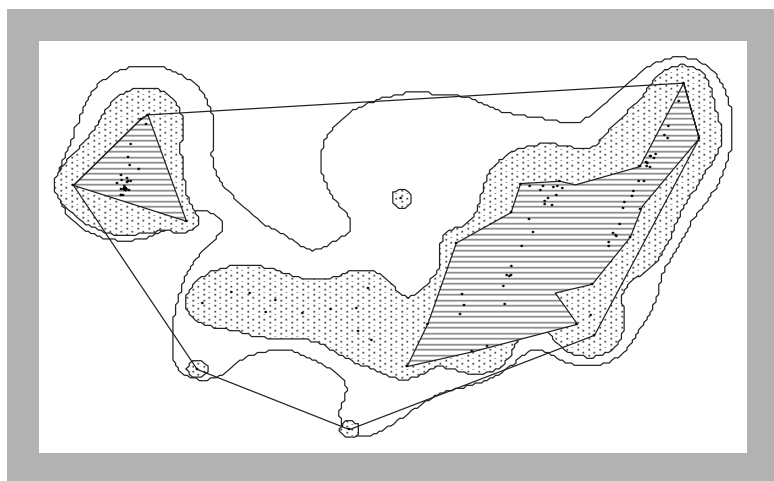


Figure 1. Range of an adult male badger (Wayne), calculated using a continuous sampling protocol and four different estimators. Rounded contours and unfilled area show 40% Brownian bridge; straight contours and unfilled area the 100% MCP; rounded contours and dotted area the 90% FK; straight contours and hatched area the 90% LCH. Black dots represent fixes.
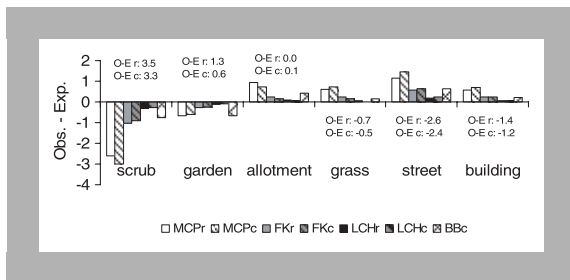
Figure 2. Average value across eight study animals of observed (O) minus expected (E) habitat coverage (in ha) using different home-range estimators and sampling protocols. Values close to zero indicate an accurate representation of habitat use. The O-E values printed above or below the histogram bars show the average use by all study animals of different habitats in relation to their availability within the entire study area, divided by the average number of fixes/ha. Positive values of O-E represent habitat preference, whereas negative values represent habitat avoidance. See text for further details. MCP gives the 100% minimum convex polygon; FK the 90% fixed kernel with smoothing factor h = 15; LCH the 90% adaptive local convex hull; c indicates continuous sampling protocol and r the rotational sampling protocol.

in Davison 2007). These habitat preferences and aversions were revealed equally clearly by both sampling protocols.

## Discussion

### Method of home-range estimation

To be able to use the BB approach at all, we had to use a very low level (40%) of the utilisation distribution, so results are not comparable to the other approaches. Despite the low level, estimated ranges were even larger than when using a kernel approach, and often extended beyond the MCP ranges. Thus, the BB approach failed completely for our kind of data. However, this may have been due to the very small home ranges of urban badgers in relation to their mobility, which meant that even fixes taken only 10 minutes apart were not autocorrelated. The BB approach may therefore only be appropriate for species with relatively large home ranges or which can be tracked using even shorter time intervals (e.g. using GPS). Preliminary inspection of contours of home ranges estimated using the BB approach also suggests that this estimator will, like kernels, produce utilisation distributions that include inaccessible features such as lakes, steep cliffs, or, in cities, blocks of housing (see Fig. 1). Unfortunately, only two studies have used the BB approach (Bullard 1991, Horne et al. 2007), both of which presented probability densities but not actual home range
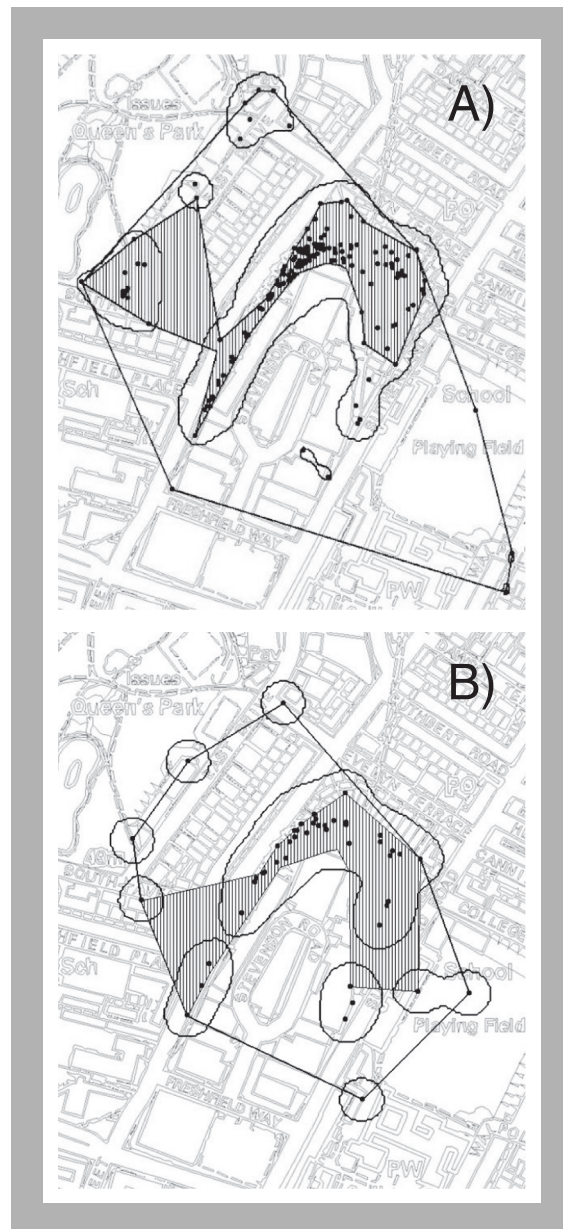


Figure 3. 100% MCP (shown by outer straight lines), 90% FK (by rounded lines) and 90% LCH (the hatched areas) home-range estimates for one female badger (Florence) under A) a continuous sampling protocol, and B) a rotational sampling protocol. Black points represent fixes.

sizes. The species used (i.e. black bear *Ursus americanus* and caribou *Rangifer tarandus*) have much larger range sizes than badgers, which might result in better estimates, even though the time interval between locations was in both cases higher than the one used in our study (20 minutes and seven hours, respectively). However, comparing the figures

474

showing the contours with those showing the probability density of estimated home ranges (Figs. 16-18 in Bullard 1991) suggests that the contour maps derived using this method may tend to be over-smoothed and not suitable for estimation of home-range size in a conventional way. We acknowledge, though, that our results are preliminary and suggest further investigation of this estimator prior to drawing strong conclusions.

As regards the other three estimators and with respect to habitat analysis, both LCH and FK performed better than 100% MCP, but LCH performed consistently better than FK insofar as it reflected most closely the actual proportions of fixes obtained in different habitats, and had the least tendency to underestimate preferred and overestimate avoided habitats. This is in line with a simulation study by Getz et al. (2004) showing that LCH gave estimates within 12% of true home-range sizes, while FK methods always performed worse. Habitat selection, as described by the difference between habitat use and the percentage of different habitat types in the study area as a whole, revealed clearly favoured habitats (scrub and garden) and clearly disfavoured habitats (grass, streets and buildings), as has already been shown by Davison et al. (2008).

However, LCH always resulted in smaller home ranges than FK and both of these were considerably smaller than MCPs. Getz et al. (2004; see their Table 2) also found that LCH usually underestimated the true area by up to 12%, while both fixed and adaptive kernels, using both $h_{ref}$ and $h_{LSCV}$ sometimes highly underestimated (by 27-98%) and sometimes highly overestimated (by 21-981%) the relevant areas. Depending on the study aim, it may be of interest to know the absolute size of the area covered by an animal or population, regardless of its internal characteristics, in which case MCPs might still be of value under certain circumstances. For example, MCPs may better reflect the area needed by animals to ensure that the range contains sufficient resources, which will be an important consideration in the management of protected species. Urban environments are particularly patchy and contain many areas that are *per se* unsuitable for animals. In more homogenous habitats, without such exclusion zones, FK might perform as well as LCH.

## Sampling protocols

The two sampling protocols led in some cases to significant differences in the distribution of fixes, leading either to differences in the pattern of ag-gregation (i.e. the precise shapes of ranges, *cf*. Figs. 3A and B) or to less than expected overlap of home ranges. However, significant differences were only found for animals where the data collection periods between the continuous and rotational protocols differed to some extent (see Table 1; in some cases at least one complete season was missed under the continuous protocol). Thus, range differences might have reflected seasonal differences in habitat use. This interpretation is supported by the finding that using 30-minute interval subsets of the continuous data never resulted in significant differences. Overall, the LCH method seemed to be more robust to the choice of sampling protocol than either FK or MCP: in contrast to these other methods, none of the home-range pairs overlapped less than could be expected using the LCH method (see Table 2). This might be an additional advantage of the LCH over the FK.

In contrast to this, and more importantly, the sampling protocols did not produce significantly different range sizes or proportions of different habitat types, even though the relevant data did not always represent seasons equally. In addition, the two sampling protocols produced the same pattern of habitat preferences. The difference between these two findings explains why Börger et al. (2006) stressed the importance of standardising the sampling regime whereas we stress the choice of estimator. Whereas their study only investigated the effects on the estimated home-range size and the potential for varying results under different sampling regimes, our main focus lay on the representation of habitat use. For the latter, the sampling protocol proved to be of minor importance compared to the estimator. We suggest that choice of estimator is likely to be more relevant to other studies since for many purposes, the exact shape of a home range will be less important than its habitat composition.

In cases where the exact shape is important, a rotational scheme involving more animals over a longer period will reflect this better, because factors such as seasons and times of day can be more easily balanced (see also Otis & White 1999). This is because the rotational method, although it provides fewer data points per individual and longer inter-fix intervals, yields data that are more evenly distributed over time for the same amount of radio-tracking effort. On the other hand, some questions and approaches specifically require autocorrelated data (e.g. the BB approach, or analysis of movement

475

trajectories; see Davison et al. 2008), in which case continuous sampling is necessary.

## Conclusions

Our results demonstrate that the choice of home-range estimator has far greater influence on conclusions relating to the relative amounts of different types of habitat within home ranges than has the choice of sampling protocol. Convex hulls performed consistently better than kernels or MCPs when estimating habitat utilisation. However, we recommend using convex hulls in combination with other methods to estimate total range size, since convex hulls tended to produce smaller estimates than any other method. Results relating to Brownian bridges are preliminary but suggest that this method is unsuitable for species in which range size is small compared to average travel speed.

## References

Blundell, G.M., Maier, J.A.K. & Debevec, E.M. 2001: Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. - Ecological Monographs 71: 469-489.

Börger, L., Franconi, N., de Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. & Coulson, T. 2006: Effects of sampling regime on the mean and variance of home range size estimates. - Journal of Animal Ecology 75: 1393-1405.

Bullard, F. 1991: Estimating the home range of an animal: a Brownian bridge approach. - M.Sc. thesis, University of North Carolina, Chapel Hill, 27 pp.

Cade, B.S. & Richards, J.D. 2005: User manual for Blossom statistical software. - Open-File Report 2005-1353, Geological Survey, Fort Collins Science Center, Fort Collins, CO: U.S. 124 pp.

Cade, B.S. & Richards, J.D. 2007: Blossom Version W2007.09.21. - Geological Survey, Fort Collins Science Center, Fort Collins, CO: U.S. Available at: http://www.fort.usgs.gov/Products/Software/Blossom/

Calenge, C. 2006: The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. - Ecological Modelling 197: 516-519.

Davison, J. 2007: Ecology and Behaviour of Urban Badgers. - PhD thesis, University of Sussex, Brighton, 141 pp.

Davison, J., Huck, M., Delahay, R.J. & Roper, T.J. 2008: Restricted ranging behaviour in a high-density population of urban badgers. - Journal of Zoology (London). doi: 10.1111/j.1469-7998.2008.00509.x.

De Solla, S., Bonduriansky, R. & Brooks, R. 1999: Eliminating autocorrelation reduces biological relevance of home range estimates. - Journal of Applied Ecology 68: 221-234.

Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J. & Wilmers, C.C. 2007: LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. - PLoS ONE 2: e207. doi: 10.1371/journal.pone.0000207.

Getz, W.M. & Wilmers, C.C. 2004: A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. - Ecography 27: 489-505.

Harris, S., Cresswell, W.J., Forde, P.G., Trewhella, W.J., Woollard, T. & Wray, S. 1990: Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. - Mammal Review 20: 97-123.

Horne, J.S. & Garton, E.O. 2006: Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. - Journal of Wildlife Management 70: 641-648.

Horne, J.S., Garton, E.O., Krone, S.M. & Lewis, J.S. 2007: Analyzing animal movements using brownian bridges. - Ecology 88: 2354-2363.

Huck, M., Davison, J. & Roper, T.J. 2008: Predicting European badger Meles meles sett distribution in urban environments. - Wildlife Biology 14: 188-198.

Jiménez, J.E. 2007: Ecology of a coastal population of the critically endangered Darwin's fox (Pseudalopex fulvipes) on Chiloé Island, southern Chile. - Journal of Zoology 271: 63-77.

Kenward, R.E., South, A.B. & Walls, S.S. 2003: Ranges 6, version 1.2: for the analysis of tracking and location data. - Anatrack Ltd., Wareham, UK.

LeMunyan, C.D., White, W., Nyberg, E. & Christian, J.J. 1959: Design of a miniature radio transmitter for use in animal studies. - Journal of Wildlife Management 23: 107-110.

Marzluff, J.M., Millspaugh, J.J., Hurvitz, P. & Handcock, M.S. 2004: Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. - Ecology 85: 1411-1427.

Miller, C.J., Genovese, C., Nichol, R.C., Wasserman, L., Connolly, A., Reichart, D., Hopkins, A., Schneider, J. & Moore, A. 2001: Controlling the false-discovery rate in astrophysical data analysis. - The Astronomical Journal 122: 3492-3505.

Otis, D.L. & White, G.C. 1999: Autocorrelation of location estimates and the analysis of radiotracking data. - Journal of Wildlife Management 63: 1039-1044.

Pope, M.L., Lindenmayer, D.B. & Cunningham, R.B. 2004: Patch use by the greater glider (Petauroides volans) in a fragmented forest ecosystem. I. Home range size and movements. - Wildlife Research 31: 559-568.

Safi, K., König, B. & Kerth, G. 2007: Sex differences in population genetics, home range size and habitat use of the parti-colored bat (Vespertilio murinus, Linnaeus 1758) in Switzerland and their consequences for conservation. - Biological Conservation 137: 28-36.

Seaman, D.E. & Powell, R.A. 1996: An evaluation of the accuracy of kernel density estimators for home range analysis. - Ecology 77: 2075-2085.

Silverman, B.W. 1986: Density Estimation for Statistics and Data Analysis. - Monographs on Statistics and Applied Probability. Chapman and Hall, London, UK, 175 pp.

Verhoeven, K.J.F., Simonsen, K.L. & McIntyre, L.M. 2005: Implementing false discovery rate control: increasing your power. - Oikos 108: 643-647.

Worton, B.J. 1989: Kernel methods for estimating the utilization distribution in home-range studies. - Ecology 70: 164-168.

Worton, B.J. 1995a: A convex hull-based estimator of home-range size. - Biometrics 51: 1206-1215.

Worton, B.J. 1995b: Using Monte Carlo simulation to evaluate kernel-based home range estimators. - Journal of Wildlife Management 59: 794-800.