Kernel-based home range method for data with irregular sampling intervals

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Abstract
Studies of habitat selection and movements often use radio-tracking data for defining animal home ranges. Home ranges (HR) can be approximated by a utilization density distribution (UD) that instead of assuming uniform use of areas within HR boundary provides a probabilistic measure of animal space use. In reality, radio-tracking data contain periods of frequent autocorrelated observations interspersed with temporally more independent observations. Using such temporally irregular data directly may result in biased UD estimates, because areas that have been sampled intensively receive too much weight. The problem of autocorrelation has been tackled by resampling data with an appropriate time interval. However, resampling may cause a large reduction in the data set size along with a loss of information. Evidently, biased UD estimates or reduction in data may prejudice the results on animal habitat selection and movement. We introduce a new method for estimating UDIs with temporally irregular data. The proposed method, called the time kernel, accounts for temporal aggregation of observations and gives less weight to temporally autocorrelated observations. A further extension of the method accounts also for spatially aggregated observations with relatively low weights given to observations that are both temporally and spatially aggregated. We test the behaviour of the time kernel method and its spatiotemporal version using simulated data. In addition, the method is applied to a data set of brown bear locations.

1. Introduction
Defining the size, shape and pattern of utilization of an animal’s home range is important for studying habitat selection and spacing of individuals. A home range can be defined as an area with a defined probability of occurrence of an animal during a specified time period (Harris et al., 1990; White and Garrott, 1990; Robertson et al., 1998; Kernohan et al., 2001a). Home ranges are often estimated from data obtained with radio-tracking techniques (Harris et al., 1990; White and Garrott, 1990; Otis and White, 1999, Kernohan et al., 2001a). Many methods have been developed to define the area used by an animal from such point location data (Dixon and Chapman, 1980; Anderson, 1982; Worton, 1989; Larkin and Harkin, 1994; Seaman and Powell, 1996; Lawson and Rodgers, 1997; Robertson et al., 1998; Kenward et al., 2001). Home range methods have been reviewed by several authors, who have often expressed concern about adequate sample size and autocorrelation of locations (Anderson, 1982; Worton, 1987; Harris et al., 1990; White and Garrott, 1990; Larkin and Harkin, 1994; Lawson and Rodgers, 1997; Robertson et al., 1998; Kenward, 2001; Kenward et al., 2001; Kernohan et al., 2001a).
Radio-tracking can be continuous or discontinuous with constant or variable time intervals between observations. Thus, techniques are needed that account for the temporal sequence of observations (Larkin and Halkin, 1994; Robertson et al., 1999).

Home range methods are based on either densities of locations or link distance between locations. Methods, such as probabilistic circles or ellipses, the kernel method and the harmonic mean method, are based on the assumption that aggregation of locations provides information about differential use of space within the home range (Dixon and Chapman, 1980; Anderson, 1982; Worton, 1989; Kernohan et al., 2001a). The minimum convex polygon (MCP) is an example of link distance methods that assume uniform use of space within the range enclosed by the outermost locations (White and Garrott, 1990; Kenward, 2001; Kernohan et al., 2001a). Kernel contours have frequently been used in habitat selection studies (Mace et al., 1996; Seaman and Powell, 1996; Tufto et al., 1996; Mace and Walker, 1997; Walker and Mace, 1997; Kernohan et al., 1998; Kenward et al., 2001; Marzluff et al., 2001; McLoughlin et al., 2002; Lumsden et al., 2003). This is done assuming that an animal uniformly uses the area inside a contour enclosing a certain proportion (e.g., 95%) of the total probability density of the locations. For clarity, here we call such a home range estimate a "flat kernel", because the original probability density is replaced by a flat distribution, and thus not all information about differential home range use is retained. However, animals are unlikely to use their home range in a uniform manner and consequently, probabilistic methods can be more useful in habitat relative studies than the MCP method or flat kernel (Worton, 1987; Harris et al., 1990; Seaman and Powell, 1996; Marzluff et al., 2001; Kenward et al., 2004).

Especially in spatially heterogeneous environments it may be important to understand the internal structure of the home range (Kernohan et al., 2001a). The probability distribution that maps an individual's relative use of space has been termed the utilization distribution (UD). Marzluff et al. (2003) suggested that the use of UD directly would enhance studies of animal movements, species interactions and resource selection. The kernel method actually provides an estimate for the UD depicting the probability of an animal occurring at each location within its home range (Worton, 1987, 1989; Kernohan et al., 2001a; Marzluff et al., 2001; Kenward et al., 2004).

The kernel method implicitly assumes statistical independence among the observations (Harris et al., 1990). The problem of temporal autocorrelation has so far been overcome by resampling the data with an appropriate time interval (Swihart and Slade, 1985; Harris et al., 1990; Rooney et al., 1998; Kenward, 2001). It is not straightforward to translate data into statistically independent observations while still retaining an adequate sample size without loss of information. Attempts to achieve statistically independent data by resampling have often resulted in severe reduction in the data and consequently significant underestimation of the range size and rates of movement (Rooney et al., 1998; Kernohan et al., 2001a; Dahle and Swenson, 2003a). At the same time, many authors emphasize that relatively many locations are needed for any home range or UD estimates to be reliable (Harris et al., 1990; White and Garrott, 1990; Arthur and Schwartz, 1999; Gisard et al., 2000). When data provide unbiased temporal coverage of the animal's movements during the study period, the issue of autocorrelation is not necessarily relevant (Otis and White, 1999; Marzluff et al., 2001). However, if the data contain periods of frequent observations with temporally more isolated and independent observations, UD estimates are likely to become biased.

Problems with temporal autocorrelation can be prevented by using a sound tracking protocol, collecting locations with regular time intervals over a long time period (Robertson et al., 1998; Rooney et al., 1998). However, in practice, bursts of data separated by gaps with no observations are often collected. We suggest a new kernel-based method for estimating UDs with data that results from uneven sampling. The method, hereafter called the "time kernel", allows the user to decide the temporal scale at which aggregated locations are weighted less in relation to temporally discrete locations. A further development of the time kernel method uses information on both temporal and spatial autocorrelation of observations when weights are calculated. Essentially, an observation gets a relatively low weight only if it is both spatially close to and temporally aggregated with other observations.

Below, we describe the new methods and test them with the help of simulated data. By using simulated data, we gain improved understanding of the potential advantages of the techniques, because the true UD is available for comparisons.

We also investigate the time kernel method and the loss of data due to resampling with real radiolocation data collected for brown bears (Ursus arctos).

## 2. Methods

### 2.1. Time kernel calculations

The time kernel (TK) method considers both the spatial and temporal aggregation of observations. The idea is to calculate the UD by the standard kernel method (Worton, 1988, 1995), but by giving less relative weight to temporally close and thus autocorrelated observations that might otherwise bias the UD estimate. Animal observations, \( i = 1, \ldots, n \), are described by two spatial coordinates \( x_i \) and \( y_i \), and by the time the observation was made, \( t_i \). We first define a function, \( D(t) \), which describes the temporal density of observations (Fig. 1A). When a 1-D Gaussian density kernel is used, \( D(t) \) is defined by:

\[
D(t) = \sum_{i=1}^{n} \exp \left( -\frac{(t - t_i)^2}{2\hat{\lambda}_t^2} \right).
\] (1)

The temporal smoothing parameter, \( \hat{\lambda}_t \), is analogous to the spatial smoothing parameter used in traditional fixed and adaptive kernel methods (Worton, 1988, 1995). With a small value of \( \hat{\lambda}_t \), the fine detail of the data are used and each observation is considered independently, whereas with a larger value the role of individual observations is decreased and temporally close locations are considered as dependent on each other (Fig. 1A).

Next we use \( D(t) \) to get a weight, \( w_i \), for each data point, \( i \), under the assumption that a comparatively high value for
D(t) indicates high temporal autocorrelation, which should be translated into a comparatively low \( w_i \). The UD estimate is eventually normalized to unity and thus only relative weights are of significance. Thus, we calculate weights \( w_i \) as:

\[
\frac{1}{D(t)}
\]

Eq. (2)

Fig. 1 demonstrates the process of obtaining weights. Where locations are temporally aggregated, \( D(t) \) receives high relative values. When \( h_s \) is small, \( D(t) \) peaks are more narrow, but with large values of \( h_s \), the curve is smoother with fewer peaks (Fig. 1A). With large \( h_t \), more observations are considered temporally dependent and consequently there are more observations that receive relatively low weights, whereas with small \( h_t \), most observations are considered independent and gain a relative weight of 1 (Fig. 1B).

Following the determination of observation weights, the calculation of the actual spatial kernel home range follows the procedure of the traditional kernel method (Worton, 1987, 1989), but with each radiolocation weighted by \( w_i \). When using a normal distribution for smoothing, the spatial kernel is thus defined as:

\[
K(x, y) = \frac{1}{2\pi h_s^2} \sum_{i=1}^{n} w_i \exp \left( -\frac{(x-x_i)^2 + (y-y_i)^2}{2h_s^2} \right)
\]

Eq. (3)

Parameter \( h_s \) controls the degree of spatial smoothing in the calculation of the kernel estimate (Worton, 1989, 1995). Biologically, \( h_s \) controls for uncertainty in the estimation of the radiolocations and in the perceptual range of an animal. In order to compare individual home ranges, \( h_s \) should be the same for all individuals (Kernohan et al., 2001a).

In some cases, taking into account only the temporal density of observations in weights calculations may not be sufficient. For example, if animals perform fast long-distance movements to the location of an important resource, using only the temporal density on obtaining time kernel weights may underestimate the value of this resource. To avoid this, weights can be calculated using a spatiotemporal variant of the time kernel (TK STW) by replacing \( D(t) \) with \( D(t, x, y) \):

\[
D(t, x, y) = \sum_{i=1}^{n} w_i \exp \left( \frac{(t-t_i)^2}{2h_t^2} \right) \exp \left( -\frac{(x-x_i)^2 + (y-y_i)^2}{2h_s^2} \right)
\]

Eq. (4)
the species (Kemohian et al., 2001a) and the accuracy of the measurement of spatial locations. The value of \( h \) should be based on the movement rate of the animal. Temporal smoothing can be regarded as comparable to time to independence (TTI), the time needed between observations in order for them to be independent from each other (Pielbarg and Slade, 1985; Swihart et al., 1988; Kemohian et al., 2001a). Techniques suggested for defining TTI can also be used for adjusting the value of \( h \) (Swihart and Slade, 1985; Swihart et al., 1988; Roncey et al., 1998). As \( h \) describes the standard deviation (Eqs. (1) and (4)), TTI can be thought to approximate \( 2h \).

Since all observations do not receive equal weight in time kernel calculations, the effective data size, \( N_{\text{eff}} \), is usually smaller than the original data size, \( N \). Effective data size can be calculated by summing the weights:

\[
N_{\text{eff}} = \sum_{i=1}^{N} \frac{w_{i}}{w_{\text{max}}} \tag{5}
\]

where \( w_{\text{max}} \) is the highest individual weight obtained for any observation.

Note that for any data there is a minimum effective number of observations, \( N_{\text{min}} \), which can be found by varying \( h \). With low \( h \), all observations are essentially independent and \( N_{\text{eff}} = N \). Increasing \( h \) starts recognizing dependency between observations, causing non-independent observations to receive less weight. Consequently, \( N_{\text{eff}} \) decreases down to some point \( N_{\text{min}} \). We call the \( h \) corresponding to the minimum effective number of observations \( h_{\text{min}} \). When \( h \) is further increased from \( h_{\text{min}} \), all observations become essentially correlated to a high degree, and thus they get essentially same relative weights following which \( N_{\text{eff}} \) increases back to \( N \). Thus, using \( h \) values larger than \( h_{\text{min}} \) is not meaningful.

\( N_{\text{min}} \) can be used for investigating the temporal correlation structure of the data; if \( N_{\text{min}} < N \), then the data contains periods of high temporal autocorrelation at some time scale and the home range estimate may be correspondingly biased unless this is taken into account in the calculations. If \( N_{\text{min}} = N \), the data are very evenly sampled and partial temporal autocorrelation is not an issue.

### 2.2. Testing time kernel method with simulated data

Testing the time kernel method was done according to the following scheme: (i) generate a true UD for a hypothetical species based on a habitat quality-biased correlated random walk. (ii) Sample movement paths of individuals in the landscapes depicting the radiolocation data. (iii) Generate UD estimates based on the sampled simulated data using different methods, including the ordinary kernel and the time kernel, and calculate the deviation from the true UD.

For the tests, we chose a landscape structure that is simple enough to allow the replication of these results but complex enough to include some common features of real home ranges (Fig. 2). The landscape we use is bimodal, allowing infrequent moves of the individual between the two high-quality core areas. Habitat is divided into three classes with respect to quality, which results in uneven habitat use within the home range. Because best habitat occurs in a ring rather than in a filled-circular (Fig. 2), the true UD is more difficult to approximate using kernels than what may be apparent on the surface.

Movement paths of individuals were generated by a correlated random walk. The length of each movement is taken from an uniform distribution \( L \sim [0, L_{\text{max}}] \). The turning angle with respect to the previous movement is normally distributed around 0°, with a standard deviation of the angle being \( \phi \). Habitat quality has the following importance in the simulation. First, a movement is proposed by the random walk. If the movement would occur to habitat of the same or higher quality, then the proposed move is always accepted. If the move would go to habitat of lower quality, the move is accepted with probability \( P_{\text{accept}} = q_{2}/q_{1} \), where \( q_{1} \) is the lower quality and \( q_{2} \) the higher quality. (Note that this condition prevents the random walk moving out into cells with \( q < 0 \)). Following a discarded move event, the correlated random walk is interrupted for the following move and the next turning angle is picked from a uniform distribution \( [0, 2\pi] \).

As a further complication, our hypothetical animal has two movement modes, a slow and less directed one (e.g., foraging) and a faster and more directed one (escape, long-distance movement, etc.). Parameters for the foraging mode are \( L_{\text{max}} = 3.0 \) for the maximum step length and \( \phi = \pi/6 \) for the turning angle parameter. Parameters for the movement mode have triple speed and more directed movement with \( L_{\text{max}} = 9.0 \) and \( \phi = \pi/18 \), respectively. After a move in the foraging mode, the individual switches to the movement mode with a probability of 0.1. Transition from movement to foraging happens with probability 0.5.

Simulated individual starts its movements from the centre of the landscape, but the first 1000 movements are ignored to remove any dependence of results on the initial location of the individual. Simulated movement was continued as many steps as was needed to sample a given number (we used 800) of hypothetical observations. Movement paths were sampled using random sampling interspersed with bursts of intense sampling. Observations were taken with random intervals with from 1 to 100 time units between. An observation was extended to a sequence of 2–20 sequential observations (taken with identical intervals of 1) with the probability of 0.2. We did not include a sampling scheme with a uni-
form interval between samplings because with such data the
time kernel would have been identical to the normal kernel method.

We compared home range estimates generated using (i) the
ordinary kernel method, (ii) the ordinary kernel with data resampling interval and temporal autocorrelation between points (resampled kernel), (iii) the time kernel (TK) and (iv) the time kernel with spatiotemporal calculation of weights (TK STW). UD estimates generated using different methods were compared with respect to the overlap of the estimated and true UD (true obtained from the converged distribution of the random walk obtained from a 10 million step a posteriori simulation). This was done by calculating the difference in the discrete probability distribution as:

\[
d(T, E) = \sum_{x} \sum_{y} (T_{xy} - E_{xy}),
\]

where E is the estimated home range matrix and T the matrix
for true UD and summation is over the x-y-coordinates of the
matrices (discrete version of the Seidel's volume of intersection
(Kernohan et al., 2001b)). If the two spatial probability distributions are completely non-overlapping, \(d(T, E)\) equals one.

When comparing home range computation methods, data
sets with different effective numbers of observations were produced by setting \(h_t = 1, 1.5, 2.25, \ldots\). Each \(h_t\) resulted in a different number of effective observations, \(N_{eff}\) (Eq. (5)), for the time kernel estimates. For each \(h_t\), we generated 200 independent observation set replicates. Importantly, the resampling interval for the resampled kernel method was for each data set adjusted so as to give a number of observations identical to that obtained using the time kernel (\(N_{eff}\)).

The spatial smoothing parameter \(h_t\) would normally be
determined from prior knowledge on the spatial accuracy of observations, behaviour of the animal and on the desired spa-
tial resolution of the home range estimate. For our hypothet-
cial case, we set \(h_t = (2A/N)^{1/3}\), where \(N\) is the number of observations and \(A\) is the number of cells with positive habi-
tat quality. Heuristically, \(A\) is an a priori estimate of the average home range size for the species and \(h_t\) is set so that \(N\) circles with the radius of 0.5 \(h_t\) cover the area of the home range.

### 2.3 Comparison of home range methods with brown bear data

We used real radio-tracking data for 35 adult individual brown bears (Ursus arctos) from years 1998 and 1999 to compare yearly home ranges produced with the MCP, kernel and time kernel methods. Both years, each bear was observed during the entire active period from April to October. These data were collected with irregular sampling interval for various purposes by the Scandinavian Brown Bear Research Project.

Since the real bear UDIs were not available, we compared the home range areas estimated with 10 different home range estimation methods. The 100% MCP and kernel without resampling were included as reference home range types. The kernel and 100% MCP with resampling represent commonly used home range estimation methods that try to avoid temporal autocorrelation. Time kernel estimates were calcul-
lated with both temporal and spatiotemporal weights using three different values for \(h_t\). Resampling of data was done with a minimum of 100 h between observations. This inter-
val has been used previously with the same data (Dahle and Swenson, 2003a,b). It corresponds to the time it takes for a bear to travel across its home range with mean speed, and the time between weekly observations often available for bears (Wielgus and Bunnell, 1994; Mace and Waller, 1997, Waller and Mace, 1997; Rooney et al., 1998; Arthur and Schwartz, 1999; Dahle and Swenson, 2003a,b). The value of \(h_t\) in kernel and time kernel calculations was set to 1500 m, which falls between the error in localizing and the median \(h_t\) calculated with LSCV (Kenward, 2001, Dahle and Swenson, 2003a,b). In the time kernel calculations, we applied a \(h_t\) of 0.2, 2 and \(h_t\) (\(N_{eff}\)) days (the temporal unit in our calculations was 1 day). Tem-
poral smoothing of 2 days is comparable to the 100-h resam-
pling used for the resampled kernel method (see Section 2.1). The 2-day interval was approximately 50 h (2 days).

For computational purposes, it is practical to use discrete space instead of the full continuous distributions underlying the kernel methods. We discretized the bear home ranges into a grid with a 1000 m × 1000 m cell size, which corresponds to the grain of a habitat map available for the region. Dimensions of the matrix used for each home range were determined by the minimum and maximum coordinates of the bear, buffered all around by a margin of 1.5 times the value of \(h_t\). This ensured that tail probabilities extending outside the borders of the matrix were sufficiently small to be negligible (<1% of total probability). The contour enclosing 95% of the total UD was used for calculating kernel and time kernel home range area estimates.

### 3. Results

#### 3.1 Simulated data

Fig 3 shows the performance of different home range compu-
tation methods. With simulated data, \(N_{min} = 80\) \((h_t\) (\(N_{eff}\)) = 64) even
then though \(N_t = 800\), which indicates significant irregular tem-
poral aggregation of observations. With very small \(h_t\), the
performance of the TK is very similar to that of the ordi-
nary kernel. The performance improves with increasing \(h_t\)
(decreasing \(N_{eff}\)), and the best performance is achieved with
\(N_{eff} = 150\) \((h_t = 320)\). With any given \(N_{eff}\), especially with low
values, the TK performs better than the resampled kernel. The
performance of the resampled kernel deteriorates rapidly with
an increasing resampling interval (corresponds to a decreas-
ing \(N_{eff}\)), whereas the performance of the TK declines only to
the point \(N_{min}\). The performance of the resampled kernel may
even be worse than that of the ordinary kernel, because it is highly sensitive to selecting a too large resampling interval.

The TK STW performs best of the presented methods. This
method takes points as correlated only if they are close both
in terms of time and space (as determined by Eq. (4)). If two
points are temporally close (as determined by the choice of \(h_t\))
but spatially clearly distinct (as determined by the choice of \(h_t\))
then the locations are taken as essentially independent.
Consequently, the TK STW is less sensitive than the TK to the
choice of \(h_t\).
Fig. 3 – The comparison of different UD modelling techniques using simulated data. Curves show the performances of the different home range calculation methods measured by the mean difference from the true UD. Straight solid line shows the performance of the kernel estimated from the whole simulated data ($N = N_{eff} = 800$). Open circles mark the situation if the home ranges would have been estimated based on TTI (resampling interval $\approx 76$ and $h_t \approx 38$). The simulated animal moved with the average speed of 1.98 in the area with largest diameter of 150, thus it takes approximately 76 time units for the animal to cross its area (TTI). Note that TK estimate together with TK STW performed considerably better than the resampled kernel, when TTI was used as a guideline.

3.2. Brown bear data

Exploring the bear data with the help of $N_{min}$ exposed severe temporal irregularity (mean $N_{min}$ of 19 ± 1 compared to mean N of 91 ± 11). However, with $h_t = 2$ the comparison of the $N_{eff}$ values for standard TK (mean 28 ± 1) with those of TK STW (mean 51 ± 4) revealed that although many observations are temporally close, they are spatially separate at the time scale used. Fig. 4 demonstrates differences between home range layouts produced with different methods. The shapes of the MCP ranges (B and C) differ markedly from those of kernel-based methods and information about the use of space inside the home range is lost. Although the profiles of the ordinary kernel and TK ranges do not differ as noticeably, the spatial arrangement of the probabilities of occurrence is somewhat different. In the ordinary kernel using all observations, emphasis is given to the large area in the middle of the home range (A). When temporal aggregation of observations is taken into account in the TK estimate, the relative importance of this area decreases and areas in the left of the home range increase in their importance (D). Most importantly, the ordinary kernel with data resampling leaves many observations outside the home range estimate (D).

Resampling of data resulted in almost 70% reduction in data points (from mean 95 ± 11 to mean of 27 ± 1). The smallest sample size after resampling was 13, which hardly is adequate for reliable home range estimation (Harris et al., 1990; White and Garrott, 1990; Arthur and Schwartz, 1999; Girard et al., 2002). This loss of information is evident in Fig. 4, where the time kernel UD estimates (Fig. 4E and F) include areas absent from the resampled kernel estimate (Fig. 4D).

In general, kernel ranges estimated from resampled data were much smaller than TK ranges with corresponding temporal smoothing, which is evident from a comparison of home range areas (Table 1). Areas estimated from resampled

Fig. 4 – Home range layouts for one brown bear produced with different home range estimates. The darker the colour is the lower is the probability of occurrence. Original observations are marked with dark dots. For both kernel and time kernel methods $h_t = 1500$ and for estimates with resampled data the sampling was made with a 100 h interval. Shown home range estimates are (A) kernel and (B) 100% MCP estimate for all locations, (C) 100% MCP and (D) kernel estimate for resampled data and (E) time kernel (TK) and (F) time kernel with spatiotemporal weights (TK STW) using $h_t = 2$ (that corresponds to 100 h sampling interval). Note that the corresponding TK and TK STW estimates reveal two areas with comparatively high utilization probabilities that are left outside the area of the resampled kernel.
data were smaller than those estimated using other home range methods (Table 1). Resampling may exclude remote observations by chance, which can affect range sizes significantly. MCP home ranges were in general considerably larger than any of the kernel-based ranges. This is because MCPs may include large unused areas between the outermost locations. Areas calculated with the TK and TK STW methods using different values for $h$ seemed to be consistent using this data.

### 4. Discussion

Home range estimates are often used for studying animal use of space. Valuable information about habitat use within the home range can be lost if only information about home range borders is used, as is done by MCPs and flat kernels. Using the UD directly, instead of a uniform probability distribution within a given probability contour, can improve our understanding of the animal’s use of space. This also evades the problem of having to choose the proportion of the UD that is used for the contour calculation. Ideally, the data for estimating animal UD should comprise a large collection of observations by chance, which can affect range sizes significantly. MCP home ranges were in general considerably larger than any of the kernel-based ranges. This is because MCPs may include large unused areas between the outermost locations. Areas calculated with the TK and TK STW methods using different values for $h$ seemed to be consistent using this data.

### Table 1

<table>
<thead>
<tr>
<th>HR method</th>
<th>Area ± S.E. (km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>100% MCP</td>
<td>977 ± 192</td>
</tr>
<tr>
<td>Kernel</td>
<td>415 ± 29</td>
</tr>
<tr>
<td>100% MCP with resampling</td>
<td>838 ± 170</td>
</tr>
<tr>
<td>Kernel with resampling</td>
<td>356 ± 19</td>
</tr>
<tr>
<td>TK $h = 2$</td>
<td>415 ± 29</td>
</tr>
<tr>
<td>TK $h = 0.2$</td>
<td>418 ± 29</td>
</tr>
<tr>
<td>TK $h = 2$ STW</td>
<td>412 ± 29</td>
</tr>
<tr>
<td>TK STW $h = 0.2$</td>
<td>435 ± 30</td>
</tr>
<tr>
<td>TK STW $h = 0.02$</td>
<td>620 ± 30</td>
</tr>
</tbody>
</table>

Note that $h_{max}^{N_{min}}$ was different for each individual (mean $h_{max}^{N_{min}}$ was 12.3 ± 1 and minimum $h_{max}^{N_{min}}$ was 2.5 days).

The time kernel (TK) method and its spatiotemporal extension (TK STW) allow the user to decide to which extent bursts of frequent observations are taken into account in the estimation of a UD without losing any information through resampling.

A long enough study period and a sampling procedure covering different behaviours of the animal are relevant for home range studies (Worton, 1987; Robertson et al., 1998; Rooney et al., 1998; Otis and White, 1999; Kernohan et al., 2001a). Especially in heterogeneous environment and in case of animals with complex behaviour it is important to have temporally unbiased data. Even if tracking protocol originally had been regular problems in detectability of species could have resulted in temporally irregular data for different individuals. If data are suspected to be irregular, we propose investigating the temporal sequence of the radiolocation data with help of TK method. The first step is to define $N_{max}$ by varying the values of $h$, in the standard TK calculations with a chosen $h$. If $N_{max} ≪ N$, data contains periods of high temporal autocorrelation that have potential to bias the UD estimates. In this case, the next step would be to identify a reasonable temporal scale ($h_t$) to work with.

Selection of $h_t$ should be based on the movement rate of the animal. For example, if animal is likely to cover most of its range within short time period, the value of $h_t$ should be set small. With small $h_t$, most of the observations are considered independent and given equal weights. Estimates of TTI and $h_t(N_{min})$ provide guidelines for deciding the value of $h_t$. Although the optimal value for $h_t$ is likely to be smaller than $h_t(N_{min})$, direct use of $h_t(N_{min})$ in time kernel calculations gave better results with our simulated data than did the ordinary kernel with resampling with any time interval (Fig. 3). Whether to use temporal or spatiotemporal weights in time kernel calculations depends on both the behaviour of the animal and the intended purpose of the UD estimates. For example, if an animal is likely to spend most of its time around one place (say nest site) but exhibits fast long distance visits to the location of some important resource, using standard weighting may underestimate the value of this resource. On the other hand, some animals may pay short visits to resource poor edges of their home ranges just to check surrounding individuals.

On the downside, the time kernel method shares some disadvantages with other kernel-based methods. A degree of subjectivity cannot be avoided in selecting values for $h_t$ and $h$. However, techniques suggested for selecting the value for spatial smoothing are also valid for the time kernel estimator (Worton, 1987; 1989, 1995; Seaman and Powell, 1996; Kenward, 2001; Kernohan et al., 2001a). Likewise, methods of defining TTI can be used for selecting an appropriate value of $h_t$ (Swihart and Slade, 1985; Rooney et al., 1998; Otis and White, 1999; Kernohan et al., 2001a). It is an implicit assumption by those advocating resampling that estimates with resampled data will describe the home range more accurately (Rooney et al., 1998). However, information can be lost because of resampling and using intensive observation procedures instead can lead to improved UD estimates (Rooney et al., 1998; Otis and White, 1999; Kernohan et al., 2001a).
The spatial organization of the landscape and different behavioral characteristics of the animal define the shape of the animal's UD. Differences in the performances of UD estimation methods are likely to become more significant with increasing complexity. We used a variant of a bimodal landscape representation to capture some complexity of the real world without losing the possibility of replicating our results. Based on our comparison of true and estimated UD's, with temporally irregular data the TK and TK STW methods always performed better than the ordinary kernel or the TTI resampled kernel. In short, it is always safe to use TK as it never performs poorer than ordinary kernel or corresponding resampling. Additionally, TK may reveal interesting details about the temporal structure of the data. A software implementation of the time kernel method is available from website www.helsinki.fi/science/metapop/. This software, R-Range, can also be used for the estimation of habitat selection based on UD's and for the comparison of different home range computation methods.

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