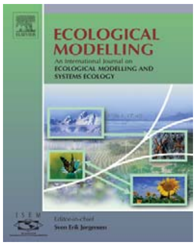
ECOLOGICAL MODELLING 194 (2006) 405–413

available at www.sciencedirect.com

journal homepage: www.elsevier.com/locate/ecolmodel



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

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ARTICLE INFO

Article history:
Received 21 October 2004
Received in revised form 17 October 2005
Accepted 4 November 2005
Published on line 27 December 2005

Keywords:
Habitat analysis
Home range
Kernel
Temporal autocorrelation
Time kernel

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 UDs 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; Kenward, 2001; 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 Halkin, 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 Halkin, 1994; Lawson and Rodgers, 1997; Robertson et al., 1998; Kenward, 2001; Kenward et al., 2001; Kernohan et al., 2001a).

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doi:10.1016/j.ecolmodel.2005.11.001

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., 1998).

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 Waller, 1997; Waller and Mace, 1997; Kernohan et al., 1998; Kenward et al., 2001; Marzluff et al., 2001; McLoughlin et al., 2002; Lyons 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 related studies than the MCP method or flat kernel (Worton, 1987; Harris et al., 1990; Seaman and Powell, 1996; Marzluff et al., 2001, 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. (2001) 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, 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; Girard et al., 2002). 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, 1989, 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:

$$D(t) = \sum_{i=1}^{n} \exp\left(-\frac{(t - t_i)^2}{2h_t^2}\right). \tag{1}$$

The temporal smoothing parameter, h_t, is analogous to the spatial smoothing parameter used in traditional fixed and adaptive kernel methods (Worton, 1989, 1995). With a small value of h_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

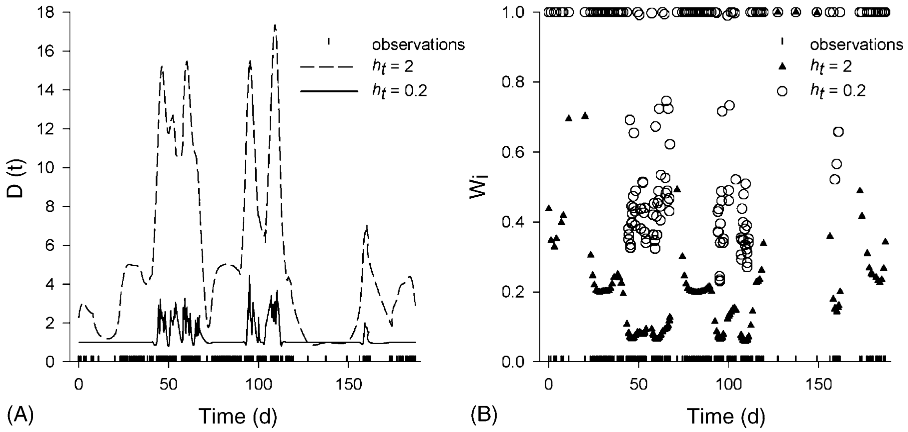

Fig. 1 – The calculation of weights for observations, which are shown by vertical lines at the bottom of panels: (A) the smoothed temporal distribution of locations $D(t)$ is calculated using the smoothing parameter values $h_t = 0.2$ and 2. (B) The corresponding relative weights (w_i/w_{max}) of individual observations.

$D(t)$ 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:

$$w_i = \frac{1}{D(t_i)}. \tag{2}$$

Fig. 1 demonstrates the process of obtaining weights. Where locations are temporally aggregated, $D(t)$ receives high relative values. When h_t is small, $D(t)$ peaks are more narrow, but with large values of h_t 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:

$$K(x, y) = \frac{1}{2\pi n h_s^2} \sum_{i=1}^{n} w_i \exp\left(-\frac{(x - x_i)^2 + (y - y_i)^2}{2h_s^2}\right). \tag{3}$$

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., 2001b).

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 $D(t, x, y)$:

$$D(t, x, y) = \sum_{i=1}^{n} \exp\left(-\frac{(t - t_i)^2}{2h_t^2}\right) \exp\left(-\frac{(x - x_i)^2 + (y - y_i)^2}{2h_s^2}\right). \tag{4}$$

Eq. (4) combines the time kernel with the ordinary spatial kernel in the calculation of weights for observations. The logic is that usually temporally close observations are autocorrelated and should be devalued to avoid an artefactual high-density aggregate in the UD. However, occasionally a fast long distance movement might occur between the temporally close observations. Correlation structure of such movement can be defined in relation to the spatial kernel that is used in home range calculations. If the spatial kernels for two observations do not overlap, there seems to be little reason to devalue the observations due to temporal autocorrelation—both give information of the preferred locations at different parts of the home range. Consequently, in the spatiotemporal calculation of weights, both temporal and spatial kernel components are multiplied. Heuristically, highest UD values are given to areas where the animal repeatedly returns to after being elsewhere for a while. Observations at such a location are spatially close but they have zero temporal autocorrelation, and therefore a high-density area is generated into the UD. For example, with brown bears, having data with 10 sequential observations 1 h apart at approximately the same location tells little more than that an observation sequence just happened to be recorded when the animal was crossing the location. In contrast, if the animal returns to the same spot 10 times with a week between, there is a strong signal of the location really being preferred by the animal.

The selection of the values for h_s, and h_t is necessarily species-dependent and somewhat subjective. Methods based on least squares cross-validation (LSCV) have been suggested for selecting the optimum value for h_s (Worton, 1989; Seaman and Powell, 1996; Kenward, 2001; Kernohan et al., 2001a). The selection of h_s should also take into account the biology of the species (Kernohan et al., 2001a) and the accuracy of the measurement of spatial locations. The value of h_t 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 (Swihart and Slade, 1985; Swihart et al., 1988; Kernohan et al., 2001a). Techniques suggested for defining TTI can also be used for adjusting the value of h_t (Swihart and Slade, 1985; Swihart et al., 1988; Rooney et al., 1998). As h_t describes the standard deviation (Eqs. (1) and (4)), TTI can be thought to approximate 2 h_t.

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

$$N_{\text{eff}} = \sum_{i=1}^{n} \frac{w_i}{w_{\max}}, \tag{5}$$

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

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

$N_{\min}$ can be used for investigating the temporal correlation structure of the data; if $N_{\min} \ll N$, 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 $N_{\min} \approx N$, 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 circle (Fig. 2), the true UD is more difficult to approximate using kernels than what may be apparent on the surface.

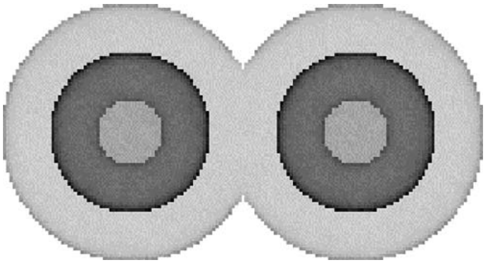

Fig. 2 – The true UD of the hypothetical species that reflects the structure of the landscape. The concentric rings have radiuses of 10, 25 and 40 grid cells. The habitat quality in the rings is 5, 10 and 2, respectively. The two centres of the home range are located at 60 and 130 in the horizontal direction. The darker the point in UD is the higher is its usage rate.

Movement paths of individuals were generated by a correlated random walk. The length of each movement is taken from an uniform distribution $L = [0, \ldots, L_{\max}]$. The turning angle with respect to the previous movement is normally distributed around 0°, with a standard deviation of the angle being φ. 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_2 is the lower quality and q_1 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 $L_{\max} = 3.0$ for the maximum step length and $\varphi = \pi/6$ for the turning angle parameter. Parameters for the movement mode have triple speed and more directed movement with $L_{\max} = 9.0$ and $\varphi = \pi/18$, 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 uniform 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 resampled using a minimum interval to reduce 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 UDs (true obtained from the converged distribution of the random walk obtained from a 10 million step simulation). This was done by calculating the difference in the discrete probability distribution as:

$$d(T, E) = \frac{\sum_x \sum_y |T_{xy} - E_{xy}|}{2}, \tag{6}$$

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_s would normally be determined from prior knowledge on the spatial accuracy of observations, behaviour of the animal and on the desired spatial resolution of the home range estimate. For our hypothetical case, we set $h_s = [2A/(N\pi)]^{0.5}$, where N is the number of observations and A is the number of cells with positive habitat quality. Heuristically, A is an a priori estimate of the average home range size for the species and h_s is set so that N circles with the radius of $0.5\,h_s$ 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 UDs were not available, we compared the home range areas estimated with 10 different home range estimation methods. The 100% MCP and the 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 calculated 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 interval 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 to 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_s in kernel and time kernel calculations was set to 1500 m, which falls between the error in localizing and the median h_s calculated with LSCV (Kenward, 2001; Dahle and Swenson, 2003a). In the time kernel calculations, we applied a h_t of 0.2, 2 and $h_t(N_{\text{min}})$ days (the temporal unit in our calculations was 1 day). Temporal smoothing of 2 days is comparable to the 100-h resampling used for the resampled kernel method (see Section 2.1; $2h_t \approx 100\,\text{h} \Leftrightarrow h_t \approx 50\,\text{h} \approx 2$ day).

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 $1000\,\text{m} \times 1000\,\text{m}$ 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 2.5 times the value of h_s. This ensured that tail probabilities extending outside the borders of the matrix were sufficiently small to be negligible ($\ll$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 computation methods. With simulated data, $N_{\text{min}} \approx 80$ ($h_t(N_{\text{min}}) \approx 44$) even though $N = 800$, which indicates significant irregular temporal aggregation of observations. With very small h_t, the performance of the TK is very similar to that of the ordinary kernel. The performance improves with increasing h_t (decreasing N_{eff}), and the best performance is achieved with $N_{\text{eff}} \approx 210$ ($h_t \approx 320$). 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 decreasing 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 proposed 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_s), then the locations are taken as essentially independent. Consequently, the TK STW is less sensitive than the TK to the choice of h_t.

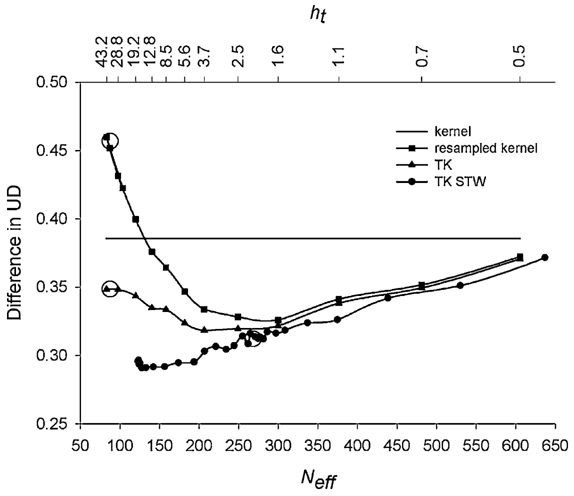

Fig. 3 – The comparison of different UD modelling techniques using simulated data. Curves show the performances of the different home range calculation methods measured by the mean difference from the true UD. Straight solid line shows the performance of the kernel estimated from the whole simulated data ($N = N_{eff} = 800$). Open circles mark the situation if the home ranges would have been estimated based on TTI (resampling interval ≈ 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 95 ± 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 (E). 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 12, 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

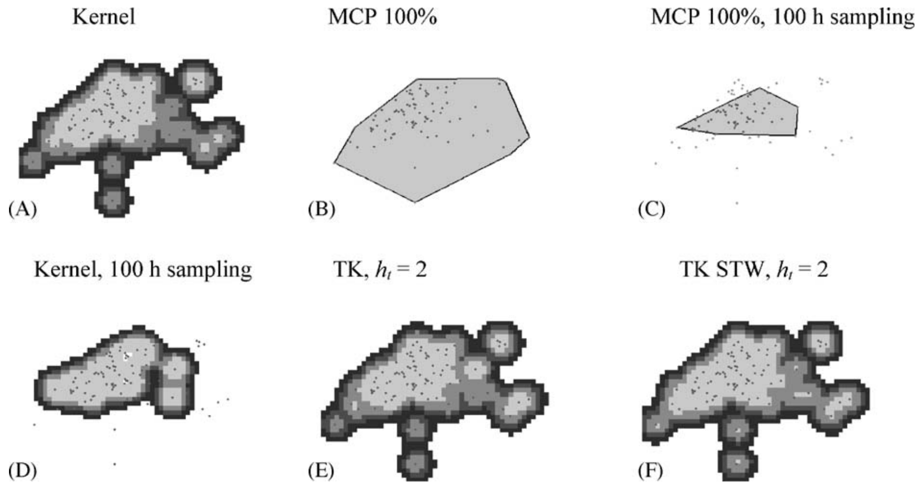

Fig. 4 – Home range layouts for one brown bear produced with different home range estimates. The darker the colour is the lower is the probability of occurrence. Original observations are marked with dark dots. For both kernel and time kernel methods $h_s = 1500$ and for estimates with resampled data 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.

Table 1 – The mean areas (km^2) of brown bear home ranges that have been estimated with different home range (HR) methods

HR method	Area ± S.E. (km^2)
100% MCP	977 ± 192
Kernel	415 ± 29
100% MCP with resampling	818 ± 170
Kernel with resampling	356 ± 19
TK $h_t = 2$	416 ± 29
TK $h_t = 0.2$	418 ± 29
TK h_t^{min}	412 ± 29[a]
TK STW $h_t = 2$	435 ± 30
TK STW $h_t = 0.2$	420 ± 30
TK STW h_t^{min}	449 ± 30[a]

[a] Note that $h_t(N_{min})$ was different for each individual (mean $h_t(N_{min})$ was 12.3 ± 1 and minimum $h_t(N_{min})$ was 2.5 days).

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_t 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 obtained over a long time period with approximately equal sampling intervals. However, often rather small data sets with irregular sampling interval are available. The probability of occurrence at any location inside a home range is an estimate of the proportion of time spent there, and thus, using such partially temporally autocorrelated data leads to overemphasizing the areas where frequent sampling happened to take place.

By definition, locations inside an animal's home range cannot be spatially or temporally independent from each other (Otis and White, 1999). Much effort has been put into detecting temporal autocorrelation and for developing methods for selecting a proper resampling interval (Swihart and Slade, 1985; Swihart et al., 1988; 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 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_{min} by varying the values of h_t in the standard TK calculations with a chosen h_s. If $N_{min} \ll N$, 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_s. 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; Kenward, 2001; Kernohan et al., 2001a). More importantly, where selecting a too large resampling interval may result in severe deterioration in the performance of the traditional kernel method, N_{min} defines a clear upper limit for h_t in time kernel estimation. Spatiotemporal weighting is even less sensitive to the overestimation of h_t than is the standard weighting.

The spatial organization of the landscape and different behavioural 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 and two movement modes to capture some complexity of the real world without loosing the possibility of replicating our results. Based on our comparison of true and estimated UDs, 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, B-Range, can also be used for the estimation of habitat selection based on UDs and for the comparison of different home range computation methods.

Acknowledgements

We thank Hanna Kokko, Bob O'Hara, Otso Ovaskainen and Jon E. Swenson for comments on the manuscript, and the Scandinavian Brown Bear Research Project for providing the bear data. Two anonymous referees are acknowledged for the valuable and inspiring comments they gave to improve the manuscript. This work was supported by the Finnish Cultural Foundation and the Academy of Finland (grant number 1206883 to A.M.) and the Finnish Centre of Excellence Programme 2000–2005 (grant number 44887).

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