22 August 2011

Jed A Long
Spatial Pattern Analysis and Research Lab
Department of Geography, University of Victoria
PO Box 3060 STN CSC
Victoria, BC, Canada, V8W 3R4
1-250-853-3271
jlong@uvic.ca

Time Geography and Wildlife Home Range Delineation

JED A. LONG, Spatial Pattern Analysis and Research Lab, Department of Geography, University of Victoria, PO Box 3060 STN CSC, Victoria, BC, Canada, V8W 3R4

TRISALYN A. NELSON, Spatial Pattern Analysis and Research Lab, Department of Geography, University of Victoria, PO Box 3060 STN CSC, Victoria, BC, Canada, V8W 3R4

ABSTRACT We introduce a new technique for delineating animal home ranges that is relatively simple and intuitive: the potential path area (PPA) home range. PPA home ranges are based on existing theory from time geography, where an animal's movement is constrained by known locations in space-time (i.e., *n* telemetry points) and a measure of mobility (e.g., maximum velocity). Using the formulation we provide, PPA home ranges can be easily implemented in a Geographic Information System (GIS). The advantage of the PPA home range is the explicit consideration of temporal limitations on animal movement. In discussion, we identify the PPA home range as a stand-alone measure of animal home range or as a way to augment existing home range techniques. Future developments are highlighted in the context of the usefulness of time geography for wildlife movement analysis. To facilitate the adoption of this technique we provide a tool for implementing this method.

KEY WORDS home range, time geography, potential path area, wildlife movement, GPS tracking, space-time

The Journal of Wildlife Management: 00(0): 000-000, 201X

Animal home ranges are used to study many aspects of wildlife ecology including habitat selection (Aebischer et al. 1993), territorial overlap (Righton and Mills 2006), and movement impacts of offspring status (Smulders 2009). Home ranges often serve as the primary spatial unit for wildlife research and represent the area to which an animal confines its normal movement (Burt 1943). Wildlife telemetry data, typically collected with radio or Global Positioning System (GPS) collars, provide a collection of space-time locations for an animal. Telemetry data are commonly converted to home ranges to identify spatial patterns in animal movement and answer specific research questions.

To derive animal home ranges, wildlife scientists have used existing methods in geometric topology and spatial smoothing to transform a set of telemetry points into a polygon animal home range. The 2 most common methods for computing animal home ranges are the minimum convex polygon (MCP), and kernel density estimation (KDE; Laver and Kelly 2008). MCP continues to be used extensively in wildlife movement analysis (Laver and Kelly 2008) despite considerable drawbacks, such as sensitivity to sampling intensity and outliers, convex assumption, and inclusion of large, unused interior areas (Worton 1987, Powell 2000, Borger et al. 2006). The prevalence of MCP is likely owing to its ease of implementation in common Geographic Information System (GIS) platforms and that it requires no input parameters. Kernel density estimation (KDE) has been influential in home range analysis since its introduction by Worton (1989). KDE remains contentious in animal movement analysis owing to issues with selecting an appropriate kernel bandwidth (Hemson et al. 2005, Kie et al. 2010), which can significantly affect results (Worton 1989). Unfortunately, KDE-based home ranges can be misleading when telemetry points are irregularly shaped (Downs and Horner 2008) or when animals occupy patchy environments (Mitchell and Powell 2008). A number of other lesser-used methods also exist (e.g., harmonic mean, Dixon and Chapman 1980; local nearest-neighbor convex hull, Getz and Wilmers 2004; Brownian bridge, Horne et al. 2007; characteristic hull, Downs and Horner 2009), but have yet to become widely adopted.

The objective of this article is to demonstrate a new approach for integrating time attributes accompanying telemetry data when calculating animal home ranges. Drawing on concepts from time geography (Hagerstrand 1970), we develop a new approach for computing animal home ranges that explicitly considers the temporal constraints of animal movement. Time is largely ignored in existing home range techniques, and used primarily for separating data into temporal groups such as seasons (Nielson et al. 2003). We discuss the value of this method in context of existing home range research, including existing examples moving towards a time-geographic approach.

METHODS

Background: Time Geography

Time determines bounds on an object's movement in space (Parkes and Thrift 1975). With time geography (Hagerstrand 1970), these constraints are represented as volumes containing all accessible locations in a 3-dimensional space-time continuum consisting of geographic coordinates x and y and time (t) (frequently termed the space-time cube, Kraak 2003; or space-time aquarium, Kwan and Lee 2004). If both starting and end points are known (as with a collection of telemetry fixes) then the space-time prism represents the set of all accessible locations to the object during that movement segment (Fig. 1). The projection of the space-time prism onto the geographic plane is termed the potential path area (PPA), and represents all locations accessible to an object given its start and end points and assumed maximum rate of travel (Fig. 1). An object's maximum traveling velocity affects the extent of these volumes into geographic space.

Potential Path Area (PPA): A New Measure of Animal Home Range

We will focus on potential uses of PPA in wildlife movement analysis, specifically the calculation of a PPA animal home range. The PPA represents the set of all accessible locations between 2 known locations in space and time (Miller 2005). Geometrically, the PPA is an ellipse with focal points located at 2 known locations, the origin and destination. The spatial extent of the PPA depends on the animal's maximum velocity (v_{max}), which may be explicitly known or empirically estimated from the data.

Visually, conceptualizing the creation of a PPA ellipse is best done using the pins-and-string method (Fig. 2a). Consider placing pins at the known start (i) and end (j) locations of an animal movement segment. A single string is then tied to each point, connecting the 2 pins. The length of the string is D_{max}, representing the maximum distance the animal can travel given its maximum velocity (v_{max}) and the time difference between points i and j (Δt).

$$D_{max} = v_{max} \times \Delta t \qquad [1]$$

The PPA ellipse is drawn by moving a pencil around the 2 points, but inside of the string, keeping the string tight at all times. Any point located along or within the PPA ellipse is reachable by the animal during this movement segment.

Mathematically, given that in unconstrained space PPA is an ordinary ellipse, we can derive PPA using parameters of an ellipse related to animal movement in time and space. We define v_{max} and Δt as above, the maximum velocity of the animal and the time difference between known telemetry locations *i* and *j*. We define a PPA ellipse using 4 parameters: a center point, a major axis, a minor axis, and a rotation angle (Fig. 2b). We calculate the center point as the midway point between the spatial (x, y) coordinates of telemetry points *i* and *j*. We define the major axis (a) as:

$$\begin{aligned} a &= D_{\max} \\ &= v_{\max} \times \Delta t \end{aligned} \quad [2]$$

With this we can define the minor axis (b) as:

$$b = \sqrt{a^2 - d^2} \quad [3]$$

Where d is the Euclidean distance between points *i* and *j*. Rotation angle (R_θ) is the angle the ellipse is rotated from the horizontal, and defined using x and y coordinates of telemetry points *i* and *j*:

$$R_\theta = \tan^{-1}\left(\frac{y_j - y_i}{x_j - x_i}\right) \quad [4]$$

Using these parameters, we can generate the PPA ellipse for any pair of known locations in space-time.

A PPA home range can be computed by generating PPA ellipses for a set of animal locations. A telemetry dataset of n recordings requires calculation of $n - 1$ PPA ellipses, which are combined to produce the PPA home range (Fig. 2c). Formally this is defined as the union of $n - 1$ PPA ellipses such that:

$$\mathrm{PPA}_{\mathrm{HR}} = \bigcup[\mathrm{PPA}_{i,i+1}], \quad i \text{ in } \{1,\ldots,n-1\} \quad [5]$$

The mathematical formulation of this method (represented by equations [1] through [5]) is easily implemented in a GIS.

Estimating v_{max}

The PPA home range method requires a single input parameter v_{max} that has obvious biological connotations and in some cases may be explicitly known based on a fine understanding of an organism's mobility. This parameter could be related to an organism's maximum velocity. For example, cheetahs have a maximum speed of up to 120 km/h (Sharp 1997); however it is unreasonable to expect a cheetah to maintain that speed over longer intervals, characteristic of telemetry datasets. It is more useful to compute the maximum distance a cheetah could cover in 30 minutes and derive v_{max} from this. In practice, v_{max} should relate biologically to the temporal frequency of recordings.

In many cases however, a biologically reasonable estimate of v_{max} will not be explicitly known and a researcher will be required to estimate it from the data. For each pair of consecutive relocation fixes we can compute the segment velocity (v_i) by:

$$v_i = \frac{d_i}{t_i} \qquad [6]$$

where d_i is the distance and t_i the time difference between consecutive fixes. Computing v_i for all $n - 1$ segments will provide a distribution of v values which can be used to generate estimates for v_{max}. The simplest would be to take $\max(v_i)$ – the maximum observed velocity as v_{max}; however, this is problematic as it produces a straight-line (degenerative ellipse) between any consecutive pair of fixes that have this maximum value. A more robust approach is to estimate a value for v_{max} based on the ordered distribution of the v_i. Following Robson and Whitlock (1964) an estimate of v_{max} could take the form:

$$\hat{v}_{\max} = v_m + (v_m - v_{m-1}) \quad [7]$$

where v_i are in ascending order such that $v_1 < v_2 < \ldots < v_{m-1} < v_m$ and $m = n - 1$. This estimate for v_{max} has an approximate $100(1 - \alpha)\%$ upper confidence limit given by:

$$\mathrm{U}_{\mathrm{Lim}}(v_{\max}) = v_m + \frac{(1-\alpha)(v_m - v_{m-1})}{\alpha} \quad [8]$$

Cooke (1979) and van der Watt (1980) have extended the work of Robson and Whitlock (1964) deriving estimates with lower mean squared errors and smaller confidence intervals, at the cost of added complexity. In the case where $v_m = v_{m-1}$, the result from [7] will equal $\max(v_i)$ and cause degenerate ellipses to be produced for pairs of consecutive points that have this maximum value. The method of van der Watt (1980) is advantageous as it avoids the problem of degenerate ellipses through careful selection of the parameter k in the equation:

$$\hat{v}_{\max} = \left(\frac{k+2}{k+1}\right)v_m - \left(\frac{1}{k+1}\right)v_{m-k} \quad [9]$$

where $1 < k < m$ representing the k^{th} ordered value of v_i. This estimate for $v_{\max}$ has an approximate $100(1 - \alpha)\%$ upper confidence limit given by:

$$\mathrm{U}_{\mathrm{Lim}}(v_{\max}) = v_m + \left(\frac{1}{1/(1-\alpha^{1/k}) - 1}\right)(v_m - v_{m-k}) \quad [10]$$

In the previously stated problem scenario where $v_m = v_{m-1}$ it would be useful to take k to be the largest value such that $v_{m-k} < v_m$. In general [9] has been shown to be an improved estimator of $v_{\max}$ over [7] (van der Watt 1980); however, it requires that the researcher select an appropriate value for k. Alternatively, a more conservative analysis could use the upper confidence interval limits (e.g., [8] or [10]) as an estimator for $v_{\max}$.

For demonstration, we simulate an animal trajectory using a correlated random walk (n = 2,000). Using these data as a surrogate for animal movement data, we calculate animal home range using 2 common, existing techniques (MCP and KDE) and the new PPA home range approach. We used the Robson and Whitlock (1964) method given by [7] for estimating the $v_{\max}$ parameter from the data. The temporal sampling interval of telemetry fixes is known to influence output home range size and shape using MCP (Borger et al. 2006) and KDE (Downs and Horner 2008), but also will influence the PPA home range. To demonstrate this effect, we re-sampled our simulated animal trajectory using only 25% (n = 500) of the points and re-estimated the $v_{\max}$ parameter using [7].

RESULTS

Estimated values for the $v_{\max}$ parameter were 10.6 for the original correlated random walk dataset (n = 2,000), and 6.8 for the re-sampled dataset (n = 500). Maps of output home ranges using the original correlated random walk (Fig. 3 a–c) and re-sampled dataset (Fig. 3 d–f) are given to view differences and similarities between MCP, KDE, and PPA. Areas of output home ranges for the original correlated random walk are: MCP – 53,739, KDE – 25,045, PPA – 37,232. For the re-sampled dataset home range areas are: MCP – 52,391, KDE – 29,110, PPA – 60,658. Coarsening of the sampling frequency (through re-sampling) caused MCP area to decrease, while both KDE and PPA increased in area.

DISCUSSION

In this example, the effect of changing sampling frequency had minimal effect on home range computed using MCP (Fig.3 a, d), however this will not always be the case (Borger et al. 2006). With KDE, fewer points lead to increased uncertainty in the bandwidth selection process, resulting in a wider bandwidth selection, and in general a larger output home range. With the PPA home range method uncertainty is a function of the time between consecutive known locations, rather than the number of points. As a result, PPA home ranges are comprised of fewer, larger ellipses to account for uncertainty in animal location between consecutive known points, and produce larger home range estimates. We suggest that PPA home ranges be employed only when telemetry data are collected using a relatively short sampling interval (e.g., dense GPS telemetry data). In these situations, uncertainty between consecutive fixes will be relatively low. In cases where the temporal duration between fixes is substantially longer (e.g., with most VHF collars), the ellipses produced by the PPA algorithm will be large, resulting in significant overestimations of home range size. We withhold from specifying an absolute threshold on sparse telemetry data where the PPA method should not be used as it will be dependant on both the species (e.g., large vs. small mammal) and application (seasonal home range vs. migratory behavior). Comparison of the PPA home range with existing methods (e.g., KDE and MCP) should provide information as to whether or not the PPA approach is appropriate with a given dataset (see Fig. 4 and the accompanying discussion below).

The conceptual and computational simplicity of the PPA home range may be its greatest asset. We define the PPA home range simply as: given a set of sampled locations (telemetry points) the PPA home range contains all locations in geographic space that the animal could have visited. The PPA method can be easily implemented in a GIS and requires only 1 input parameter, maximum travelling velocity – v_{max}, that can be derived using biological knowledge or estimated directly from the data (e.g., using [7] or [9]). If telemetry data are categorized into distinct behavioral segments (e.g., Jonsen et al. 2005, Gurarie et al. 2009) where differing v_{max} would be expected, PPA home range analysis could be further enhanced.

Despite the intuitive structure of ideas from time geography, they are largely absent from wildlife movement research. In one example, Baer & Butler (2000) use time geographic theory for modeling wildlife movement building upon Hagerstrand's (1970) concept of bundling, representing animals congregating in space-time. Regions where bundling occurs can be used to identify specific ecological activity in groups of animals (e.g., locating scarce resources). Wentz et al. (2003) implement time geographic constraints for animal movement, interpolating between sampled telemetry locations to model movement paths. Time geography volumes are used by Wentz et al. (2003) to constrain random walks between sampled locations. More recently, Downs (2010) presents a novel approach for incorporating time geographic principles, specifically the potential path area (termed geo-ellipse), into kernel density estimation. Downs (2010) uses the geo-ellipse in place of a circular kernel in the density estimation. Several advantages of this approach are identified, such as replacing subjective selection of kernel bandwidth by an objective parameter – maximum travelling velocity. Time geographic kernel density estimation assigns zero density to regions outside of the PPA home range, creating a utilization distribution density allocated only to accessible regions.

Wildlife do not use the space within their home range evenly motivating use of an intensity surface (utilization distribution) to analyze animal space use (Jennrich and Turner 1969). Utilization distributions more adequately portray patterns of space use within wildlife home ranges and provide more reliable estimates of overlap and/or fidelity compared with discrete home range methods (Fieberg and Kochanny 2005). However, these advantages come at the cost of added complexity in deriving the utilization distribution with many researchers continuing to use discrete measures of home range over utilization distributions in analysis due to their simplicity (Laver and Kelly 2008). Kernel density estimation remains the most popular method for computing utilization distributions despite considerable drawbacks with newer (temporally dense) telemetry data (Hemson et al. 2005, Kie et al. 2010). Horne et al. (2007) propose the Brownian bridge approach for computing the utilization distribution. A Brownian bridge is simply defined as the probability a random walk passes through a location given the known start and end points. Like the PPA home range, with the Brownian bridge approach telemetry data are analyzed using pairs of consecutive telemetry fixes. This method relies on a variance parameter (σ_m) that is difficult to interpret but can be estimated from the data using an optimization algorithm. The PPA method is essentially the discrete equivalent of the Brownian bridge approach, but with simple, intuitive, and easy to estimate parameters that can be straightforwardly computed in a GIS. Getz and Wilmers (2004) propose the use of overlapping local convex hulls to generate a utilization distribution. A similar approach could be adopted with PPA ellipses to generate a utilization distribution based on the areas under overlapping ellipses. The derivation of an overlap-based utilization distribution for PPA ellipses remains an area for future investigation.

Wildlife researchers now routinely collect temporally dense telemetry data using sophisticated tracking technologies (e.g., GPS; Tomkiewicz et al. 2010). Such temporally dense telemetry data provide a more detailed and informative view of animal movement.

Given continued advancements in technology in the future it is likely that we will be analyzing (near) continuous animal trajectories. This improved representation of animal movement necessarily results in highly autocorrelated movement data. Much attention has been given to the problems autocorrelated telemetry data pose with traditional methods for studying wildlife movement (Swihart and Slade 1985, Otis and White 1999, Fieberg et al. 2010). Many existing methods, developed for use with temporally sparse telemetry data, are ill equipped for dense telemetry data. The PPA home range method is advantageous with temporally-dense telemetry data, as it is capable of including rich temporal information into the derivation of home range. With few exceptions (e.g., Horne et al. 2007) existing home range techniques ignore rich temporal information contained in telemetry datasets. Including temporal information in analysis is beneficial as points are no longer considered independent observations, but rather as a sequence of recordings taken over time.

Certain land cover types (e.g., dense forest; Rempel et al. 1995) can interfere with locating technologies resulting in missing recordings. Missing data points are problematic in subsequent analysis as bias towards specific cover types can occur (Frair et al. 2004). By explicitly considering the temporal sequencing of points, PPA home ranges adjust for missing telemetry recordings by way of a larger Δt value in these areas, providing an unbiased estimator of home range.

Commission errors (locations included in the home range but never visited) and omission errors (locations visited but not included in the home range) are important properties of output home range polygons that require careful consideration (Sanderson 1966). All home range methods short of a direct trace of an animal's movement path will include commission errors. Omission errors occur with most methods, but can be avoided by substantially overestimating home range size. This is equivalent to selecting an overly large bandwidth with KDE. Substantial overestimation limits utility for wildlife research as the signature of animal behavior is masked. The PPA home range method can be used in tandem with other methods to examine commission and omission errors. Consider a simple comparison, by intersecting the PPA home range with commonly employed home range techniques MCP and KDE (Fig. 4). The PPA home range represents the largest spatial unit such that no omission error occurs, due to explicit consideration of the time geography constraints on animal movement. Potential omission errors are then easily represented as those areas included in the PPA home range, but not in other techniques. Areas not included in the PPA home range but included in other methods can be considered inaccessible regions and an unnecessary source of commission error. With MCP, potential omission errors are likely to occur near edges of MCP home ranges. Due to the convex assumption, MCP home ranges almost always include inaccessible areas as well (Powell 2000). KDE home range polygons are not guaranteed to include all sampled telemetry points, therefore explicitly known errors of omission may exist.

All measures of home range are indirect and based on specific properties of the telemetry data from which they are derived. Most existing methods use only the spatial properties of telemetry data represented as points. The PPA method provides a complementary view that not only considers spatial information but also temporal information. Using the demonstrated intersection technique, omission errors and inaccessible regions (unnecessary commission error) using existing home range methods can be mapped and quantified. This represents a significant contribution towards home range analysis that carefully considers these types of errors as has been previously suggested (Sanderson 1966). Often studies employ multiple methods when delineating wildlife home ranges to evaluate a range of possibilities (e.g., Righton and Mills 2006). The PPA home range should be included in such studies as it can be used to augment other techniques by providing information on omission and commission errors.

In this derivation of PPA home range, all geographical space is considered equally navigable. In reality, environmental factors (e.g., topography, land cover, water bodies) influence an animal's ability to traverse the landscape. As well, external factors such as inter- and intra-species competition (Schwartz et al. 2010), and habitat requirements (Sawyer et al. 2007), motivate wildlife movement, and subsequent home range delineations. Optimally, PPA home ranges would be based on the time geography constraints across an unequal surface (see Miller and Bridwell 2009), that considers competition, habitat, topography, and barriers to wildlife movement. Future work should investigate combining available environmental datasets into animal specific movement cost surfaces. Movement cost surfaces could then be integrated into time geographic analysis to compute more realistic PPA home ranges. However, incorporating movement cost surfaces may take away from the attractiveness of time geography methods due to added complexity.

MANAGEMENT IMPLICATIONS

We have presented a new technique for deriving animal home ranges that is simple and intuitive, but also designed specifically for use with emerging temporally-dense telemetry datasets, such as those now routinely collected with GPS collars. However, we suggest the PPA approach not be adopted with temporally-coarser telemetry data (e.g., VHF collars) as it can lead to overestimation of home range size and misleading interpretations. The PPA home range can be used as a stand-alone measure of animal home range, or to augment existing techniques by identifying potential omission errors and inaccessible areas making it flexible for use with both novel and existing analyses. When performing PPA home range analysis the method for obtaining the v_{max} parameter (e.g., through biological reasoning or by 1 of the estimation approaches we provide) along with the parameter value should be explicitly stated, as it will influence the resulting home range area. To those wishing to implement the PPA home range technique in their own research we have provided access to a tool for implementing the PPA home range. For more information please go to: http://www.geog.uvic.ca/spar/tools.html.

ACKNOWLEDGMENTS

Funding for this work was provided by Canada's Natural Science and Engineering Research Council (NSERC) and GEOIDE through the Government of Canada's Networks of Centres of Excellence program. Thanks to B. Stewart for assistance in programming the implementation tool. The comments and suggestions we received from G. White, N. Lichti, and 1 anonymous reviewer greatly improved the presentation of this article.

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Baer, L. D., and D. R. Butler. 2000. Space-time modeling of grizzly bears. Geographical Review 90:206–221.

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

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.

Cooke, P. 1979. Statistical inference for bounds of random variables. Biometrika 66:367–374.

Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040–1044.

Downs, J. A. 2010. Time-geographic density estimation for moving point objects. Lecture Notes in Computer Science 6292: 16-26.

Downs, J. A., and M. A. Horner. 2008. Effects of point pattern shape on home-range estimates. Journal of Wildlife Management 72:1813–1818.

Downs, J. A., and M. A. Horner. 2009. A characteristic-hull based method for home range estimation. Transactions in GIS 13:527–537.

Fieberg, J., and C. O. Kochanny. 2005. Quantifying home-range overlap: The importance of the utilization distribution. Journal of Wildlife Management 69:1346–1359.

Fieberg, J., J. Matthiopoulos, M. Hebblewhite, M. S. Boyce, and J. L. Frair. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity? Philosophical Transactions of the Royal Society B 365:2233–2244.

Frair, J. L., S. E. Nielson, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. M. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. Journal of Applied Ecology 41:201–212.

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

Gurarie, E., R. D. Andrews, and K. L. Laidre. 2009. A novel method for identifying behavioural changes in animal movement data. Ecology Letters 12:195–408.

Hagerstrand, T. 1970. What about people in regional science? Papers of the Regional Science Association 24:7–21.

Hemson, G., P. Johnson, A. South, R. Kenward, R. Ripley, and D. MacDonald. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. Journal of Animal Ecology 74:455–463.

Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movement using Brownian bridges. Ecology 88:2354–2363.

Jennrich, R. I., and F. B. Turner. 1969. Measurement of non-circular home range. Journal of Theoretical Biology 22:227–237.

Jonsen, I. D., J. Mills Flemming, and R. A. Myers. 2005. Robust state-space modeling of animal movement data. Ecology 86:2874–2880.

Kie, J. G., J. Matthiopoulos, J. Fieberg, R. A. Powell, F. Cagnacci, M. S. Mitchell, J.-M. Gaillard, and P. R. Moorcroft. 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? Philosophical Transactions of the Royal Society B 365:2221–2231.

Kraak, M. J. 2003. The space-time cube revisited from a geovisualization perspective. Pages 1988–1995 *in* Proceedings of 21st International Cartographic Conference.

International Cartographic Association, 10–16 August 2003, Durban, South Africa.

Kwan, M. P., and J. Lee. 2004. Geovisualization of human activity patterns using 3D GIS: A time-geographic approach. Pages 48–66 *in* M. F. Goodchild, and D. G. Janelle, editors. Spatially integrated social science: examples in best practice. Oxford University Press, Oxford, United Kingdom.

Laver, P. N., and M. J. Kelly. 2008. A critical review of home range studies. Journal of Wildlife Management 72:290–298.

Miller, H. J. 2005. A measurement theory for time geography. Geographical Analysis 37:17–45.

Miller, H. J., and S. A. Bridwell. 2009. A field-based theory for time geography. Annals of the Association of American Geographers 99:49–75.

Mitchell, M. S., and R. A. Powell. 2008. Estimated home ranges can misrepresent habitat relationships on patchy landscapes. Ecological Modelling 216:409–414.

Nielson, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2003. Development and testing of phenologically driven grizzly bear habitat models. Ecoscience 10:1–10.

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

Parkes, D. N., and N. Thrift. 1975. Timing space and spacing time. Environment and Planning A 7:651–670.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65–110 *in* L. Boitani, and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, New York, USA.

Rempel, R. S., A. R. Rodgers, and K. F. Abraham. 1995. Performance of a GPS animal location system under boreal forest canopy. Journal of Wildlife Management 59:543–551.

Righton, D., and C. Mills. 2006. Application of GIS to investigate the use of space in coral reef fish: a comparison of territorial behaviour in two Red Sea butterflyfishes. International Journal of Geographical Information Science 20:215–232.

Robson, D. S., and J. H. Whitlock. 1964. Estimation of a truncation point. Biometrika 51:33–39.

Sanderson, G. C. 1966. The study of mammal movements: A review. Journal of Wildlife Management 30:215–235.

Sawyer, H., R. M. Nielson, F. G. Lindzey, L. Keith, J. H. Powell, and A. A. Abraham. 2007. Habitat selection of Rocky Mountain Elk in a nonforested environment. Journal of Wildlife Management 71:868–874.

Schwartz, C. C., C. L. Cain, S. Podruzny, S. Cherry, and L. Frattaroli. 2010. Contrasting activity patterns of sympatric and allopatric black and grizzly bears. Journal of Wildlife Management 74:1628–1638.

Sharp, N. C. C. 1997. Timed running speed of a cheetah (*Acinonyx jubatus*). Journal of Zoology 241:493–494.

Smulders, M. C. A. 2009. Spatial-temporal analysis of grizzly bear habitat use. Thesis, University of Victoria, Victoria, British Columbia, Canada.

Swihart, R. K., and N. A. Slade. 1985. Influence of sampling interval on estimates of home-range size. Journal of Wildlife Management 49:1019–1025.

Tomkiewicz, S. M., M. R. Fuller, J. G. Kie, and K. K. Bates. 2010. Global positioning system and associated technologies in animal behaviour and ecological research. Philosophical Transactions of the Royal Society B 365:2163–2176.

van der Watt, P. 1980. A note on estimation bounds of random variables. Biometrika 67:712–714.

Wentz, E. A., A. F. Campbell, and R. Houston. 2003. A comparison of two methods to create tracks of moving objects: linear weighted distance and constrained random walk. International Journal of Geographical Information Science 17:623–645.

Worton, B. J. 1987. A review of models of home range for animal movement. Ecological Modelling 38:277–298.

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

Associate Editor: Gary White.

Figure Captions:

Figure 1: Diagram of Hagerstrand's (1970) time geography. The space-time prism contains the set of all locations accessible to an individual given telemetry fixes at t_1 and t_2, and a velocity parameter (v_{max}). The projection of the space-time prism onto the geographical plane is called the potential path area (PPA), used here for delineating wildlife home ranges.

Figure 2: a) Pins-and-strings method for generating potential path area (PPA) ellipses. The length of the string is equal to the longest distance the animal could travel (D_{max}) given parameter v_{max} and the time difference between points. b) Geometric properties of a PPA ellipse with telemetry points i and j. CP is the center point and d is the Euclidean distance between points i and j; a and b are lengths of the major and minor axis respectively; and R_θ is the rotation angle. c) Computation of the PPA home range involves combining multiple (n–1) PPA ellipses.

Figure 3: Home range polygons for a simulated dataset with n = 2,000 (top) re-sampled to n = 500 (bottom) using minimum convex polygon (MCP; a, d), kernel density estimation (KDE; b, e), and potential path area (PPA; c, f).

Figure 4: Intersections between a) minimum convex polygon (MCP) and potential path area (PPA) and b) kernel density estimation (KDE) and PPA (for n = 2,000); demonstrating how PPA home ranges can be used to augment existing techniques by identifying omission errors and inaccessible areas.

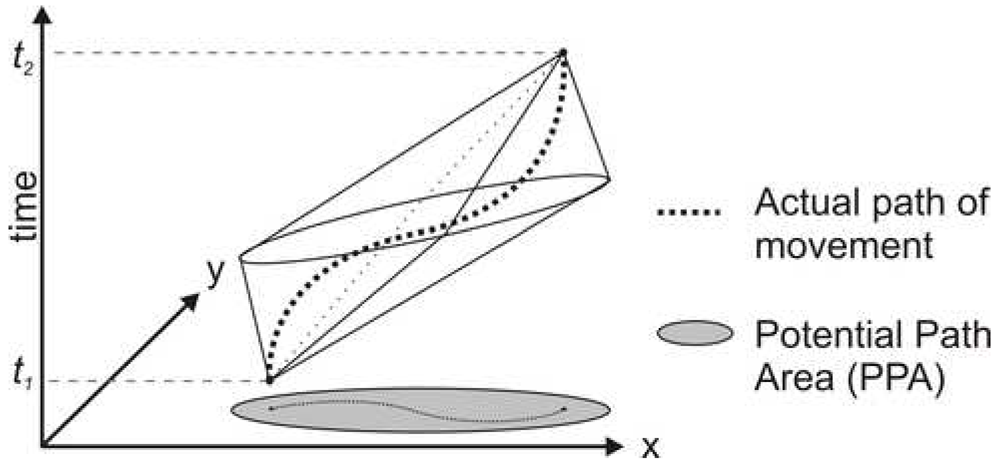

Figure 1: Diagram of Hagerstrand's (1970) time geography. The space-time prism contains the set of all locations accessible to an individual given telemetry fixes at t1 and t2, and a velocity parameter (vmax). The projection of the space-time prism onto the geographical plane is called the potential path area (PPA), used here for delineating wildlife home ranges.
41x19mm (300 x 300 DPI)

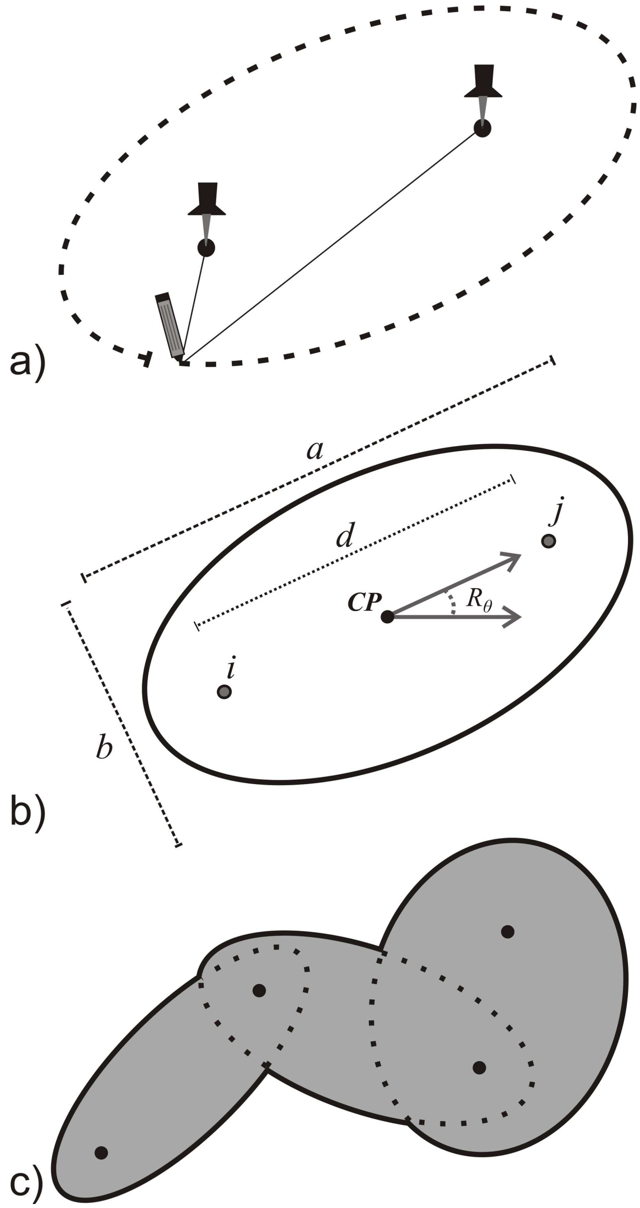

Figure 2: a) Pins-and-strings method for generating PPA ellipses. The length of the string is equal to the longest distance the animal could travel (Dmax) given parameter vmax and the time difference between points. b) Geometric properties of a PPA ellipse with telemetry points i and j. CP is the center point and d is the Euclidean distance between points i and j; a and b are lengths of the major and minor axis respectively; and Rθ is the rotation angle. c) Computation of the PPA home range involves combining multiple (n-1) PPA ellipses.
161x309mm (300 x 300 DPI)

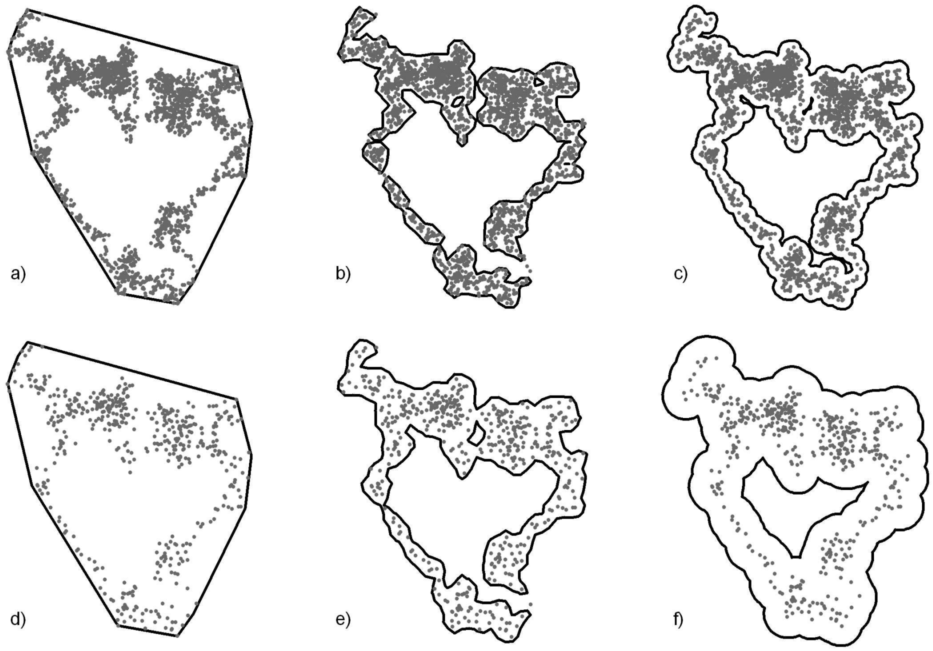

Figure 3: Home range polygons for a simulated dataset with n = 2000 (top) re-sampled to n = 500 (bottom) using MCP (a & d), KDE (b & e) and PPA (c & f).
190x127mm (300 x 300 DPI)

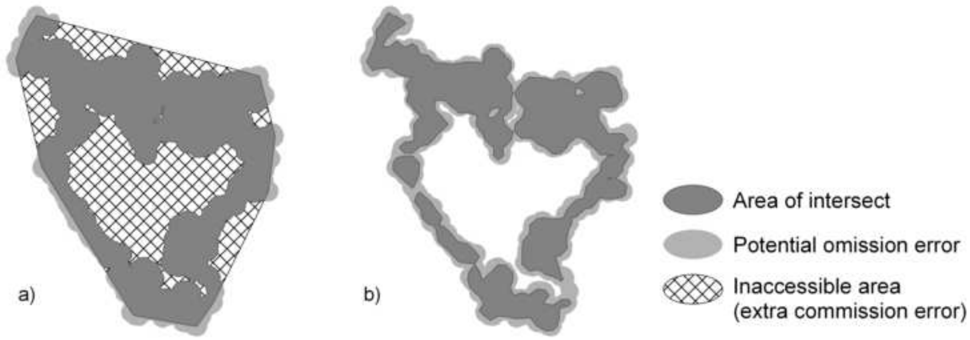

Figure 4: Intersections between a) MCP & PPA and b) KDE & PPA (for n = 2000); demonstrating how PPA home ranges can be used to augment existing techniques by identifying omission errors and inaccessible areas.
63x22mm (300 x 300 DPI)