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The home-range concept: are traditional estimators still relevant with modern telemetry technology?

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Recent advances in animal tracking and telemetry technology have allowed the collection of location data at an ever-increasing rate and accuracy, and these advances have been accompanied by the development of new methods of data analysis for portraying space use, home ranges and utilization distributions. New statistical approaches include data-intensive techniques such as kriging and non-linear generalized regression models for habitat use. In addition, mechanistic home-range models, derived from models of animal movement behaviour, promise to offer new insights into how home ranges emerge as the result of specific patterns of movements by individuals in response to their environment. Traditional methods such as kernel density estimators are likely to remain popular because of their ease of use. Large datasets make it possible to apply these methods over relatively short periods of time such as weeks or months, and these estimates may be analysed using mixed effects models, offering another approach to studying temporal variation in space-use patterns. Although new technologies open new avenues in ecological research, our knowledge of why animals use space in the ways we observe will only advance by researchers using these new technologies and asking new and innovative questions about the empirical patterns they observe.

Keywords: home ranges; utilization distributions; mechanistic models; GPS; telemetry; space use

1. INTRODUCTION

Recent advances in tracking and telemetry technology, such as the widespread use of the global positioning system (GPS), have allowed scientists to collect location data for animals at an ever-increasing rate and accuracy (Tomkiewicz *et al.* 2010). These technological advances have allowed, and in some cases necessitated the development of, new methods of data analysis. Large datasets are permitting the use of data-intensive statistical approaches such as kriging and nonlinear generalized regression models to characterize animal habitat use, and new approaches such as mechanistic home-range models (Moorcroft *et al.*

1999, 2006; Moorcroft & Lewis 2006; Smouse *et al.* 2010) are having a considerable impact on the home-range literature. In this article, we briefly review these approaches, but, in tandem, we seek to answer the question: are traditional statistical home-range estimators still relevant following the advent of these new technologies, and, if so, in what way?

The concept that individual animals restrict their movements to finite areas known as home ranges is perhaps as old as ecology itself (Darwin 1859). Seton (1909, p. 23) observed that ‘No wild animal roams at random over the country; each has a home-region, even if it has not an actual home.’ The most commonly cited definition of an animal’s home range is that of Burt (1943, p. 351): ‘that area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should

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not be considered as in part of the home range.' This definition presents well-recognized problems, among them that an 'occasional sally' can only be defined in relation to a well-defined home range. In addition, Burt's definition does not specify how to delineate the boundary of the home range, nor does it recognize the importance of variations in the intensity of space use within a home range (Powell *et al.* 1997; Powell 2000). Still, Burt's definition acknowledges that space use can arise from different behavioural activities such as finding food, shelter and partners, and where they survive, reproduce and maximize their fitness (Krebs & Davies 1997). In this sense, the home range is not just spatial use by an animal. Use of space, however, is what could be historically quantified most easily and reliably.

Home-range analysis has evolved from early attempts to identify an area via minimum convex polygons (Blair 1940; Odum & Kuenzler 1955) to methods that describe the animal's home range as a utilization distribution: a multi-dimensional relative frequency distribution of animal locations (Jennrich & Turner 1969; Van Winkle 1975; Worton 1989; Getz & Wilmers 2004; Keating & Cherry 2009). Since the publication of Worton's (1989) seminal paper, density estimation techniques such as kernel smoothing have become the method of choice for quantifying utilization distributions (Kernohan *et al.* 2001; Laver & Kelly 2008).

The question remains, however: without complete knowledge of an animal's trajectory over a period of time, what is its home range or utilization distribution? If uncertainty exists from sampling the trajectory, then a home range will be estimated with uncertainty. If the trajectory has no error or the error is negligible, and if the animal uses a strip around the travelled path, then the buffered path may serve as a useful estimate of the home range or measure of use of space for the time period of observation. This approach was taken by Pulliainen (1984) and Ostro *et al.* (1999) for estimating home ranges of pine martens (*Martes martes*) and black howler monkeys (*Alouatta pigra*). They concluded that the width of the area around the path should be based upon biological information. Recording the continuous occurrence of animals, however, can be labour-intensive or impossible if the animal moves too fast or is secretive in nature (Turchin 1998; Kernohan *et al.* 2001), or if recording is limited by battery drain in case of automatic localization devices (Tomkiewicz *et al.* 2010). Therefore, occurrence is usually estimated from a sample of estimated locations that describe where an animal might have been while it was not being observed (Kernohan *et al.* 2001).

Over the years, a variety of statistical home-range estimators have been developed with increasing complexity and sophistication. Prior to the advent of GPS locations, the combination of location data derived from very high-frequency (VHF) radio telemetry and kernel home-range estimators produced widely accepted and intuitive interpretations of a home range as a probability density surface or utilization distribution, depicting the likelihood that any point in space was going to be occupied by the animal of interest at any given time. This probability surface offered

the unique ability to go beyond simply describing an animal's home range and draw inferences on why it had the home range it did because probabilities of use can be correlated with environmental characteristics such as habitat features (Marzluff *et al.* 2004; Moorcroft & Barnett 2008). With increasing use of geographical information systems (GIS), the capacity to draw such inferences has increased manifold, such that a wide variety of GIS tools currently exist to facilitate the estimation and analyses of home ranges with unprecedented data availability and ease of use (Urbano *et al.* 2010).

The advent of GPS telemetry data poses both fundamental advances and challenges to the home-range paradigm developed over decades of VHF telemetry. One advance is obvious: the number and accuracy of locations obtainable from GPS devices greatly exceed those collectible from VHF telemetry, often by several orders of magnitude. However, GPS devices are still subject to a trade-off between frequency of data collection and battery life in small vertebrate species for which device weight is a significant issue. The more frequent sampling afforded by GPS collars is likely to capture occasional use of areas or resources that are important to an animal (Kochanny *et al.* 2009). Further, the absence of observer-based sampling limitations, including observations during night and bouts of inclement weather, and the possibility of an evenly distributed sampling protocol throughout days and seasons, ensure a more representative sample of an animal's space use. GPS technology also extends the possibility of gathering remote locations for species otherwise difficult to track either because of long-distance movements (such as in some birds) or because of environmental constraints (e.g. in fossorial or marine species). Nevertheless, missing data and location bias are still problems requiring data imputation or weighting to account for differential observability in various habitat types and landscape characteristics (Frair *et al.* 2004, 2010; Horne *et al.* 2007).

With increases in the duration, frequency and accuracy of observations, it may be argued that we are approaching near-perfect knowledge of locations that an animal has visited, as required by Burt's (1943) definition. Indeed, many field studies of home ranges seek to achieve little else. Description, however, does not address the remainder of Burt's (1943) definition: '... in its normal activities of food gathering, mating, and caring for the young'; that is, why an animal has the home range it does. Considered uncritically, detailed GPS data offer the chance to describe in increasingly minute detail something we still cannot explain satisfactorily. Recent deployments, however, (Wilson *et al.* 2008; Tomkiewicz *et al.* 2010; Urbano *et al.* 2010) have coupled GPS boards with other biosensors (activity, body temperature, heart rate, light, proximity) to create new opportunities for interpretation of space using other animal-based data.

The volume and detail of GPS telemetry data offer considerable challenges to traditional analytical approaches, which were developed with VHF telemetry in mind. An obvious challenge is how one analyses all the data. This issue arises especially

when a prior hypothesis and questions have not been carefully thought out. A less obvious challenge, but perhaps more critical, is what such data can tell us about the home ranges of animals.

2. ESTIMATING HOME RANGES AND UTILIZATION DISTRIBUTIONS: HOW TO PUT GPS TELEMETRY DATA TO GOOD USE

Home-range estimation techniques can be divided into two types: statistical models based purely on empirical data, and mechanistic models. The latter, although based on empirical observations that describe movement vectors of individual animals, are in close alignment with the concept of home range expressed by Burt (1943) as an 'area traversed'. Historically, few authors have used mechanistic models to estimate home ranges, although this is changing (Moorcroft & Lewis 2006). Inferentially, mechanistic models are certainly an important response to this issue, examining the processes that determine emergence of a home range (Moorcroft & Lewis 2006; Börger *et al.* 2008; Smouse *et al.* 2010) and taking into account resource distribution (Moorcroft & Barnett 2008; Van Moorter *et al.* 2009). Statistical models based purely on empirical data may complement this information, analysing the spatio-temporal determinants of home ranges. Statistical models for estimation of home ranges, however, were mainly developed with VHF telemetry in mind, and therefore could be challenged by the volume and detail of GPS data.

Purely statistical models can be classified as: (i) those involving graphic techniques or other types of data summary; (ii) utilization distribution approaches; or (iii) methods employing spatial statistics and trend fitting. Despite subtle differences between the definitions of home range and utilization distribution (an animal's home range may be thought of as a contiguous two-dimensional polygon, whereas a utilization distribution may consist of multiple polygons and portray intensity of space use in a third dimension), they are often used interchangeably (Smouse *et al.* 2010). We argue that a home range is a biological concept that can be studied using a variety of statistical constructs (aerial polygons, utilization distributions, mechanistic movement models or others). One cannot expect that a single statistical construct will cover all relevant aspects of the biological concept, and one might expect statistical constructs to lead to questions that are not covered by the biological concept.

To explore connections between the biological concept of a home range and statistical measures used to study this concept, consider Powell's (2000) definition of home range as the cognitive map (the area an animal knows and maintains in its memory because the area has some value) of where an animal lives. This cognitive map would integrate contour maps for 'food resources, escape cover, travel routes, home ranges of members of the other sex, and so forth' (Powell 2000, p. 66). A utilization distribution (Worton 1989) depicts the intensity of use by an animal, either within its home range or within a study area. An estimate of the intensity of use, such as using a

kernel density estimator, might provide an approximation of a cognitive map, albeit a poor one, when a sparse set of locations is the only available information of an individual. Alternatively, the estimate of the utilization distribution could be sliced to reveal a two-dimensional surface (for example, by taking a 95% volume contour); the equivalent of a traditional definition of a home range. Such two-dimensional slices may be not contiguous but disjoint, made up of multiple polygons that more accurately indicate intensity of space use (Powell 2000).

Both statistical concepts (the utilization distribution itself and the 95% volume contour) have utility depending on the question at hand. Certainly, the intensity with which an animal uses space is critical in determining those areas that are needed for foraging, resting and reproduction (Powell 2000). Previous descriptions of a home range do not provide such information. Conversely, a disjoint utilization distribution, while minimizing the importance of areas seldom used by an animal, may fail to indicate important travel corridors; for example, between important feeding and resting areas.

(a) *Statistical methods based on utilization distributions: how to choose smoothing factors with high-volume data*

Currently, kernel density estimates are the most popular statistical approach to characterizing and visualizing animal home ranges (Laver & Kelly 2008). Choosing the appropriate smoothing parameter (or bandwidth) is the single most important issue in a kernel analysis (Wand & Jones 1995). The actual shape of the kernel (Gaussian, Epanechnikov, other) has little effect on its statistical efficiency (Silverman 1986). Bandwidth, however, is particularly critical in determining outer contours (home-range estimate) and, to a lesser extent, also affects estimation of the utilization distribution (Seaman & Powell 1996; Fieberg 2007b). No single best method of choosing a bandwidth *a priori* exists (Worton 1989). Although kernel smoothing in general makes few or no assumptions about the underlying distribution of data points (Silverman 1986), if one assumes animal location data are normally distributed in bivariate space, then a reference bandwidth can be calculated (Worton 1989). If locations are clumped, however, as animal locations frequently are, then the reference bandwidth will be too large, the data over-smoothed and the areal estimate of the utilization distribution too large, with excess space around the outermost points.

Conversely, it is possible to try different bandwidths iteratively and pick the one that minimizes least-squares cross-validation (Stone 1984) or likelihood-cross validation scores (Matthiopoulos 2003; Horne & Garton 2006; Horne *et al.* 2007). Least-squares cross-validation, however, tends to be especially sensitive to sample size. Animal locations numbering in the thousands, such as those derived from GPS devices, often result in under-smoothing and a utilization distribution consisting of small perimeters around individual data points.

A compromise is to reduce the reference bandwidth to a fixed proportion such as 0.70 (Bertrand *et al.* 1996) or 0.80 (Kie & Boroski 1996; Kie *et al.* 2002), thereby reducing over-smoothing. Indeed, 80 per cent of the reference bandwidth is nearly unbiased for certain data types (Worton 1995, p. 797). If the objective is to estimate a contiguous home-range boundary, it is possible to reduce the reference bandwidth just prior to the point where that estimate starts to fragment into multiple polygons (Berger & Gese 2007; Jacques *et al.* 2009). This technique is repeatable and defensible given that the proper biological questions are posed prior to analysis. ‘There are many situations where it is satisfactory to choose the bandwidth subjectively by eye’ (Wand & Jones 1995, p. 58). A natural method for choosing the smoothing parameter is to plot several curves and choose the estimate that is most in accordance with one’s prior idea about the density. ‘For many applications this approach will be perfectly satisfactory’ (Silverman 1986, p. 44).

Newer techniques for choosing a bandwidth have been developed, such as the ‘solve-the-equation plugin’ and smoothed bootstrap methods (Jones *et al.* 1996), but more work is needed to investigate their performance. Occasionally, information additional to the distributional data is available, such as natural history or historical data that can be used to supervise kernel smoothing. Model-supervised kernel smoothing (Matthiopoulos 2003) requires synthesizing all available information except telemetry data into a usage surface (the model), which is then combined with kernel-smoothed telemetry data into a weighted-average hybrid surface. Such information might simply include empirical opinions from people working with the animals in the field, or more systematic data such as output of a statistical or mechanistic model derived from studies at other regions in space or points in time. The technique requires few additional calculations, and where the usage surface estimated *a priori* fails to bring significant information to the final model its results are equivalent to simple kernel smoothing (Matthiopoulos 2003).

Kernel smoothing ignores the temporal sequence of occurrence of individually referenced data by assuming that animal locations are spatially autocorrelated and that observing an animal at a particular point implies a heightened probability that it frequents neighbouring locations as well. It is possible to weight the locations to give less consideration to points that are closely spaced and thus more highly autocorrelated (Katajisto & Moilanen 2006). In general, however, the spectre of autocorrelation can be a bit of a red herring, and subsampling data to eliminate it often reduces the value of the resulting estimate (De Solla *et al.* 1999; Fieberg 2007b). More importantly, sampling for locations should be done systematically over the time period of interest rather than trying to achieve independent locations (McNay *et al.* 1994; De Solla *et al.* 1999; Fieberg *et al.* 2007b); GPS technologies excel at this type of sampling design.

Since not all regions of an animal’s distribution are necessarily characterized by the same degree of spatial autocorrelation (Osborne & Suárez-Seoane 2002),

using a single smoothing parameter may over-smooth in some regions and under-smooth in others (Hemson *et al.* 2005). In adaptive kernel smoothing, as opposed to fixed kernel approaches, areas with low densities of observations receive more smoothing (Silverman 1986; Worton 1989). It is also possible to use weighting to account for non-random sampling and missed observations (Fieberg 2007a). Alternatively, Brownian bridges can be used to estimate the probability of an animal being at a specific location in between fixes. A Brownian bridge is a continuous-time stochastic process with an expected value of the bridge of zero at points in time where animal locations are obtained (ignoring small locational errors associated with modern GPS data). Conversely, the height of the bridge is minimal and its breadth maximal midway between two sequential location estimates and, hence, uncertainty about the actual location of an animal is maximal at midway locations (Horne *et al.* 2007). When sequential locations are independent, Brownian bridges collapse to kernels at each location, meaning that Brownian bridges contribute to utilization distributions only when sequential locations are autocorrelated. The closer locations are in time, as obtained using GPS technology, the closer locations are in space, and kernel estimators can estimate utilization distributions well without the need for Brownian bridges.

The sheer volume of animal location data derived from GPS technologies offers new ways of visualizing home ranges, but also poses additional analytical problems. For example, the 95 per cent probability contour from a kernel home range calculated using 100 VHF locations may look very different from the one calculated for the same animal using 3000 GPS locations—an artefact of smoothing parameter choice (figure 1; but see Pellerin *et al.* 2008). Attempts to explain home ranges by correlating habitat features potentially important to food gathering, mating and caring for young are influenced quite strongly by whether one’s home-range estimate looks like figure 1a or b. If figure 1a and b were derived from the same animal, differing only in frequency of sampling, it would be inferentially problematic, and biologically disturbing, that explanatory analyses of the two estimates yielded substantively different results.

Most data-based rules for choosing smoothing parameters result in smaller parameters as sample sizes increase (Fieberg 2007b). Choice of smoothing parameters reflects a bias–variance tradeoff, with larger smoothing parameters leading to more biased estimators with better precision (measured in terms of the mean squared error integrated over the home range; Fieberg 2007b). As one collects more data, precision improves, so less bias is optimal and thus smaller smoothing parameters are suggested as optimal. As a result, kernel-based estimates of utilization distributions can vary greatly as a function of the number of sample locations (figure 1).

Conversely, estimates of utilization distributions may not change much once some minimal level of sampling intensity is reached. For example, Kochanny *et al.* (2009) compared estimates of home-range size for white-tailed deer using VHF sampling 2–3 times

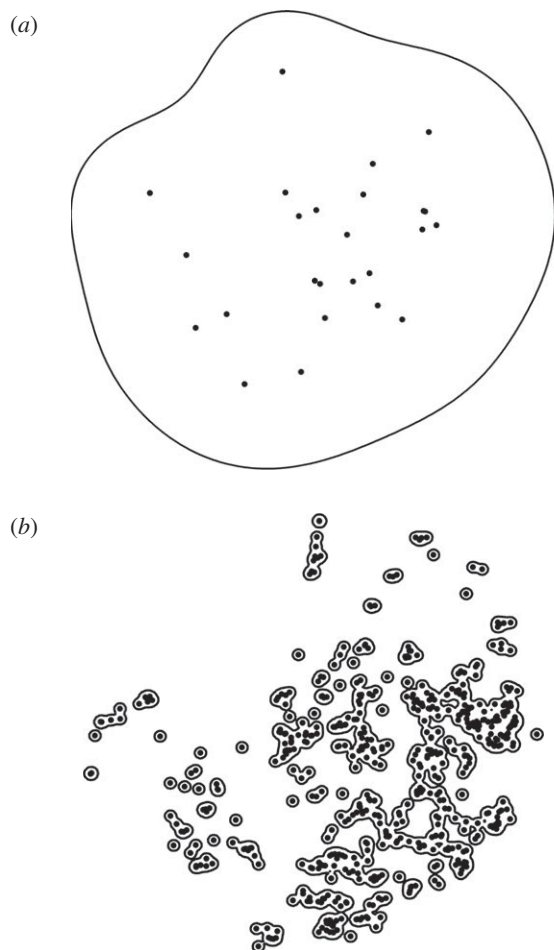


Figure 1. Home-range estimates for a North American elk (*Cervus elaphus*) on the Starkey Experimental Forest and Range, OR, USA, calculated using a fixed bivariate normal kernel with a choice of smoothing parameter that minimized the least-squares cross-validation score (Worton 1989). Analyses performed with home-range tools (HRT) for ARCGIS (Rodgers *et al.* 2007), rescaling X , Y data to unit variances, 95% isopleths, and raster size set to 30 m cells. Data represent multiple locations collected over a single month, (a) sub-sampled at $n = 25$ representing typical VHF-based data obtained on a daily basis, and (b) data sub-sampled at $n = 603$ representing GPS data collected at high sampling frequencies. Autocorrelation indices were (a) 1.66 and (b) 2.39, with values of more than 0.6 representing significant autocorrelation (Swihart & Slade 1985).

per week to those using hourly GPS sampling for the same animals. The GPS datasets resulted in estimates that were, on average, equal to the VHF estimates, despite the difference in sampling intensities. Börger *et al.* (2006a) characterized the variation in estimated home ranges (among individuals and across various sampling frequencies) using mixed-effects models. Variation among individuals was substantial, whereas estimates of home range using kernel density estimators were relatively stable when using at least 10 fixes per month. Thus, they suggested that following a larger numbers of individuals for longer periods of time is preferable to increasing sampling frequencies. More frequent sampling of animal locations made possible by GPS technologies, however, may be more apt to capture corridors and connecting paths and to

capture occasional use of areas or resources that are important to an animal (Kochanny *et al.* 2009).

Recently, Getz & Wilmers (2004) proposed an alternative kernel method (LoCoH) for estimating utilization distributions based on local nearest-neighbour convex hulls. As originally described, LoCoH kernels were constructed from $k - 1$ nearest neighbours of focal locations (Getz & Wilmers 2004). Subsequent variations include kernels constructed from all points within a fixed radius of each reference point (Getz *et al.* 2007). Testing with empirical data has suggested that LoCoH methods outperform traditional kernel-smoothing techniques; that is, they did a better job of excluding areas known not to be used in simulations where home ranges incorporated distinct habitat, geographical or physiographic boundaries (Getz *et al.* 2007).

(b) Statistical methods based on geostatistics and trend fitting

The ability of GPS technology to generate very large numbers of locations for individual animals has provided the opportunity to estimate space use based on geostatistics and other data-intensive techniques. Like kernel-smoothing methods, techniques based on geostatistics assume that animal locations are spatially autocorrelated. In contrast to kernel techniques, which make few other parametric assumptions, geostatistics require normality, stationarity and isotropy. One such technique is kriging (Krige 1951). Although kriging is often applied to geophysical variables, it can also be employed to estimate the density of use by a single animal or a group of animals by binning locations on a spatial grid (Stewart *et al.* 2006).

Kriging requires that the statistical properties of the process are independent of absolute location (stationarity assumption) and independent of direction in space (assumption of isotropy; Fortin & Dale 2005). Where stationarity is violated, it is possible to detrend the data using trend surface analysis, kriging the residuals, then add the resulting individual response surfaces together to get a final modelled surface. Once done manually, this process is implemented automatically by software packages such as ARCGIS (ESRI 2001). Where isotropy is violated, anisotropic kriging enables the modulation of directional dependence between spatial locations so that points lying along a given directional axis are similar over greater distances. An extension of kriging called co-kriging makes use of covariate information to determine similarity between two points, giving it potential as a method to incorporate habitat variables and the ability to model environmental heterogeneity.

Kriging has potential advantages and disadvantages. The background theory is well developed, the techniques are designed to give unbiased estimates with minimum associated uncertainty, and it can operate both as a smoother and a spatial interpolator. On the other hand, the method assumes normally distributed response variables. In practice, observations of usage are presences/absences, counts or frequencies that do not adhere to normality. Similar geostatistical methods for non-normal data do exist (Diggle *et al.*

1998) but are computationally demanding. Conversely, a drawback of kriging is the need for many well-spaced data points along both horizontal and vertical axes. Difficulties arise when data are highly clumped in space, which is typical of information on animal locations, and result in empty grid cells, or bins.

Modern statistical modelling approaches offer an alternative to kernel smoothing and geostatistics. These models are extensions of classic linear trend-fitting methods (Ripley 2004) and special cases of generalized regression models for habitat use (Boyce & McDonald 1999; Guisan *et al.* 2002). The idea is to use longitude and latitude as the only covariates of usage in a flexible regression model, in what constitutes a parametric form of spatial smoothing. To capture the fine-scale features of the home range, the approach needs to be implemented with functions of unlimited flexibility such as spatially global polynomials (Buckland 1992) or trigonometric functions (Anderson 1982). Alternatively, local smoothers such as splines can be used as part of a generalized additive model, or GAM (Wood 2006). GAMs are extensions of the linear regression model that allow locally non-linear features of the utilization distribution to be fully specified from the data. In contrast to global polynomial/trigonometric functions, GAMs are able to redirect model flexibility towards the data-rich regions of space. This increases their capability to describe the fine-scale features of often-visited regions of the home range, but also makes them prone to overfitting. In any event, GPS technology with its ability to collect large amounts of animal location data has opened the door to new and innovative statistical techniques for portraying space use.

(c) Mechanistic home-range models

Coincident with the development of GPS technologies and new statistical models of animal home ranges has been the development of mechanistic home-range models (Mitchell & Powell 2004; Moorcroft & Lewis 2006). Mechanistic models acknowledge that how an animal uses space is a function of its underlying patterns of movement behaviour over a specified period of time (Smouse *et al.* 2010) based on the spatial distribution of critical or limiting resources. A simple model of animal movement might involve an individual moving at random across a landscape but returning to a central place such as a nest, den or roost (Holgate 1971; Okubo 1980), although multiple areas of attraction comprising a variety of resources can also be modelled (Dunn & Gipson 1977; Blackwell 1997) dependent on specific behaviours such as foraging, resting and seeking mates or refuge.

Analyses of space use by coyotes (*Canis latrans*) and black bears (*Ursus americanus*) illustrated how such approaches can provide insights into the factors controlling patterns of space use by individuals (Moorcroft & Lewis 2006; Moorcroft *et al.* 2006; Mitchell & Powell 2007). The analysis of coyote movements showed that a model incorporating a foraging response to prey availability, in which individuals' movement rates decreased in areas of high prey density, and a conspecific avoidance response, in which

individuals biased their movements towards their home-range centres following encounters with scent marks, was sufficient to explain the home-range patterns of coyotes in Yellowstone National Park, USA. Including these behavioural and movement responses resulted in realistic multimodal utilization distributions for each pack (Moorcroft & Lewis 2006; Moorcroft *et al.* 2006). Analyses of black bear selection of resource-bearing patches for their home ranges showed an optimal balance between the value of resources contained in patches and average travel costs to realize these resource values. Modelling optimal selection of patches based on this balance resulted in accurate estimates of geographical shape and extent of utilization distributions for black bears living in the Pisgah Bear Sanctuary in the southern Appalachian Mountains (Mitchell & Powell 2007).

An important power of mechanistic home-range models is that once the mechanisms underlying the genesis of an animal's utilization distribution are understood, they can be used to predict how space use will change in response to changing landscapes or animal populations. For example, Moorcroft *et al.* (2006) and Moorcroft & Lewis (2006) showed that their model was able to successfully predict how adjacent coyote packs altered their patterns of space use after the break-up of one of the packs within the study area. Mitchell & Powell (2007) showed that resource depression by conspecifics influenced patch use of black bears according to a dominance hierarchy among females within the population. They hypothesized that this could be the mechanism underlying the ideal pre-emptive distribution of bears on the landscape; thus, changes in the distribution and abundance of resources on a landscape, or age structure, abundance and distribution of the population, would have cascading effects on patch selection, movements and distribution of bears within the population.

Mechanistic movement and home-range models can also inform analyses of habitat selection (Fieberg *et al.* 2010). Often, kernel density estimates are used to define habitat availability in these studies (e.g. by using the outer 95 per cent probability contour; Sjöberg & Ball 2000; Hastie *et al.* 2004; Breed *et al.* 2006). Although selection of specific patches of habitat by an individual is dictated by resource preference, such selection can be further constrained by travel costs, which can be depicted as the distance from the individual's current location, but also as the distance of a patch from the centre of the individual's home range (Arthur *et al.* 1996; Hjermann 2000; Mitchell & Powell 2004; Rhodes *et al.* 2005). The models of Mitchell & Powell (2004) explicitly include how selection of habitat is constrained by distance of those patches from a home-range centre. Their analyses showed how such travel costs, combined with spatial distribution and quality or resource-bearing patches, as well as abundance of conspecifics, can ultimately structure site fidelity and habitat selection within home ranges. Recently, Moorcroft & Barnett (2008) have incorporated habitat selection into a mechanistic movement model. Their analyses showed that when habitat preferences are spatially localized, the relative intensity of space use at any location is equal to the

square of the preference function at that location, but as scale of habitat preference increases the intensity of space use becomes proportional to preference (Barnett & Moorcroft 2008).

A key issue in mechanistic home-range models is behavioural mechanisms responsible for the formation of a characteristic home range by individuals. Note that this issue is closely aligned to the conceptual question of how animals develop their cognitive map of their environment. Mitchell & Powell (2004, 2007) showed how such a cognitive map could be a function of an animal's knowledge of available resources, discounted for travel costs, and the extent to which those resources are influenced by conspecific competitors. In the model analysed by Moorcroft *et al.* (2006) and Moorcroft & Lewis (2006), encounters with conspecific scent marks biased the movements of individuals towards a prescribed home-range centre. While this may be appropriate for coyotes and other carnivores that have den sites or other clearly identifiable centres of attraction, other behavioural mechanisms can also give rise to home ranges. For example, Briscoe *et al.* (2002) showed that if animals reduce their rate of movement and increase their scent marking rate in response to encounters with familiar scent marks, individuals can develop stable home ranges in the absence of any focal point of attraction. Tan *et al.* (2002) have shown how memory, in conjunction with preferential movement towards a previously visited area, can give rise to characteristic home ranges for individuals. Additional details of mechanistic movement models are available elsewhere in this issue (Fieberg *et al.* 2010; Smouse *et al.* 2010).

(d) Temporal changes in home ranges and utilization distributions

Temporal changes in space-use patterns may result from age- or stage-dependent behavioural responses, environmental variability (such as changes in temperature, precipitation, photoperiod, predator density) or other factors affecting the distribution or importance of resources (Börger *et al.* 2006a). Changes may be gradual or abrupt (in the case of migratory species and dispersal), and the existence of a stable home range may be time-scale dependent (Börger *et al.* 2008). With VHF data, temporal changes in space use (e.g. among seasons) have sometimes been examined using static measures of home-range overlap (Fieberg & Kochanny 2005). Although useful for quantifying differences in space use among temporally discrete, biologically meaningful time periods such as summer and winter home ranges for seasonally migrating species, GPS data should provide additional opportunities for exploring variation in space-use patterns at finer temporal scales, thus allowing for a more dynamic view of the home-range concept. We highlight two analysis techniques that may be useful to this end.

First, high sampling rates available with GPS technology make it possible to estimate home ranges over relatively short time periods such as weeks or months, which in turn may be used as a response variable in repeated-measures mixed-effects models to

explore temporal variation in space-use patterns (Börger *et al.* 2006a). For example, Börger *et al.* (2006a) fitted mixed effects models that included climatic variables, dominant habitat type (within the home range), individual characteristics (age, sex) and interactions among factors to home-range estimates for roe deer obtained using different smoothing methods and defined using different isopleths (50%, 70% and 90% contours). The relationship between these factors and home-range estimates depended on the time scale and isopleth. For example, climatic variables (precipitation, photoperiod) interacted with habitat characteristics (dominant habitat type within the home range), and their effects were more pronounced over shorter time scales (bi-weekly to half-year scales versus yearly scale). By modelling home ranges as a function of time-varying covariates, mixed effects models have the potential to address problems associated with variable sampling durations (among individuals). In addition, covariates (e.g. number of locations) may also be included to adjust for variable sampling efforts (Börger *et al.* 2006b). Although this approach uses traditional methods such as kernel density estimators, the ability to apply them at finer temporal scales makes it possible to study how large-scale patterns emerge over time.

In the limit (of increasingly smaller time intervals), one may view the utilization distribution as continuous in time. Keating & Cherry (2009) take this viewpoint, suggesting the need to extend Van Winkle's (1975) definition of the utilization distribution to four dimensions (three spatial dimensions and one time dimension). They developed a product-kernel density estimation method for characterizing temporal patterns in space use, using a circular time scale (0 to 24 h or 0 to 365 days) based on a wrapped Cauchy distribution to facilitate modelling recurrent patterns of space use in time, such as seasonal migrations. They applied the approach to data collected on two social groups of bighorn sheep (*Ovis canadensis*) in Glacier National Park using video of daily utilization distribution contours overlaid on habitat maps to capture the time evolution of each group's space-use patterns. Estimates of the four-dimensional utilization distribution varied within time periods normally used to define seasonal patterns. For example, the utilization distribution became increasingly concentrated in late winter, with a peak concentration lasting for only a short period of time. This level of detail is lost by typical approaches that estimate average space use over discrete time periods, often defined using rather arbitrary or subjective dates.

Although both of these approaches open the door for viewing home ranges more dynamically, they also may prove useful in the design of follow-up studies. Several authors have argued for the use of well-defined, biologically meaningful sampling periods as a means of addressing problems associated with temporal autocorrelation (Otis & White 1999; Fieberg 2007b). The mixed-effects approach of Börger *et al.* (2006b) and the space-time utilization approach of Keating & Cherry (2009) may help to define biologically meaningful study periods and sampling frequencies for future telemetry studies.

3. CONCLUDING REMARKS

We begin with some summarizing thoughts about the concept of an animal's home range. Let us consider a home range as the area an animal knows and maintains in its memory because the area has some value. The individual then applies this memory or cognitive map across a landscape that contains habitat patches of varying utility with respect to its resource needs (Folse *et al.* 1989; Dalziel *et al.* 2008). Thus, some parts of a home range may be visited seldom and perhaps never during a period of data collection. Other areas that are of little interest to a mammal may be traversed or visited occasionally but not be considered a part of the home range. Those places have no intrinsic value except that the animal passed through them going somewhere else that it wanted to visit. From this perspective, GPS data alone (separate locations connected by lines) do not constitute an animal's cognitive map. Kernel home ranges do a decent job of telling us the probability of being reasonably close to an animal if we stand in a given place; yet kernel density estimates include areas that may be of little value to an animal if those areas are close to areas that are important.

The advent of GPS technologies that can sample animal locations systematically throughout the day and night with high precision raises the question of whether the near-perfect knowledge of an animal's movements based on GPS data obviates the need for kernel-based or other statistical home-range estimators. If collected at a sufficiently high sampling rate, and if they are representative of space use by the animal, GPS locations can closely approximate the actual continuous path taken by an animal in near-real time. The closer the GPS data come to being continuous data, the less the information each additional data point provides. In such cases, one needs to look at movement paths, not data points. A relevant example is provided by the track of a forest-dwelling carnivore such as a fisher (*Martes pennanti*) during winter (Powell 1994). If one looks at each track as it is embedded in its landscape, one can determine the habitats and other resources to which a fisher had direct access and one gains insight into habitats and resources the fisher may have perceived. With data on many fishers, one can also test hypotheses regarding why fishers travel through their home ranges as they do—hypotheses of optimal foraging, memory and energy expenditure. Likewise, testing hypotheses for why and how animals move using GPS data as tracks embedded within their landscapes can provide new knowledge about how resources shape individual animals' lives (Lovari *et al.* 2008). Present GPS technology, however, is incapable of providing data equivalent to tracks for more than a few days in the case of small mammals and many birds. To sample a fisher's movements over weeks or months, present GPS technology provides no more data than conventional VHF telemetry collected using a representative sampling design (Hebblewhite & Haydon 2010). Another concern is that obtaining enough data to answer population-level questions is usually prevented by the prohibitive cost of GPS technology and the limited number of data points possible for all but large mammals.

When the parameters of statistical home-range models (such as kernel type and bandwidth or k parameter of LoCoH estimator) match well with pertinent aspects of an animal's biology (such as its perceptual distance, foraging abilities or areas of indirect interaction with other individuals), then the resulting utilization distribution can help to identify resources important to an individual (Fieberg & Kochanny 2005). Regardless of whether utilization distributions are estimated using VHF or GPS data, they will be useless without additional contextual data (habitat, foraging behaviour, memory, perception, resources, locations of conspecifics, locations of predators and more). Determining *how* and *why* an animal uses space in the way that it does may require complex analytical tools such as mechanistic home-range models that seek to identify the underlying behavioural mechanisms for an observed pattern of use. Conversely, the technical expertise required to implement these methods nearly ensures that simpler, traditional modelling approaches will continue to be important in home-range studies. For example, methods that incorporate models of animal movement into habitat selection studies have the potential to provide new insights into fine-scale patterns of habitat selection, but are computationally demanding and typically require custom-written computer code (Fieberg *et al.* 2010). As a result, more traditional use-availability designs for the study of habitat selection are likely to continue to be of value (Boyce & McDonald 1999; Manly *et al.* 2002; Lele & Keim 2006; Beyer *et al.* 2010; Fieberg *et al.* 2010). The need will remain to find the appropriate spatial scales for defining availability when making inferences at individual and population levels (Johnson 1980; Boyce 2006; Fryxell *et al.* 2008; Fieberg *et al.* 2010), and utilization distributions offer one objective approach towards this end (Johnson 1980).

In studying animal home ranges and constructing utilization distributions, one must design research questions carefully to test theoretical predictions; simply collecting animal locations and then searching for appropriate analytical technique does not yield new knowledge. Powell *et al.* (1997) and Mitchell *et al.* (2002) developed *a priori* hypotheses for how productivity of food should affect home-range overlap of black bears if bears are food-limited (hypothesized for females) or not (hypothesized for males) and used utilization distributions to quantify home-range overlap. *Post hoc* analyses would have had little power, whereas testing *a priori* hypotheses establishes the strength of our knowledge. In all cases, authors must provide adequate details for others to replicate their work. If existing software is used, one should provide information on all options chosen (figure 1), even if default values are used (Laver & Kelly 2008).

Emerging GPS technologies open new avenues in ecological research. Ultimately, however, technologies and techniques are merely tools in the hands of research scientists. Our knowledge of why animals use space in the ways we observe will only advance if we ask new and innovative questions (Schwartz 2008). We anticipate that GPS technologies will in future allow tests of hypotheses not presently testable.

At present, however, traditional home-range estimators can still be used well to advance our knowledge of why animals have evolved the behaviours and use of space we document.

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