

Could you please phrase “home range” as a question?

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Statisticians frequently voice concern that their interactions with applied researchers start only after data have been collected. The same can be said for our experience with home-range studies. Too often, conversations about home range begin with questions concerning estimation methods, smoothing parameters, or the nature of autocorrelation. More productive efforts start by asking good (and interesting) research questions; once these questions are defined, it becomes possible to ask how various design and analysis strategies influence one's ability to answer these questions. With this process in mind, we address key sample-design and data-analysis issues related to the topic of home range. The impact of choosing a particular home-range estimator (e.g., minimum convex polygon, kernel density estimator, or local convex hull) will be question dependent, and for some problems other movement or use-based metrics (e.g., mean step lengths or time spent in particular areas) may be worthy of consideration. Thus, we argue the need for more question-driven and focused research and for clearly distinguishing the biological concept of an animal's home range from the statistical quantities one uses to investigate this concept. For comparative studies, it is important to standardize sampling regimes and estimation methods as much as possible, and to pay close attention to missing data issues. More attention should also be given to temporally changing space-use patterns, with biologically meaningful time periods (e.g., life-history stages) used to define sampling periods. Last, we argue the need for closer connections between theoretical and empirical researchers. Advances in ecological theory, and its application to natural resources management, will require carefully designed research studies to test theoretical predictions from more mechanistic modeling approaches.

Key words: home range, kernel density, local convex hull, minimum convex polygon, mixed model, space use, study design, telemetry, territory, utilization distribution

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All resident mammals restrict their movements to fairly well-defined areas instead of wandering randomly, and thus the concept of a home range, as an area routinely used by an animal to meet its daily needs, serves as a useful concept for studying animal behavior (Burt 1943; Powell 2012). Home ranges have been explored using a variety of methods, including both empirical and theoretical studies (Börger et al. 2008). Theoretical inquiries frequently aim to discover causes and consequences of home-range (or restricted space-use) behavior. For example, one might ask “why or under what conditions does home-range behavior evolve (i.e., when is it adaptive to restrict movements to a well-defined area)?” This type of question is arguably best addressed using mathematical models of animal-movement and foraging behaviors, as well as interactions among individuals of the same and different species (Börger et al. 2008; Moorcroft 2012; Moorcroft and Lewis 2006). We refer readers to Mitchell and Powell (2012)

and Spencer (2012) for illustrative examples. By contrast, we were asked to contribute a review of statistical home-range estimators to this Special Feature on home ranges.

Although several such reviews exist (e.g., Kernohan et al. 2001; Kie et al. 2010; Laver and Kelly 2008), new methods for estimating home-ranges continue to be developed, and thus, an inclusive review seemed like a worthy objective. A plethora of simulation studies have been used to compare home-range estimators (e.g., Getz and Wilmsers 2004; Huck et al. 2008; Seaman et al. 1999). Other papers have been devoted to the lack of adequate reporting of estimation methods used in home-range studies (Laver and Kelly 2008; Lawson and Rodgers 1997). Although much of this literature serves a useful



purpose, the advice given regarding sample size considerations, autocorrelation, and estimation methods is often conflicting. These inconsistencies have in turn led to confusion among some biologists regarding appropriate sampling designs and analytical methods in home-range research. We strongly believe that there is no “best” method for estimating home ranges (much to the chagrin of practicing ecologists, including ourselves, who seem to have an innate desire to find an estimator that universally outperforms all others in common data scenarios); the “best” or most appropriate analytical method will be question-dependent. We felt it necessary to highlight this facet upfront. Further, we expected many of the current disagreements and confusion in the home-range literature could be resolved by a question-driven review of home-range estimators and recognition that the spatiotemporal structure of animal-movement data must be considered when evaluating study designs and inferential approaches.

We have observed a tendency for researchers to approach home-range studies from the bottom up, with much emphasis and consternation related to choosing methods for data collection and analysis that are “statistically valid,” before finally asking “what can my data tell me about animal home ranges?” For example, it is not uncommon for researchers to justify sampling intervals (between observed locations) by the need to avoid problems associated with autocorrelation. Thus, rather than allowing research questions to drive sample-design and analysis choices, statistical concerns may end up limiting the types of data researchers collect and the questions they ask. We felt it important to emphasize a top-down, question-driven approach to research design. Yet, we also thought it might be possible to offer some general principles to help to guide researchers as they evaluate the potential implications of various design and analysis choices.

Our primary objective in writing this paper is to encourage ecologists interested in studying home ranges to use a top-down approach to research design and analysis. We begin the paper with a motivating example to demonstrate the importance of the top-down approach. Secondly, we aim to provide a review of statistical home-range estimators, including several recently proposed alternatives to classical kernel density estimators (KDEs) and minimum convex polygon (MCP) estimators. Hence, in the 2nd section of the paper, we review home-range metrics commonly used in empirical research (e.g., home-range size, intensity of space use, etc.), and discuss the relative performance of various (old and new) statistical home-range estimators in this context. We extend this discussion by considering the implications of estimator choice for comparative studies. In the last section of the paper, we offer guiding principles useful for evaluating sampling design and analysis choices in home-range studies.

MOTIVATING EXAMPLE

Top-down approach to research design.—To illustrate a top-down approach that begins with clearly defined research questions, consider the following scenario (see also the

summary in Table 1 for further considerations during each step of the process). A biologist hypothesizes that white-tailed deer (*Odocoileus virginianus*) will use dense conifer stands more frequently when snow depths exceed 40 cm, a threshold determined based on energetic costs of deer moving in deep snow (conifers retain much snow in their crowns, so deer should be able to move more easily in these stands than in open habitat). To test the hypothesis, the researcher recognizes the need to observe deer movements during both severe and mild winters, and thus, he commits to a long-term study. Ideally, he would like to observe the same deer in both types of winters. More realistically, he will need to follow many deer (in each year) to make sure that any conclusions are robust to among-animal variability in space-use patterns. In addition, he will want to observe deer throughout the winter to determine if changes in seasonal movement patterns occur close to the identified snow-depth threshold.

The researcher next selects a few different metrics to quantify space-use patterns during each of several winters: amount of time spent in conifer stands; mean step lengths (distance moved between locations) in various habitat patches (conifer stands, deciduous habitat, and open habitat); the areal extent of habitats visited by deer, estimated using a kernel density estimate of home-range size; and the percent of the 3rd metric composed of conifer cover. The 1st metric provides arguably the most direct behavioral response measure to correlate with snow depth. Its main advantages are its simplicity and interpretability. The 4th metric is similar, but it substitutes area for time when quantifying the importance of coniferous habitat. The 2nd and 3rd metrics are aimed more at mechanisms underlying the specific research hypothesis (deer should alter their movements and possibly avoid more-open habitat in deep snow). To help interpret the 2nd metric, the researcher also plans to collect snow-depth measurements in these different habitat types.

Having selected possible metrics to test the researcher’s hypotheses, and armed with pilot data (or information from the literature), the researcher could then conduct a formal power analysis to determine how various sample-design choices influence hypothesis tests that rely on these metrics. Of particular importance are questions about the number of animals to follow, the monitoring frequency, and the required accuracy of spatial location data. Different sampling designs could be evaluated by simulating movement of multiple animals under varying snow-depth scenarios, with location data “collected” at different sampling intervals. Hypothesis tests could then be constructed using the 4 proposed metrics to determine the likelihood of detecting a behavioral effect under a range of possible simulated environments (and, assumptions regarding how deer respond to those environments). In lieu of conducting a simulation study, we explore sample-design trade-offs as well as additional steps in the research process using data from a previous telemetry project (Kochanny et al. 2009).

Sample-design trade-offs.—The optimal sampling design will depend on one’s research hypotheses and the metrics

TABLE 1.—Key steps and considerations required to successfully implement a question-driven approach to home-range studies.

1. Define precise research questions	<ul style="list-style-type: none"> • Aim to test specific a priori hypotheses • Hypotheses developed from exploratory studies and post hoc analyses need to be tested using independent data • Aim to establish closer connections between theoretical and empirical studies (e.g., test predictions of theoretical models) • Research questions should drive sample design and analysis choices • Other movement metrics may be more informative than home-range estimates for addressing certain research questions
2. Identify spatiotemporal scales and units of analysis	<ul style="list-style-type: none"> • Home ranges are dynamic, emergent patterns of animal space use, resulting from interactions between individuals and the external environment • Reporting a home-range measure without its associated temporal unit is akin to reporting travel speeds using only distance travelled • Research questions should determine appropriate temporal scale(s), allowing one to sample from well-defined and biologically meaningful time periods • Consider a finite population-sampling framework when evaluating the implications of sampling design choices <ul style="list-style-type: none"> ○ The population is composed of locations visited by the study subject(s) and the sampling intensity determines how well the population can be estimated ○ Varying the sampling duration changes the population
3. Select space-use metrics and covariates to test specific research hypotheses	<ul style="list-style-type: none"> • The most appropriate metrics and methods for testing hypotheses will be context-specific, depending on the underlying properties of the movement data and the question(s) asked • Use multiple, complementary metrics (e.g., home-range size, intensity of space use, and movement characteristics) when possible to determine if conclusions are sensitive to the choice of metric • Location-only data have a very limited information content <ul style="list-style-type: none"> ○ Identify environmental or biological covariates, or both, necessary to answer questions ○ Attempt to collect data on the behavior or individual state, or both, associated with each location ○ Direct observations may be more informative than large numbers of locations collected using automated telemetry systems
4. Define sampling design and inferential approach	<ul style="list-style-type: none"> • The optimal sampling design will depend on the research hypotheses and the metrics chosen to test them • Use simulations to explore how various sample design choices influence hypothesis tests: <ul style="list-style-type: none"> ○ Number of animals to follow; ○ Monitoring frequency or intensity, or both, and impact of missing data; ○ Required accuracy of spatial location data ○ Trade-offs between sampling frequency and duration • Often more can be learned by focusing on temporal dynamics, rather than conducting a static home-range analysis • Simple models may perform better than complex ones, even when the latter are biologically more realistic
5. Assess the strength of conclusions	<ul style="list-style-type: none"> • Determine if conclusions are robust to various analysis choices and if there are alternative explanations for observed data patterns
6. Archive data	<ul style="list-style-type: none"> • Archive raw location data, covariates, and metadata information, not estimates of home-range size, in databases such as Movebank

chosen to test these hypotheses. For example, tests that rely on movement paths or movement characteristics (e.g., mean step lengths) will generally require more-frequent monitoring and more-precise location data than tests that rely on estimates of broadscale patterns of space use or size of areas used by animals. Consider, for example, trade-offs between using very-high-frequency (VHF) and global positioning system (GPS) monitoring tools (Hebblewhite and Haydon 2010). These trade-offs are illustrated nicely by a recent study of white-tailed deer in Minnesota in which individual animals were observed using both sampling techniques during the same time period (Kochanny et al. 2009). For the animal depicted in Figs. 1a and 1b, VHF observations were made 2 or 3 times per week and GPS locations were made every hour from 15 February to 12 May 1999.

In this example, estimates of broadscale space-use patterns using VHF and GPS data were similar. For example, the 2 methods give identical point estimates (to 2 decimal places) of time spent in the 2 patches defined by the 95% kernel density contours from the VHF analysis (Fig. 1c): 57% of the time, the animal was in the northeastern patch. The GPS data result in a

more precise estimate (the *SEs* are 0.11 and 0.03 for the VHF and GPS data, respectively). Nonetheless, upfront costs for GPS collars are significantly higher, which may reduce the number of individuals that can be followed (relative to a VHF study). Thus, estimates of population-level parameters may still be more precise when using VHF data, particularly if among-animal variability is substantial. The ability to obtain a representative sample of locations also is important. Locations can more easily be obtained throughout the day and night as well as in inclement weather with GPS collars, but tests should be conducted to determine the frequency of missed fixes. Lastly, location error may be an important consideration. If conifer stands are small relative to the likely error in VHF location data, then VHF data may provide little power to detect shifts in habitat use relative to snow depth (e.g., see Montgomery et al. 2010). Again, pilot data (and more specifics about the study area) would allow one to quantify trade-offs between VHF and GPS techniques more precisely.

How robust are conclusions to the choice of metric?—Once data have been collected and hypothesis tests have been conducted, it is important to evaluate the robustness of one's

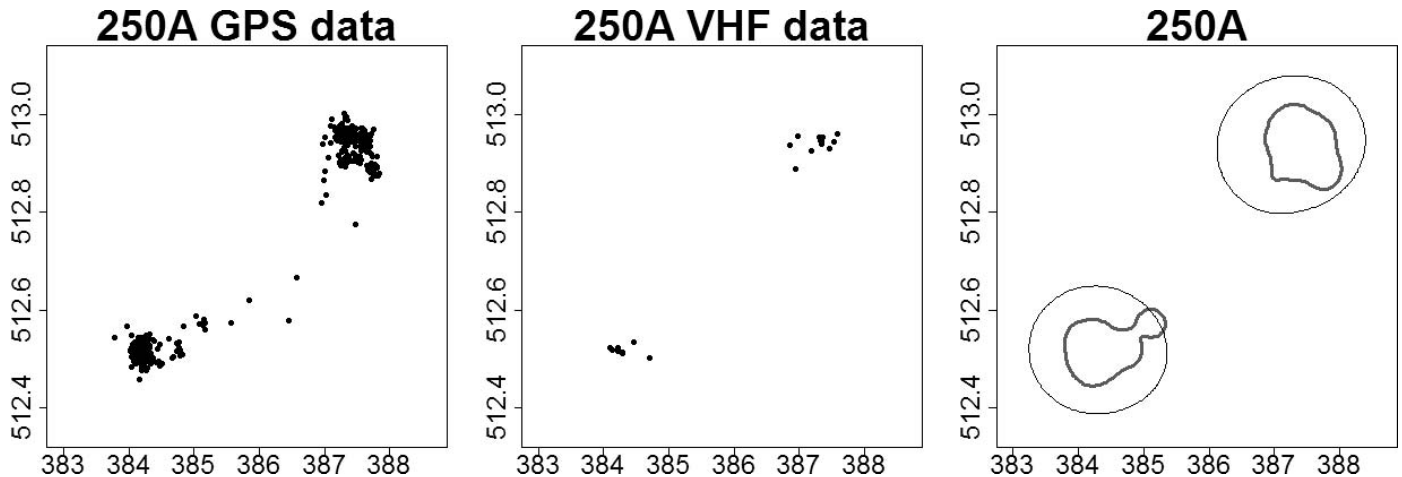


FIG. 1.—Diurnal locations of an adult (≥ 1.5 years old) female white-tailed deer collected by global positioning system (GPS) and very-high-frequency (VHF) telemetry during 15 February–12 May 1999, Camp Ripley, Little Falls, Minnesota. The 3rd column depicts 95% probability contours from kernel density estimators applied to the GPS (gray wide lines) and VHF (black thin lines) data.

conclusions to various analysis choices and also to explore alternative explanations for observed patterns in the data. In the deer example (Fig. 1), estimated home-range areas differed widely (GPS area = 294 ha versus VHF area = 945 ha). Suppose VHF collars were used in the 1st year of the study and GPS collars in 2nd, with the latter year being a more-severe winter. In this case, the researcher might incorrectly conclude that the data support his hypothesis (seasonal home ranges decreased in the 2nd, more-severe winter year). However, plotting the location data would show that this animal largely used the same habitat; the noted difference in home-range areas is due to a statistical artifact. Specifically, KDEs of home range require specification of 1 or more smoothing parameters, which have long been known to strongly influence estimates of home-range size (Powell 2000). As discussed by Fieberg (2007a), data-based methods for choosing these parameters involve a bias–variance trade-off; larger parameters (i.e., greater smoothing) are optimal in terms of minimizing the mean-integrated squared error of the estimated probability density when data are sparse or spatial variance is high. The example in Fig. 1 is an extreme case in which the VHF data exhibited large spatial variance with a small sample size; comparisons involving 13 other sets of paired observations from the same study suggested VHF- and GPS-based areas were, on average, similar (Kochanny et al. 2009). A consequence was that home-range sizes, estimated using outer 95% probability contours, differed considerably even though the estimated probability density functions largely agreed (Kochanny et al. 2009). This example also serves to illustrate that not all metrics are equally robust to various sample-design and analysis choices.

HOME-RANGE METRICS AND THEIR ESTIMATORS

Empirical home-range studies most frequently rely on estimates of animal locations over time (although continuous tracking via direct observation or by following animal tracks also is possible [Powell and Mitchell 2012]). Questions

addressed by these studies tend to emphasize 1 or more of the following characteristics:

1. Areas that are used (or not used) by an animal (without regard to frequency of use).
2. The total area used by an animal (i.e., home-range size).
3. Variation in the amount of time spent in geographical space (i.e., x and y coordinates). This variation is typically quantified by a spatial probability density function called the utilization distribution (UD—Van Winkle 1975). Alternatively, one might quantify spatial variation in some measure of utility (e.g., energy gained) with a utility distribution (Powell 2012; Powell and Mitchell 2012).
4. Areas of concentrated space use within the home range, that is, so-called “core areas.” Unfortunately, most studies estimate core areas using ad hoc definitions (e.g., 50% isopleths from the estimated UD). We refer readers to Powell (2000, 2012), Seaman and Powell (1990), and Wilson et al. (2010) for individual-based alternatives.

Researchers sometimes use the term “home range” to refer to each of these general characteristics of animal space use. To avoid confusion, however, it is useful to define questions (and metrics) as precisely as possible, particularly because the relative performance of statistical home-range estimators (and of animal-movement metrics in general) will depend on which (if any) of these characteristics are most appropriate for testing one’s specific research hypotheses.

Traditional emphasis on areas that are used or not used.—Many comparisons of statistical home-range estimators in the literature emphasize the 1st characteristic (areas used or not used). In particular, the 2 most commonly applied estimators of home-range size, KDEs and MCP estimators (Laver and Kelly 2008), are often criticized because they do not include areas known to be used by animals or they include areas known not to be used (Getz et al. 2007; Getz and Wilmers 2004; White and Garrott 1990), type I and type II errors, respectively.

Probably less well known to most ecologists, however, is that the general problem of estimating bounded areas from a random sample of points is of interest to many fields of research (e.g., cluster analysis and pattern recognition), and falls under the theory of set estimation (Cuevas 2009; Molchanov 2005). Because of their well-established statistical properties, convex hulls (which form the basis of the MCP approach) and KDEs are frequently proposed as estimators in this general context. Specifically, KDEs with typical data-based rules of bandwidth selection, in which smoothing goes to 0 as sample size goes to ∞ , provide consistent (asymptotically unbiased) estimates of the UD (Wand and Jones 1995). Similar convergence properties apply to estimates of bounded areas from KDEs (e.g., Cuevas and Fraiman 1997), despite claims otherwise (Getz et al. 2007; Getz and Wilmsers 2004)—for a nice exemplification see Lichti and Swihart (2011). MCPs also will converge as sample sizes increase provided the area one is trying to estimate is convex (Molchanov 2005).

Almost always, however, home ranges do not take simple geometric forms (Burt 1943), and MCPs typically result in type II errors when the UD is not convex—a nice example is given by figure 7.3 in White and Garrott (1990) in which a lake falls partly within the convex polygon encompassing an animal's locations. Therefore, the suggestion by Harris et al. (1990) to use MCPs for comparative purposes because they are "assumption-free" is misleading. Lastly, MCPs have been shown to increase with sampling duration (Belant and Follmann 2002; Moorcroft and Lewis 2006; Worton 1995a), suggesting that they are likely to result in type I errors with data sets of short sampling duration (Bekoff and Mech 1984). By contrast, estimates of home-range size obtained from the 95% probability contour of a KDE often decrease with sample size (Barg et al. 2005; Belant and Follmann 2002; Fieberg 2007a), and estimates may fragment into multiple, small polygons with large data sets, leaving out travel corridors between habitat patches. Thus, KDEs may result in type II errors (due to oversmoothing) with small data sets and type I errors (when restricted to a 95% contour) with large data sets. Depending on how the estimates are ultimately used (i.e., the motivating question), the cost of these errors may or may not be large.

When the cost of type I and type II errors is large, alternatives to MCPs and KDEs may be worth considering. Generalizations of the convex hull that converge to a wider class of shapes (not just convex sets) may prove useful for home-range studies (e.g., Pateiro-López and Rodríguez-Casel 2010). Recently developed approaches using local convex hulls have outperformed MCPs and KDEs in simulation studies (in terms of type I and type II errors), particularly when simulated space-use patterns had sharp boundaries (Getz et al. 2007; Getz and Wilmsers 2004).

Importance of the home-range metric.—Although KDEs have sometimes been criticized for relatively high type I or type II error rates, KDEs may outperform local convex hull approaches if the true UD varies smoothly over space, especially if the underlying biological questions require a

continuous measure of space use rather than an estimate of home-range size (Lichti and Swihart 2011); an example is the extent to which 2 home ranges overlap (Fieberg and Kochanny 2005). These points were illustrated in a recent study by Lichti and Swihart (2011), in which they compared KDEs (with various bandwidth choices) to local convex hull approaches using data simulated from a variety of UDs (Fig. 2). Although local convex hull methods resulted in lower type II errors than KDEs, differences were less pronounced when the UD varied smoothly (compare UD1 and UD2 in each series of Fig. 2). On the other hand, KDEs almost always resulted in more-accurate estimates of the UD. The best method for estimating home-range size depended on the true UD and the available sample size. Together, these results reinforce the conclusion that the most-appropriate method will be question-specific, that is, it will depend on which home-range characteristic(s) (area used, total area, or intensity of space use) is most appropriate for testing one's research hypothesis.

Use of auxiliary information to improve home-range estimators.—Like KDEs, local convex hull methods also require tuning parameters that influence their performance. Getz and Wilmsers (2004) and Getz et al. (2007) suggested choosing the smallest tuning parameter that does not result in holes (i.e., lacunae) corresponding to unused areas (e.g., lakes for terrestrial species) to be included in the home range. Incorporating useful auxiliary information will typically improve the performance of estimators, and the relative performance of local convex hulls (to KDEs) in these simulation studies may be partly attributable to using this extra information to choose tuning parameters (but see Lichti and Swihart 2011). In fact, similar ideas have been proposed for use with KDEs (e.g., choosing the smallest smoothing parameters that result in a contiguous area [Berger and Gese 2007; Jacques et al. 2009]). Further, if there are areas known not to be used, then any probability associated with these areas can be reassigned to the rest of the home range (this is the approach taken by the kernel-based "density.ppp" function in the R package spatstats [Baddeley and Turner 2005]). One also could reassign the probability locally, by redistributing the probability mass of those kernels associated with locations near unused areas—that is, kernels that would otherwise overlap the unused areas (e.g., Benhamou and Cornelis 2010; Hines et al. 2005). Similarly, lacunae can be removed from MCP and other home-range estimators (e.g., Knight et al. 2009; White and Garrott 1990:153).

In addition to lacunae, impermeable boundaries to movement can result in type II errors. Recently, Barry and McIntyre (2011) proposed a lattice-based home-range estimator that can account for a priori specified lacunae as well as boundaries that impede movement (e.g., the shoreline for aquatic species). Smoothing is accomplished by allowing probability mass associated with the observed locations to flow according to a constrained random walk among grid cells in the lattice, with the amount of smoothing controlled by the number of steps in the random walk. Similar to traditional KDEs, however, their approach ignores the temporal nature of the observation

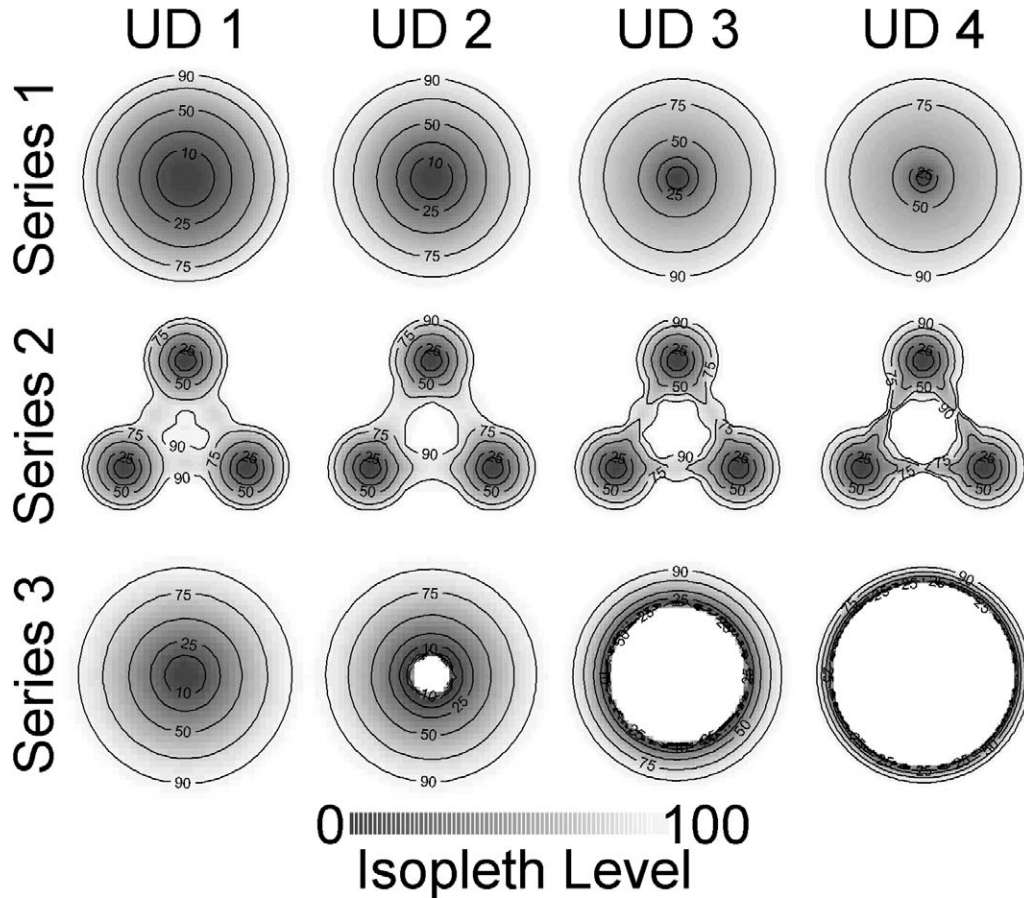


FIG. 2.—Utilization distributions (UDs) used by Lichti and Swihart (2011) to compare kernel density estimators (KDEs) and local convex hull (LoCoH) approaches to estimating home-range sizes, UD, and type II errors (probability mass associated with unused areas). UD were arranged into 3 series, with each series used to represent a different space-use pattern. Within each series, the intensity of the pattern increased from UD 1 to UD 4. Reproduced from Lichti and Swihart (2011).

process. Benhamou (2011) and Benhamou and Cornelis (2010) also developed a movement-based kernel density estimation approach that allows one to incorporate movement constraints. Their approach is similar to the Brownian bridge model proposed by Bullard (1999) and Horne et al. (2007a), in which an underlying movement model is used to create a smooth bridge between serially correlated observations. Conceptually, this approach is appealing if boundaries to movement are prominent and known a priori, and data exhibit a high degree of serial correlation. Nonetheless, performance of the movement-based kernel density estimators should be evaluated using data simulated under expected study conditions to determine if it improves upon other methods with respect to testing one’s research hypotheses.

All of the above approaches assume unused areas can be identified without error, which will be difficult except for obvious cases, like fenced areas or water bodies (or terrestrial areas for aquatic animals). Alternatively, model-supervised kernel smoothing (Matthiopoulos 2003) provides a general approach to incorporating auxiliary information (prior expectations or data). Model-supervised kernel smoothing uses a weighted combination of 2 estimators, a traditional KDE and a

model of space use built from the auxiliary information. The relative weight of the 2 models is determined using likelihood cross-validation. Simulations in Matthiopoulos (2003) suggest that model-supervised kernel smoothing will improve upon traditional KDEs when the auxiliary model is informative, and perform similar to traditional KDEs when the auxiliary model is not. Implementing model-supervised kernel smoothing and modifications to KDEs require custom-written code, whereas local convex hulls, the lattice-based estimator, and the movement-based KDE may be implemented with publicly available software (Barry and McIntyre 2011; Benhamou 2011; Benhamou and Cornelis 2010; Getz et al. 2007).

**STATISTICAL INFERENCES
FROM COMPARATIVE STUDIES**

Research hypotheses are frequently tested using comparative studies, involving several individuals or populations of a particular species or average species-specific estimates compared across a range of species (e.g., Bordes et al. 2009; Indermaur et al. 2009; Saïd et al. 2009). Relative comparisons (among animals or among species) are used for inference, and

thus a consistent bias (e.g., a tendency to consistently over- or underestimate home-range size) will often be less of a concern than obtaining estimates that are precise and robust to sampling conditions (Börger et al. 2006a). Again, the importance of home-range estimator and of sampling-related effects is likely to depend on the underlying research question. Nilsen et al. (2008) suggest that among-species comparisons are likely to be robust to many sampling and analysis considerations because the signal (differences among species) is likely to be large relative to the noise (sampling variance and nonconstant estimation biases). For example, choice of home-range estimator (KDE or MCP) had little effect on estimated regression lines relating species-specific estimates of body size to estimates of home-range size. By contrast, choice of estimator explained as much variance as did sex in the within-species comparative examples considered by Nilsen et al. (2008). Progressing from classical studies involving the relationship between home-range size and body size will, however, very likely require access to less-noisy home-range estimates, ideally obtained from a joint analysis of the raw movement data for all species compared.

Within-species comparative studies are often fraught with additional challenges. Unlike among-species comparative studies that are typically motivated by a precise theoretical question or a priori hypothesis (e.g., the scaling of body size and home-range size), within-species studies frequently aim to examine a large suite of potential explanatory variables using multivariable regression techniques (we refer readers to Platt [1964], Romesburg [1981], and Williams [1997] for a discussion of the import role of a priori hypotheses in scientific research). Oftentimes, variables are chosen based on the availability of large-scale geographical information system databases, rather than from a mechanistic understanding (or theory) of how these variables influence animal behavior. Further, most telemetry studies follow a small number of individuals, which has implications for learning from regression studies—this can be especially problematic for GPS-based studies because of the high cost of GPS collars (Hebblewhite and Haydon 2010). General sample-size guidelines suggest limiting the number of predictor or candidate variables (including nonlinear effects and interactions among variables) to $m/10$ or $m/20$, where m is the effective sample size (Burnham and Anderson 2002; Harrell 2001). The number of animals will give a good approximation to the effective sample size when predictor variables do not vary within an animal (e.g., sex). Thus, typical telemetry studies involving 10–20 animals provide little information for sorting out the influence of multiple animal-specific variables. On the other hand, mixed-effects models applied to multiple estimates of home-range size over time may provide a useful approach to looking at variables that are temporally varying (e.g., environmental covariates) because effective sample sizes will be larger for variables that change within individuals (e.g., Börger et al. 2006a, 2006b; Pinheiro and Bates 2000). Regardless, we would argue that more resources should be spent on studies designed to test specific a priori hypotheses. In addition, hypotheses

generated by exploratory studies and post hoc analyses need to be tested using independent data.

Of particular concern for drawing statistical inferences from comparative studies is the previously noted relationship between sample size and estimates of home-range size from MCPs and KDEs (Worton 1995a). As will be discussed in the next section, sample-size effects are best understood by considering the separate effects of sampling duration and sampling intensity, and if possible both should be standardized in comparative studies (Börger et al. 2006b). Alternative indexes of animal movement that are less sensitive to sample size also may prove useful for comparative studies. For example, Worton (1995a) proposed MCPs encompassing 50% of the observed locations (i.e., peeled convex polygons) as a useful metric related to home-range size. Using simulated data, he found that estimators could be scaled (using factors that depended on sample size) to allow comparisons across data sets with varying numbers of locations; the same scale factors worked well across a range of simulated UD. Moorcroft and Lewis (2006) also provide theoretical support for using peeled MCPs as well as mean-absolute and mean-squared displacement as indexes for animal movement. Ultimately, it is wise to analyze data using multiple metrics and methods and thus, to test whether conclusions are robust to various analysis choices. In general, however, we advocate that researchers choose a primary metric and analysis a priori, and then treat additional analyses as a sensitivity analysis.

DESIGN AND ANALYSIS PRINCIPLES

We reiterate that optimal design and analysis strategies will be question-dependent. We attempt, however, to provide some general guidance on design issues, largely based on principles from randomized experiments and finite population sampling.

Randomized experiments.—Randomized experiments typically focus on a small number of important variables (e.g., those defining treatments), with randomization and blocking used to control for other systematic variation. In the context of home-range studies, these principles suggest we should try to test important theoretical predictions involving a small number of key variables, sampling effort should be allocated to maximize variation in these variables (e.g., to understand how winter conditions affect space use, we need a study that is long enough to capture both mild and severe winters), and we should attempt to control for sampling characteristics that influence home-range estimators but are not of direct importance.

Finite population sampling (fixed sample size versus sampling duration and intensity).—Several authors have put forth guidelines regarding minimum sample sizes necessary for estimating home ranges. These guidelines have typically been derived from simulation studies that sampled from stationary distributions (e.g., mixtures of multivariate normal distributions [Seaman et al. 1999]), which do not capture the temporal nature of animal location data. Ultimately, this way of thinking led to a strong focus on autocorrelation and the need

to gather independent data so that the observed number of locations was a good measure of information content (effective sample size). By contrast, viewing the problem from a survey sampling viewpoint (with well-defined population and sample units) alleviates many of the concerns related to autocorrelation, by highlighting the importance of sampling duration and sampling intensity rather than the total number of locations (Fieberg 2007a; Otis and White 1999). In the context of a telemetry study, the population is composed of locations visited by an animal (or group of animals). Varying the sampling duration changes the population. Longer sampling durations may result in larger used areas, especially when longer studies encompass a wider range of environmental conditions. Similarly, animals may use different areas as they age, grow, and enter new life-history stages (Burt 1943). Thus, whenever possible, researchers should sample from well-defined (e.g., specified start and end dates) or biologically meaningful (e.g., encompassing specific life-history stages) time periods.

Sampling intensity, by contrast, determines how well we can characterize the population of visited locations. Larger samples (for a fixed study duration) are always better, provided that they are representative, and thus there is no need to subsample data already collected as sometimes has been done to avoid autocorrelation (Fieberg [2007a] and references therein). To further see the utility of a finite population sampling perspective, consider common guidelines for sample-size requirements stated in terms of the total number of locations (e.g., 50 observations per animal for estimating home-range size, as suggested by Seaman et al. [1999]). Clearly, 50 observations collected over 1 week is not the same as 50 observations collected over a period of a year or more, and researchers might suspect that autocorrelation in some way invalidates the former data set. A finite population sampling perspective provides a much clearer way to view these 2 data sets: the former data provide a rich source of information for inferring space-use patterns over a very short time period, whereas the latter data likely provide less-precise estimates of space use over a longer but maybe more biologically meaningful time period. Continuous monitoring, by direct observation of study animals or by following tracks in the snow, also may be beneficial depending on one's research questions (Powell 2012; Powell and Mitchell 2012). In such cases, the population becomes a known quantity, but whether this quantity is interesting or not may depend on the sampling duration.

Trade-offs involving sampling frequency versus sampling duration.—Although having more data is nearly always better, the rate of information gain is likely to asymptote as sampling intensities increase to the point where little to no movement occurs between observations (Turchin 1998). Trade-offs involving information gains and costs, as well as trade-offs involving sampling frequency and sampling duration (e.g., associated with battery life of GPS collars) deserve more attention (Powell 2012). These trade-offs can be investigated by simulating observed locations along continuous movement

paths, thereby introducing temporal correlation among observations, rather than sampling locations from a stationary probability distribution (Fieberg 2007a, 2007b). For many problems, we expect variable sampling intensities to be of less concern than variable study durations. For example, Kochanny et al. (2009) found that KDEs for white-tailed deer using VHF data with 1–3 observations per week were generally similar to those based on hourly GPS samples. When KDEs were applied to VHF data, larger smoothing parameters were chosen and the additional smoothing largely fill in gaps between observations that were otherwise filled in by more-frequent sampling in the GPS data. Börger et al. (2006a) also found KDEs of home-range size were relatively stable with sampling intensities of ≥ 10 observations per month for roe deer (*Capreolus capreolus*), particularly when compared to observed among-animal variability.

Missing data, variable sample duration, and dynamic home-range analysis.—Although a finite population sampling framework largely alleviates concerns associated with autocorrelation, this framework assumes one can define and obtain a representative (or random) sample from a biologically meaningful time period (Fieberg 2007a, 2007b; Otis and White 1999). Two potential concerns arise in typical telemetry studies: obtaining a representative sample can be difficult because of logistical constraints that limit or restrict one's ability to obtain locations (e.g., inclement weather may prevent one from obtaining a location with VHF collars) and also because of technological issues (e.g., missed fixes may occur in dense cover with GPS collars); and the process of capturing, collaring, and tracking animals often leads to considerable among-animal variability in monitoring start and end dates. In essence, these challenges can be thought of as creating missing data (where a "full" data set would contain an equal number of observations, taken from identical time frames, for all animals).

At a minimum, one should qualitatively assess the likely impact of missing (or nonrepresentative) data on results derived from a telemetry study. To do this, one needs to study the pattern of missing data (e.g., timing within a day or seasonally) along with diurnal and seasonal patterns in the location data to determine how systematic biases might influence metrics of interest. For example, if most missing data occur during the middle of the day when animals are assumed to be resting in heavy cover, then areas of dense cover will be underrepresented; further, movement rates will likely be overestimated in the middle of the day. In some cases, stationary tests may help elucidate covariates (e.g., canopy cover) that influence the probability of a successful fix (see Frair et al. [2010] for a review). In these cases, a model for the probability of detection can sometimes be used to fill in missing locations or statistically correct for sampling biases associated with missing data (Frair et al. 2004; Horne et al. 2007b; Nielson et al. 2009).

To understand the implications of variable sampling durations, one needs to understand how animal space use varies temporally. Börger et al. (2006b) demonstrated how mixed-effects models applied to repeated home-range estimates

across multiple temporal scales can provide insight into factors that may be responsible for temporal variation in space-use patterns. For example, they found that climatic variables (precipitation and photoperiod) interacted with habitat characteristics (dominant habitat type within the home range) and were more pronounced over shorter timescales (biweekly–half-year scales versus yearly scale). Recently, Rivrud et al. (2010) used this approach to understand how climate affects animal behavior, by investigating how local climate variables explained estimates of home-range size over different temporal scales. Temporal variation in patterns of space use also may be studied using space–time KDEs, as recently suggested by Keating and Cherry (2009). Specifically, they illustrate smoothing approaches that utilize a circular timescale (0–24 h or 0–365 days) to facilitate modeling recurrent patterns of space use in time, such as seasonal migrations. These approaches to studying temporally changing space-use patterns provide a more dynamic picture of animal behavior than static home-range analyses, and they also may prove useful for designing future studies (e.g., by providing an objective means for deriving biologically meaningful sampling periods).

Assigning a temporal unit to home ranges and connections to other types of animal space use.—Home ranges are emergent, dynamic patterns of space use and memory, determined by complex interactions between individuals and their environment (Börger et al. 2008; Mitchell and Powell 2012; Moorcroft and Lewis 2006; Powell and Mitchell 2012; Spencer 2012). Because environments (and individual state) are constantly changing, we may expect space-use patterns to change too (e.g., Edwards et al. 2009; Moorhouse and Macdonald 2005; Spencer 2012). Thus, we argue that home-range estimates should be ascribed a temporal unit (area for a given unit of time [White and Garrott 1990]). Although it is common to attach seasonal labels (e.g., summer and winter) to home-range estimates, variable sampling durations within these seasonal categories can have implications for home-range estimates (the longer an animal is followed, the more space it will likely use, which can translate into larger home-range estimates). Thus, we stress that reporting a home-range measure without its associated temporal unit is akin to reporting total distance traveled without a temporal frame of reference.

Considering the temporal scale of home-range estimates also allows for broader comparisons of space-use patterns than normally afforded by traditional static notions of home range. For example, home ranges can shift or slowly drift over time (Doncaster and Macdonald 1991; Edwards et al. 2009; Spencer 2012) and animals may alternate between different space-use behaviors (e.g., dispersal, migration, or nomadism). Current research increasingly highlights the need to better understand these dynamics by considering specific space-use patterns in the wider context of animal-movement models (e.g. Börger et al. 2011). Spatiotemporal UD estimators (e.g., the KDE proposed by Keating and Cherry [2009]) may have utility for studying these space-use patterns, particularly when combined

with fine-scale temporal data (e.g., as provided by GPS technology or direct observation).

Inherent limitation of location-only data.—The widespread availability of GPS technology has led to the collection of vast amounts of location data, and these data have in turn fueled the development of new quantitative methods for modeling animal movement, resource selection, and home range (Fieberg et al. 2010; Kie et al. 2010; Patterson et al. 2008). In an attempt to understand why animals visit specific locations, latent (unobserved) variables representing an animal's behavioral state at the time of observation can be included in these models (e.g., Morales et al. 2004). Inferring processes (e.g., movement dynamics) from patterns in location data is difficult, however, because multiple, contrasting models can often fit the data equally well (e.g., see discussion in Börger et al. [2011]). To understand why an animal uses a certain location or area will almost certainly require direct observation of animal behavior (Powell 2012). When behavioral data are available, separate UDs can be estimated (for each behavior) to investigate if individuals use different areas of the home range for different behaviors and if so, why (e.g., Marzluff et al. 2001). Unfortunately, such studies are very rare and we highlight this as a crucial avenue for future research.

Simplicity (independent observations) versus complexity (modeling correlation due to animal movement).—Historically, ecologists almost always treated location data as being independent, leading to relatively simple estimators of home range. Although location data are usually autocorrelated, the assumption of independence can be justified when inferences are limited to the fixed sampling period and observation times are random (or, alternatively, locations are evenly distributed over the sampling period [Breunig 2001; Buskirk 1998; Fieberg 2007a]). In addition, various weighting schemes can be derived either to reduce bias when oversampling certain time periods (Fieberg 2007b) or to improve efficiency when sampling intensity varies temporally (Hines et al. 2005; Katajisto and Moilanen 2006).

Alternatively, density estimators have been developed that explicitly acknowledge the temporal nature of animal location data. These approaches usually incorporate models of animal movement into the estimation approach. The earliest applications assumed animal movement could be modeled as a diffusion process with an attraction to an activity center, formally a bivariate Ornstein–Uhlenbeck process, which in the long-run results in a multivariate normal UD (Dunn and Brisbin 1985; Dunn and Gipson 1977; Worton 1995b). Brownian bridge estimators offer a similar approach to home-range estimation, by assuming animals move according to a random walk (similar to a diffusion process) between observed locations (Bullard 1999; Horne et al. 2007a).

Estimators that model movement between locations, thereby accounting for temporal correlation in the data, are appealing—for example, Horne et al. (2007a) provide a nice example of using a Brownian bridge estimator to explore travel routes and highway crossings of black bears (*Ursus americanus*) in Idaho. Nonetheless, these methods require the estimation of move-

ment parameters (e.g., travel speed) that are not present in traditional estimators built under an independence assumption. Further, models of animal movement (e.g., random diffusion or constant travel speed) may be too simplistic to provide a good fit to location data. As a result, these methods may not be as accurate or precise as estimators that ignore the temporal nature of the animal locations. Accordingly, Fieberg (2007a) found that an estimator based on the multivariate normal distribution assuming independent observations performed as well as the bivariate Ornstein–Uhlenbeck estimator even when data were autocorrelated and simulated according to the bivariate Ornstein–Uhlenbeck model. Similarly, Powell (2012) found, using simulated data, that a Brownian bridge estimator was less accurate than traditional KDEs when data were sparse, and performed only slightly better than traditional KDEs when data were sampled more intensively (resulting in highly autocorrelated data). The Brownian bridge estimator also performed poorly in a recent study comparing MCPs, KDEs, Brownian bridges, and local convex hulls for estimating badger (*Meles meles*) home-range size (Huck et al. 2008). Yet, methods that allow for more realistic movement patterns between sequential locations offer an interesting and potentially promising avenue for future research (see Benhamou [2011] and Benhamou and Cornelis [2010] for recent examples).

Similar findings with respect to model complexity have been made in natural resource management and population modeling, that is, simple models may perform better than complex ones, even when the latter are biologically more realistic (Adkison [2009] and references therein). For home-range studies, we suggest that trade-offs associated with model complexity offer an interesting line of research, but anticipate that conclusions regarding the most appropriate methods will be context-specific, depending on the underlying properties of the movement data and the question(s) asked (Powell and Mitchell 2012). We expect movement-based methods to be most useful when data are collected with a high sampling frequency, when animal movement can be adequately described by relatively simple models, and when an understanding of temporal dynamics is necessary for answering research questions of interest.

Establishing connections between theoretical and empirical research.—Much progress in understanding animal home ranges could be obtained by establishing closer connections between theoretical and empirical studies. For instance, it would be particularly interesting to design an empirical study to test some of the theoretical predictions made by Spencer (2012). Spencer's models predict that animals should forage in relatively concentrated areas, but these areas should randomly drift or shift over time when the value of information (gained from previous visits to a site) is high but the environment changes rapidly (see also Van Moorter et al. 2009). On the other hand, highly predictable resource distributions should lead animals to maximize time between revisits to sites, allowing resources to renew nearly fully (Davies and Houston 1981). One could test these predictions by experimentally manipulating resource distributions (to represent varying

magnitudes of predictability along with varying rates of resource renewal). Spatiotemporal UD estimates or path recursion analyses (e.g., Bar-David et al. 2009) could then be used to look for a shift in space-use patterns in response to these manipulations (e.g., from drifting patterns to systematic exploration and revisiting areas within the home range). Importantly, this topic serves to illustrate the importance of and potential for cross-fertilization between theoretical and empirical research (Börger et al. 2008).

Implications of question-specific approaches to home-range analysis.—We have argued that the best approach to analyzing location data will depend on the research question posed. For example, one may prefer KDEs for addressing questions that rely on estimated UDs, whereas using local convex hulls to explore the importance of habitat-edge features on the use of space (Getz et al. 2007; Lichti and Swihart 2011). The assertion that methods should be question-dependent has several other implications for home-range research. First, we may expect researchers to apply a variety of methods for analyzing location data. For comparative studies, however, it is important to standardize sampling and analytical approaches as much as possible (Börger et al. 2006b; Nilsen et al. 2008). Thus, to aid future comparative studies, it will be important to archive raw location data in databases such as Movebank (<http://www.movebank.org/about/index.html>), rather than archive estimates of home-range size (Börger et al. 2006a). Similarly, all relevant metadata and the associated environmental data should be archived. Recently developed software platforms for managing location data may prove useful for this task (e.g., Cagnacci and Urbano 2008). At the same time, we caution against uncritical, automated analyses of data in these systems.

We expect continual development of new approaches to analyzing location data (e.g., Getz et al. 2007; Horne et al. 2007a); one reviewer suggested that the recent availability of high-resolution digital imaging and high-resolution digital elevation maps provide exciting opportunities for exploring home ranges in 3 dimensions (see also Keating and Cherry 2009). Ultimately, new methods should be evaluated in terms of their ability to provide useful answers to specific research questions. Last, we predict that searches for the holy grail of home-range estimators, one that will provide a “one size fits all” approach to data analysis, will continue to fail.

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