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What Is the Proper Method to Delineate Home Range of an Animal Using Today's Advanced GPS Telemetry Systems: The Initial Step

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1. Introduction

The formal concept of an animal's home range, or derivations thereof, has been around for over half a century (Burt 1943). Within this time frame there have been countless published studies reporting home range estimators with no consensus for any single technique (Withey et al., 2001; Laver & Kelly 2008). Recent advances in global positioning system (GPS) technology for monitoring home range and movements of wildlife have resulted in locations that are numerous, more precise than very high frequency (VHF) systems, and often are autocorrelated in space and time. Along with these advances, researchers are challenged with understanding the proper methods to assess size of home range or migratory movements of various species. The most acceptable method of home-range analysis with uncorrelated locations, kernel-density estimation (KDE), has been lauded by some for use with GPS technology (Kie et al., 2010) while criticized by others for errors in proper bandwidth selection (Hemson et al., 2005) and violation of independence assumptions (Swihart & Slade 1985b). The issue of autocorrelation or independence in location data has been dissected repeatedly by users of KDE for decades (Swihart & Slade 1985a; Worton 1995, but see Fieberg 2007) and can be especially problematic with data collected with GPS technology.

Recently, alternative methods were developed to address the issues with bandwidth selection for KDE and autocorrelated GPS data. Brownian bridge movement models (BBMM), which incorporate time between successive locations into the utilization distribution estimation, were recommended for use with serially correlated locations collected with GPS technology (Bullard 1999; Horne et al., 2007). The wrapped Cauchy distribution KDE was also introduced to incorporate a temporal dimension into the KDE (Keating & Cherry 2009). Improvements were developed in bandwidth selection for KDE

(e.g. solve-the-equation, plug-in; Jones et al., 1996; Gitzen et al., 2006) and biased random walk bridges were suggested as movement-based KDE through location interpolation (Benhamou & Cornelis 2010; Benhamou 2011). Other methods incorporated movement, habitat, and behavior components into estimates of home range that included model-supervised kernel smoothing (Matthiopoulos 2003) or mechanistic home-range models (Moorcroft et al., 1999). Finally, local convex hull nonparametric kernel method, which generalizes the minimum convex polygon method, was investigated for identifying hard boundaries (i.e. rivers, canyons) of home ranges but has not been evaluated with GPS datasets with >1,000 locations (Getz & Wilmers 2004; Getz et al., 2007). The multitude of advanced methods, lack of standardized procedures for setting input parameters, and advancements in theory makes it an arduous task for researchers to select the methods that best suit their needs.

As GPS technology advances so has the software available. Several researchers have summarized software available to analyze KDE, most often as extensions for Geographic Information System (GIS) software such as the Home Range Tools extension (Rodgers & Kie 2010) for ArcMap 9.x (ArcMap; Environmental Systems Research Institute, Redlands, CA; Lawson & Rodgers 1997; Kernohan et al., 2001). For details on software cost, operation systems compatibility, distributors, and bandwidth selection available for KDE see Larson (2001), however, some of these software have since been updated or lost technical support within the past several decades. Also in the past decade, the increased popularity of the freely available, open-source software Program R (R Foundation for Statistical Computing, Vienna, Austria; hereafter referred to as R) resulted in the development of R packages to estimate KDE home ranges. Estimates of BBMM home range can be calculated in R packages (BBMM, Nielson et al., 2011; adehabitat, Calenge 2006) and the independent Animal Space Use software (beta version 1.3; Horne et al., 2007). Here, we restricted our analyses to use of adehabitat (Calenge 2006) and ks (Duong 2007) R packages for KDE and package BBMM (Nielson et al., 2011) to calculate BBMM home range. We acknowledge that some estimation methods (e.g. LoCoH) or software (e.g. BBMM function in adehabitat) are absent from our analyses; however, our goal was not to provide a complete comparison of all methods, but rather to use freely available methods and software to highlight the challenges of estimating home range with large GPS datasets.

Our review detailed proposed methods to use on autocorrelated locations that are common in GPS datasets and explain the abilities of software, or lack thereof, to calculate home range of animals. Specifically, we focused on 4 key considerations researchers must address during the study design stage that include: 1) GPS collar function parameters, 2) bandwidth selection for KDE, 3) Brownian bridge movement models, and 4) comparison of methods to estimate home range. We used 5 large datasets collected on 2 terrestrial mammalian species [black bears (*Ursus americanus*), Florida panther (*Felis concolor coryi*)] and 3 avian species [black vulture (*Coragyps atratus*), turkey vulture (*Cathartes aura*), American White Pelicans (*Pelecanus erythrorhynchos*)] to explore relationships between the 4 key considerations outlined above (Table 1). When feasible, we will discuss the topic with examples and will suggest pertinent literature for additional details. Our attempt here is to assist researchers using GPS technology for home range analysis by recommending current methods to analyze data but is not intended to be a validation of any method described herein.

Species (sample size)	Number of locations		GPS schedule
	Mean (median)	Range (min-max)	
Black bear (n=10)	5,898 (5,577)	4,057–7,856	1 point per 15 min to 1 hr (variable season schedule)
Florida panther (n=10)	4,536 (3,370)	1,154–10,730	1 point per 15 min to 7 hr (variable collar schedule)
Black vulture (n=5)	7,257 (7,182)	5,690–9,477	1 point per 1 hr (dawn-dusk)
Turkey vulture (n=5)	8,078 (8,593)	2,377–11,455	1 point per 1 hr (dawn-dusk)
American White Pelican (n=10)	4,000 (3,399)	1,579–10,536	1 point per 1hr (dawn-dusk)

Table 1. Species, number of locations, and GPS collection schedule for datasets used for estimating size of home range.

2. GPS collar function parameters

Rapid development of GPS-based telemetry systems during the past two decades has led to numerous improvements in size, performance, and data transfer capabilities (Tomkiewicz et al., 2010). Potential disadvantages of GPS telemetry are substantial costs of GPS radiocollars, which often leads to smaller sample sizes and potentially inappropriate population-level inferences (Hebblewhite & Haydon 2010). In certain instances, manufacturers of GPS radiocollars may not understand the need of wildlife professionals and research objectives or the GPS technology may limit the desired data precision. Fix rates for GPS technology are beyond the control of manufacturers and, in some instances, related to movement rates (Dennis et al., 2010; Cappelle et al., 2011), habitats occupied (Lewis et al., 2007; Nielson et al., 2009), topographical ruggedness (D'Eon et al., 2002; Cappelle et al., 2011), type of battery power (e.g. solar vs. lithium; Cappelle et al., 2011), and temporal duration of the study (Kernohan et al., 2001). Here we discuss the nature, and the spatial and temporal context of the data collected that researchers need to consider when using GPS data for home range estimation.

2.1 Data truncation

Some GPS platform transmitter terminals lack the required precision needed for closely spaced points, truncating locations onto a grid of points thus eliminating accurate representation of animal location regardless of GPS accuracy (Fig. 1). Radiotelemetry and

GPS transmitter error has long been documented in wildlife research (D'Eon et al., 2002; Gilsdorf et al., 2008), however, manufacturer programmed or hardware limitation truncation of location coordinates is poorly understood. Truncation or rounding of decimal places will result in many duplicate locations for species that roost or den in the same location repeatedly. Most researchers are likely not aware of this issue that has significant implications to the final conclusions drawn from collection of GPS locations. Researchers need to know that truncated locations exist by some GPS radio-collars and that complications during data analysis and estimates of home range may result (see section 3.2). There are possible methods to address this issue (i.e. random generation of locations within a certain distance from duplicate locations), however, reliability of estimates of home range have not been evaluated.

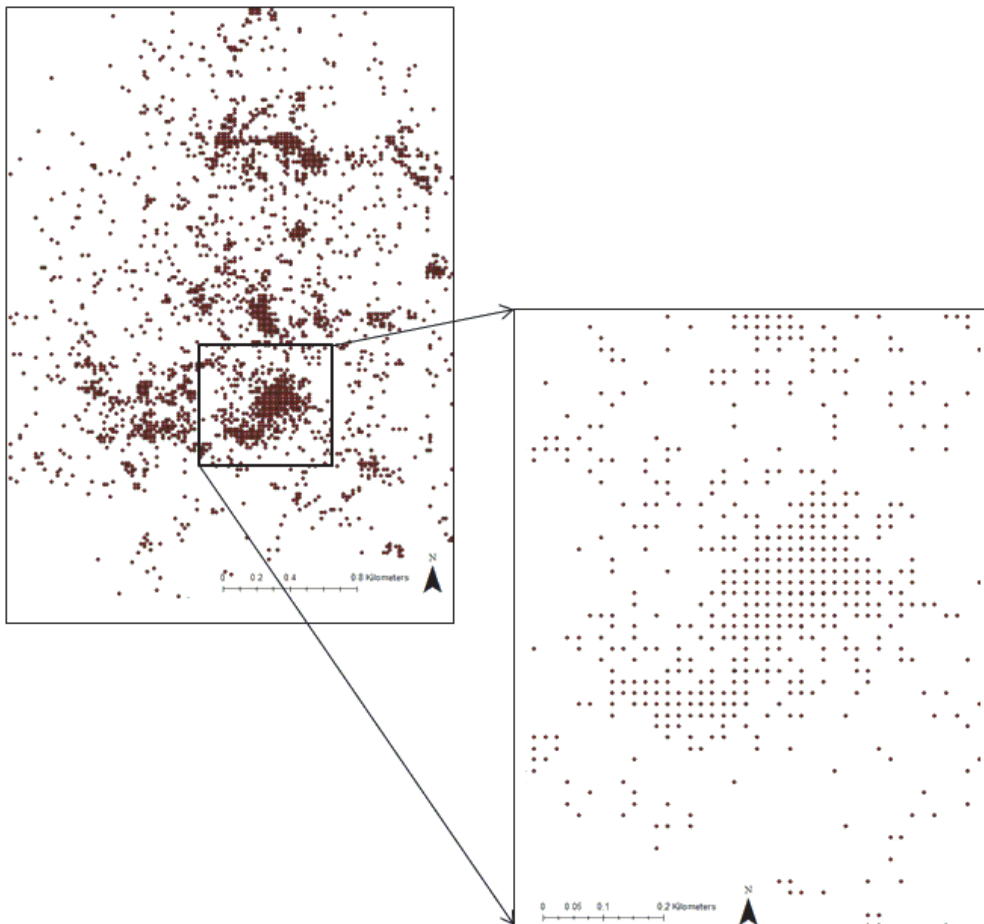


Fig. 1. Locations of a black vulture displaying the grid structure resulting from truncation of GPS coordinates.

2.2 Temporal context of data

When designing a study to analyze home ranges, time duration between successive locations is an important component to consider. Attempts at fix rates can be decreased to extend battery life for most GPS units or increased to identify detailed, real-time movements. Several manufactures provided the option of remotely downloading data to a server so locations are gathered weekly, approaching study animals within a certain distance to download locations, or store-on-board GPS units with drop-off mechanisms and VHF signals that researchers use to track and retrieve collars (Clark et al., 2006). Beyond the obvious trade-off between increased sampling effort and decreased battery life, seasonal and diel behavior of the species should be considered as it can greatly affect the resulting home range estimate depending on the data collection schedule used. For example, large data intervals can occur from failed GPS fixes or when the collar was programmed to turn off. Failed fixes can also occur for species fitted with solar-powered GPS collars that failed to charge the battery or for species that den or hibernate that had transmitters that were turned off to conserve battery life and to decrease duplicate locations. Therefore, depending on collection schedule, ecology of the species, and method of home range analysis, greater uncertainty can be associated with certain areas of the home range resulting in different levels of inference.

2.3 Spatial context of data

Various coordinate systems have been developed for different areas of the world that provides a common geographic framework to perform spatial analysis. Choosing the correct coordinate system for data analysis requires knowledge of the spatial distribution and extent of GPS points. Use of the geographic coordinate system (i.e. latitude, longitude) is recommended in cases of long distance movements and is often the default geographic collection method for GPS collar data. However, some home range software (e.g. BBMM package in R) requires input coordinate data to be in meters. This is challenging when global positioning system technology has been used to document movements of wildlife that migrate long distances (Mandel et al., 2008; Sawyer et al., 2009; Takekawa et al., 2010). For example, American White Pelicans captured in Louisiana, USA were tracked into southern Canada (D.T. King, National Wildlife Research Center, unpublished data). With such movements, a single American White Pelican could occupy 5 Universal Transverse Mercator (UTM) zones during migrations from southern to northern latitudes (Fig. 2). Therefore, BBMM analysis of home range of American White Pelican in the USA might be best depicted using Albers Equal Area or Lambert Conformal. Home range can be estimated for many animals within their respective UTM zone if GPS locations do not extend outside of more than one zone.

3. Bandwidth selection for kernel density estimation

In KDE, a kernel distribution (i.e. a three-dimensional hill or kernel) is placed on each telemetry location. The height of the hill is determined by the bandwidth of the distribution, and many distributions and methods are available (e.g. fixed versus adaptive, univariate versus bivariate bandwidth; for a complete review see Worton 1989; Seaman & Powell 1996). The study extent is then gridded with evaluation points in which different kernels are summarized to produce a utilization distribution across the area of interest. The resulting utilization distribution is therefore sensitive to the resolution of the evaluation grid, and more importantly, to the bandwidth selection (i.e. smoothing parameter) of the kernels.

Because GPS data are autocorrelated, they can pose difficulties in estimating the bandwidth (Gitzen et al., 2006) and violate the assumption of independence of locations that is inherent to KDE (Worton 1989). Therefore, although previous research on principles of bandwidth selection and selection of software is suitable for some datasets (e.g. VHF sampling protocols; Seaman et al., 1999; Gitzen et al., 2006; Kie et al., 2010), GPS datasets present additional challenges that need to be addressed (Amstrup et al., 2004; Hemson et al., 2005; Getz et al., 2007).

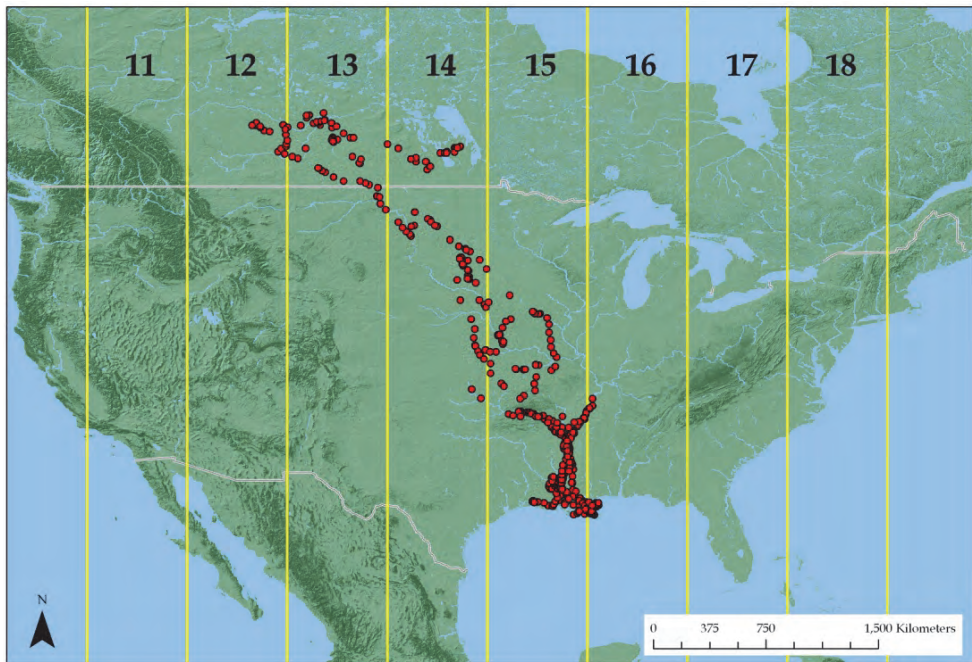


Fig. 2. Multiple Universal Transverse Mercator zones traversed by a migratory American White Pelican in the U.S.

3.1 Default (reference) bandwidth estimation

Datasets for avian and mammalian species can include as many as 10,000 locations and only the reference or default bandwidth (h_{ref}) was able to produce KDE in both Home Range Tools and adehabitat. Estimation with h_{ref} typically is not reliable for use on multimodal datasets because it results in over-smoothing of home ranges and multimodal distribution of locations is typical for most species (Worton 1995; Seaman et al., 1999). An important point to consider with previous investigations on bandwidth selection is that analyses used simulated data on only 10–1,000 locations for assessing reliability of h_{ref} (Seaman et al., 1999; Lichti & Swihart 2011). Still, results from simulated datasets and real-world examples concluded that h_{ref} should not be used on multimodal data typical for most mobile species (Worton 1995; Seaman & Powell 1996; Hemson et al., 2005). Our results confirmed that over-smoothing is considerable, especially for migratory avian species that migrate across vast geographic areas. For example, a turkey vulture that traversed from South Carolina to

Florida, USA, had a 95% home range calculated with h_{ref} that extended inland and into the Atlantic Ocean to areas locations were not even identified (J.W. Fischer, National Wildlife Research Center, unpublished data; Fig. 3).

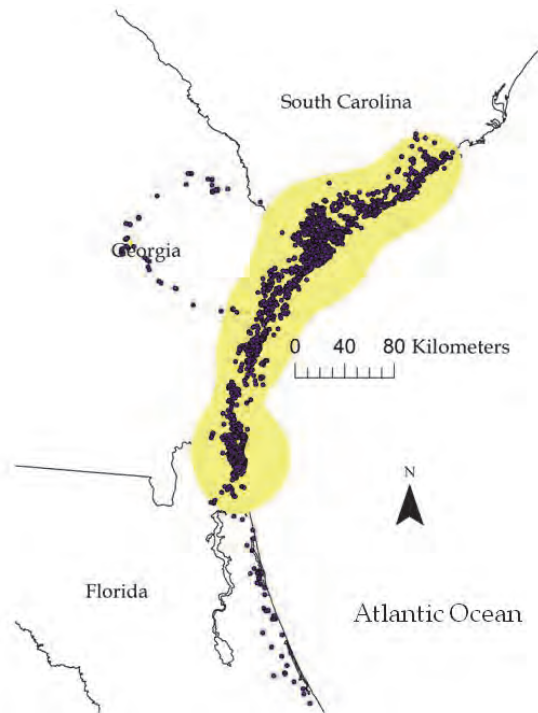


Fig. 3. Home range (yellow polygon) of a migratory turkey vulture from South Carolina to Florida, USA as estimated using KDE with h_{ref} bandwidth selection over-layed on actual GPS locations. Note that KDE occurs inland and into Atlantic Ocean where no GPS locations were collected.

An additional practical problem we encountered with h_{ref} in adehabitat is that the extent of the generated home range polygon was truncated or not generated at all because a greater extent for evaluation points needed to be specified. To work around this issue, we created an evaluation grid of increased extent and iteratively re-estimated the home range until a large enough extent was specified and all isopleth (i.e. probability contour) polygons were successfully created.

3.2 Least squares cross-validation bandwidth estimation

Both the least squares cross-validation (h_{lscv}) and bias crossed validation (h_{bcv}) have been suggested instead of h_{ref} in attempts to prevent over-smoothing of KDE (Rodgers & Kie 2010). However, h_{lscv} and h_{bcv} have been minimally evaluated on GPS datasets because previous literature only evaluated datasets collected on VHF sampling protocols or simulated data that included at most 1,000 locations and did not represent actual animal distributions (Worton 1995; Gitzen et al., 2006; Lichti & Swihart 2011). Least-squares cross

validation, suggested as the most reliable bandwidth for KDE (Worton 1989), was considered better than plug-in bandwidth selection (for description see 3.3) at identifying distributions with tight clumps of points but risk of failure increases with h_{lsbv} when a distribution has a “very tight cluster of points” (Gitzen et al., 2006; Pellerin et al., 2008). Several of our species could be classified as having “very tight cluster of points” because American White Pelican locations were truncated to a grid with multiple overlapping points, vultures occupied the same roosts at dusk and dawn, or black bears rested in day beds. Considering that none of our datasets resulted in converged h_{lsbv} or h_{bcv} estimates for home range calculation, our results on several species further supported the contention that h_{lsbv} and h_{bcv} bandwidths are not suitable for GPS-derived datasets, unless convergence issues at sample sizes $>1,000$ locations and with clumped distributions can be resolved (Amstrup et al., 2004; Hemson et al., 2005). One way to address lack of convergence due to large datasets is subsampling (Avery et al., 2011) that can be used for crude estimates of home range using KDE with h_{lsbv} . We conclude with others in cautioning against subsampling as it only serves to potentially remove important movement parameters or habitats used and will not result in the same estimate of home range size as the complete GPS dataset (Blundell et al., 2001; Pellerin et al., 2008; Rodgers & Kie 2010).

3.3 Plug-in bandwidth selection

Most first generation methods of bandwidth selection for density estimation (i.e. h_{lsbv} , h_{bcv}) were developed before 1990 but advances in theory and technological capabilities has opened the door for second generation methods (Jones et al., 1996). Second generation methods, such as the smoothed bootstrap and plug-in methods (often combined into the solve-the-equation plug-in method; Jones et al., 1996), appear to be an improved alternative because of better convergence and reasonable tradeoffs between bias and variance compared to first generation methods (Jones et al., 1996; Duong & Hazelton 2003, but see Loader 1999). Debate about the appropriateness of second generation methods still exists with some claiming the estimates obtained with bivariate plug-in bandwidth selection ($h_{\text{plug-in}}$) performs poorly compared to first-generation methods (Loader 1999) while others showed it performed well even when analyzing dependent data (Hall et al., 1995).

Using $h_{\text{plug-in}}$ in ks, we were able to calculate KDEs for the sample GPS datasets on 3 avian species and 2 mammalian species where first generation methods (h_{lsbv}) failed or generated a considerably over-smoothed KDE (h_{ref}). While home range polygons generated with $h_{\text{plug-in}}$ appeared fragmented, they may be appropriate when studying a species in highly fragmented landscapes such as urban areas. Based on our results and previous research, conclusions presented in Loader (1999) should be re-evaluated for analyses of large GPS dataset because sample size and clumping of locations has consistently failed using h_{lsbv} , while $h_{\text{plug-in}}$ estimates converged for large multimodal datasets and resulted in reasonable estimates (Girard et al., 2002; Amstrup et al., 2004; Gitzen et al., 2006).

4. Brownian bridge movement models

The concept of BBMM is based on a Brownian bridge with the probability of being in an area dependent upon the elapsed time between the starting and ending locations (Bullard 1999; Horne et al., 2007). The BBMM “fills in” the space between sequential locations irrespective of the density of locations where the width of the Brownian bridge is

conditioned only on the time duration between the beginning and ending locations for each pair of locations and GPS location error. As such, BBMM is able to predict movement paths that otherwise would not be observed with KDE methods. While some authors have suggested using $\leq 90\%$ home range contours (Borger et al., 2006; Getz et al., 2007) to remove outliers or exploratory movements for KDE, increasing size of home range from 95% to 99% for BBMM does not over-smooth the utilization distribution but rather serves to more accurately define the area of use for some species (e.g. Fig. 4; Lewis 2007). Therefore, BBMM intuitively appears better suited for mammalian and avian species that migrate or travel long distances (Sawyer et al., 2009; Takekawa et al., 2010; J.W. Fischer, National Wildlife Research Center, unpublished data).

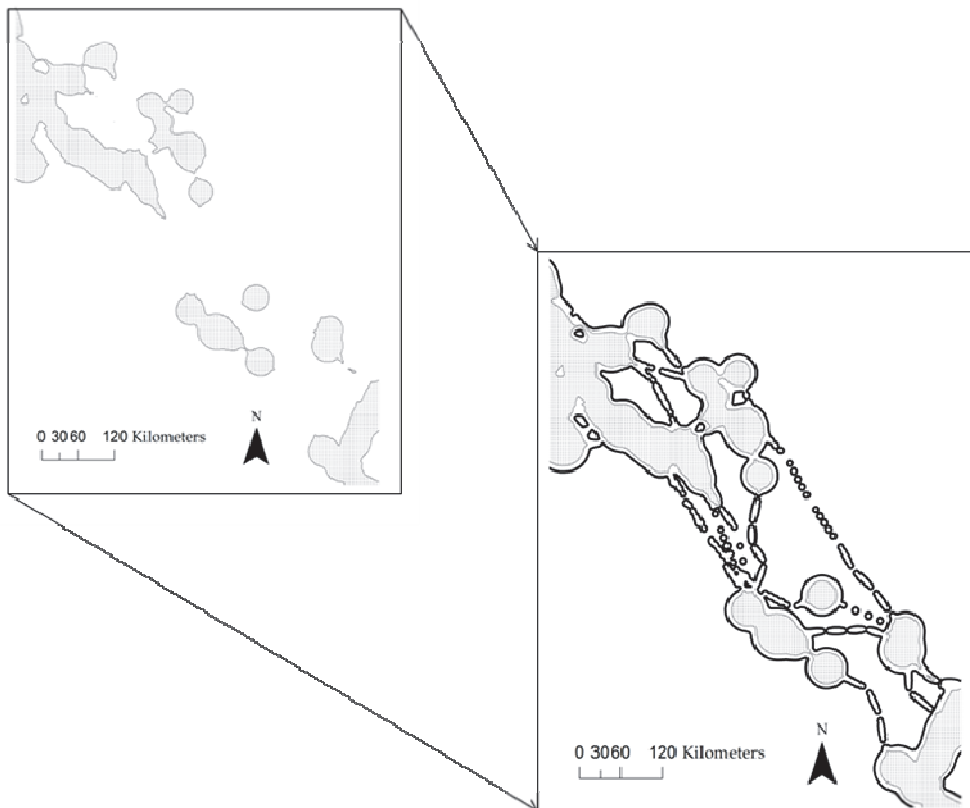


Fig. 4. Home range of an American White Pelican using 95% BBMM (outset) with 99% BBMM connecting potential used habitats in some areas of the home range (inset).

4.1 Time interval between locations

Although equal time intervals between successive relocations are not, in theory, a requirement of BBMM, the method uses a Brownian bridge to estimate the probability density that the animal used any particular pixel, given its relocations. The "shape" of the

Brownian bridge characterizing two successive relocations is adjusted as a function of the time lag separating these two relocations: if the time lag is short, the bridge will be narrower than if the time lag is long. Even though this approximation may be useful to account for movement constraints (e.g. an animal cannot move 20 km in two minutes), its implications may be problematic if the time lag between successive relocations is highly variable such as with relocations separated by time lags distributed over several orders of magnitude (e.g. days to weeks).

The variability in time lag between successive locations was important to consider for several of our species and resulted in size of home range 1.5 to 2 times larger when not accounting for time lag (Fig. 5). The GPS collars deployed on vultures were programmed to only turn on during the local dawn-dusk period, thus time lags occurred for black vultures (mean = 114 min \pm 229 SD) and turkey vultures (mean = 103 min \pm 162 SD) while on roost during nocturnal hours (Beason et al., 2010). Time lag was important for black bears (mean = 49 min \pm 199 SD; Fig. 5a) due to screening and removal of position dilution of precision of GPS fixes and lack of GPS fixes for Florida panther (mean = 214 min \pm 152 SD) in upland forest and cypress swamps. American White Pelican (mean = 359 min \pm 1,633 SD; Fig. 5b) covered up solar panels of the GPS harness or occupied habitats that prevented the battery from maintaining a full charge thereby not allowing GPS data logging upon fix attempt (Cappelle et al., 2011). To improve results, we chose a crude approach to eliminate the top 1% of outliers of time difference such that 99% of the original data were included (O_{REM}). We estimated O_{REM} for each individual animal so inclusion criterion varied across individual for each species. After implementing O_{REM} that resulted in removal of locations, we re-calculated BBMM for black bear (Fig. 5c) and American White Pelican (Fig. 5d), that represented more realistic home ranges by only including time intervals ≤ 182 min and ≤ 69 hours for an individual black bear and American White Pelican, respectively.

We followed this method for all species and present the ratio of sizes of home range for the full dataset with all locations to a limited dataset after implementing O_{REM} (Table 2). An alternative approach could be to use the median distance between successive locations as suggested by Benhamou (2011). While O_{REM} may seem reasonable for some species and studies in eliminating large time differences and resulting in tighter home ranges, we caution researchers from using such an approach without considering its implications to the ecological questions at hand and prior to determining distribution of time differences with locations from each study animal.

Home range	Black bear	Florida panther	Pelican	Black vulture	Turkey vulture
50%	2.5 (1.3)	1.0 (0.04)	2.3 (2.3)	1.4 (0.4)	1.3 (0.5)
95%	2.2 (1.6)	1.0 (0.02)	1.6 (0.8)	1.3 (0.5)	1.1 (0.1)
99%	2.3 (1.7)	1.0 (0.04)	1.5 (0.8)	1.3 (0.4)	1.1 (0.2)

Table 2. Mean (SD) ratio (full/limited) of average 50%, 95%, and 99% home range areas calculated for each species using Brownian bridge movement models with full and limited datasets, where for the latter the top 1% outlier time intervals were removed.

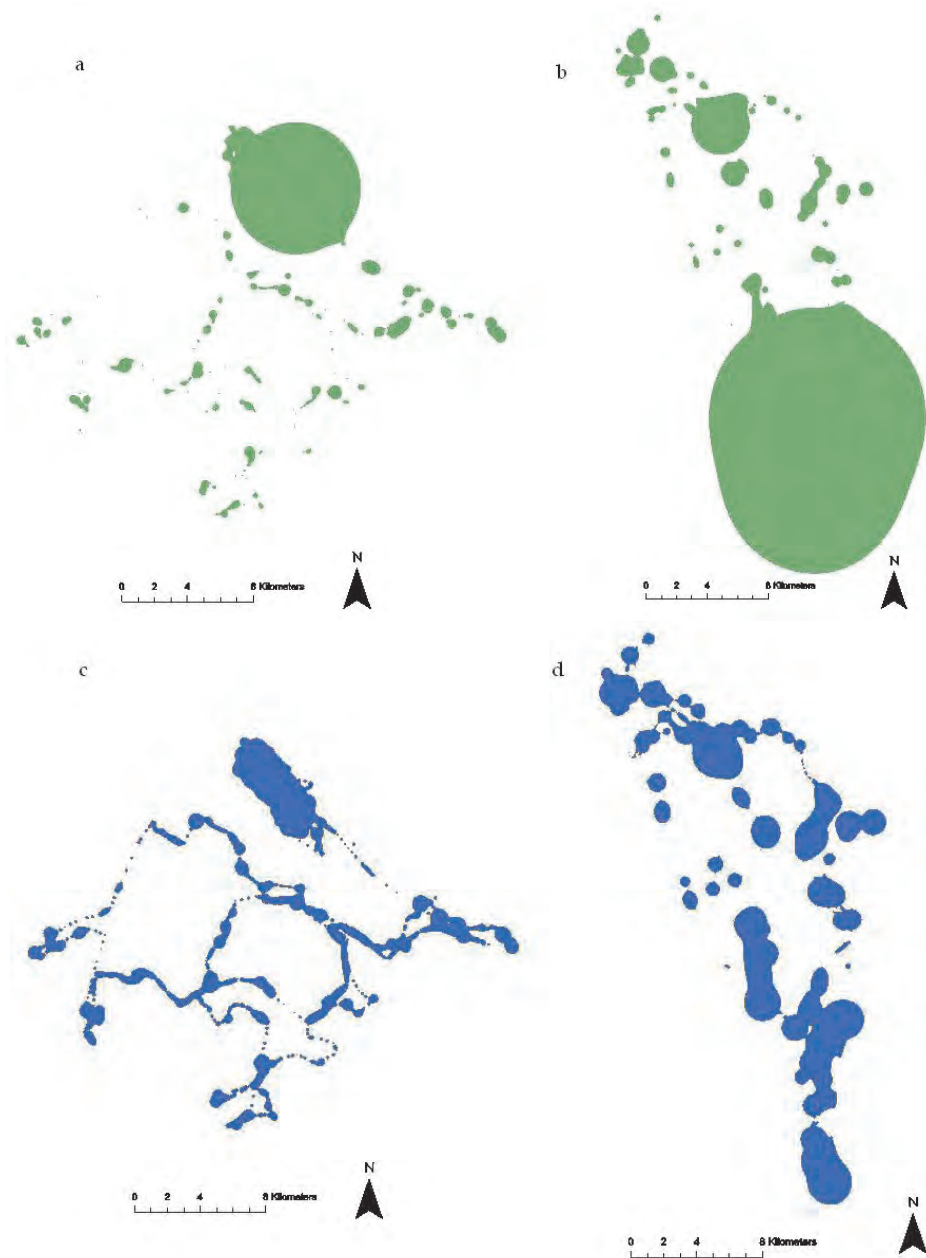


Fig. 5. Example of Brownian bridge movement models with full dataset for an individual a) black bear and b) American White Pelican resulting in a bolus in home range that was removed by excluding the top 1% of time interval for both c) black bear (time interval ≤ 182 min) and d) American White Pelican (time interval ≤ 69 hours).

5. Comparison of home range estimators

Use of BBMM or KDE is dependent on study objectives and should not be considered a similar method to an end result as previously suggested (Kie et al., 2010). Brownian bridge movement models were intended for data correlated in space and time to document the path followed and used by animals (Bullard 1999). Conversely, researchers have stressed the importance of using independent locations to accurately determine areas of use with KDE (Swihart & Slade 1985a; Worton 1989, but see Blundell et al., 2001). Animals that migrate several kilometers or avian species that cover large areas simply are not properly represented using traditional KDE and bandwidth selection common in available home range estimation software. Conversely, KDE with $h_{\text{plug-in}}$ would be better suited for less mobile species occupying patchy environments or small geographic areas because $h_{\text{plug-in}}$ is more conservative resulting in less smoothing than h_{scv} (Gitzen et al., 2006). Use of $h_{\text{plug-in}}$ may also be an appropriate method compared to BBMM when the study focus is on resident or seasonal animal habitat use and exploratory movements are not of interest and should be excluded.

Species	KDE _{href} /KDE _{plug-in}	KDE _{href} /BBMM	KDE _{plug-in} /BBMM
<i>50% contours</i>			
Black bear	7.4 (6.9)	5.0 (7.7)	0.5 (0.3)
Florida panther	2.7 (0.5)	1.0 (0.5)	0.4 (0.1)
White pelican	39.6 (26.0)	15.6 (22.3)	0.3 (0.3)
Black vulture	26.4 (15.4)	2.1 (2.4)	0.1 (0.05)
Turkey vulture	14.9 (17.3)	1.4 (0.9)	0.1 (0.1)
<i>95% contours</i>			
Black bear	4.5 (2.9)	4.5 (6.4)	0.8 (0.6)
Florida panther	2.0 (0.4)	1.3 (0.4)	0.7 (0.1)
White pelican	13.5 (9.5)	10.4 (15.3)	0.5 (0.5)
Black vulture	6.8 (3.6)	1.7 (1.7)	0.2 (0.1)
Turkey vulture	6.9 (3.8)	1.9 (1.2)	0.3 (0.1)
<i>99% contours</i>			
Black bear	3.6 (1.8)	4.6 (6.1)	1.1 (0.9)
Florida panther	1.9 (0.4)	1.5 (0.5)	0.8 (0.2)
White pelican	8.8 (4.9)	9.1 (12.9)	0.7 (0.6)
Black vulture	5.4 (1.9)	1.7 (1.6)	0.3 (0.2)
Turkey vulture	5.7 (2.9)	2.4 (1.6)	0.4 (0.2)

Table 3. Mean (SD) ratio of 50%, 95%, and 99% isopleth home range areas calculated using fixed-kernel home range with default bandwidth (h_{ref}), fixed-kernel home range with plug-in bandwidth selection ($h_{\text{plug-in}}$), and the limited dataset for Brownian bridge movement models (BBMM) for black bears ($n = 10$), Florida panthers ($n = 10$), pelicans ($n = 10$), and black ($n = 5$) and turkey ($n = 5$) vultures equipped with GPS technology.

Ratios of home range areas varied considerably depending on size of home range estimated (50%, 95%, 99%), species studied, and method of home range analysis (Table 3). For all species, all KDE home ranges calculated with h_{ref} were from 2 to 40 times larger than $h_{\text{plug-in}}$ regardless of isopleth (Table 3). These differences were especially pronounced for avian species, and are likely a reflection of the challenges of the univariate kernel bandwidth estimator h_{ref} to capture

the linear movement patterns generated by migratory American White Pelicans and black and turkey vultures, regardless of isopleth. Size of home range using KDE with h_{ref} would likely lead to over-smoothing between migratory locations (but see Blundell et al., 2001). Although we did not separate migratory and resident avian, differences in estimates likely would not be as considerable for avian species with minimal migratory movements. Conversely, we would expect greater differences in estimates for mammalian species that exhibit greater migratory movements such as seasonal migrations in mule deer (*Odocoileus hemionus*; Sawyer et al., 2009) and caribou (*Rangifer tarandus*; Bergman et al., 2000) that are not restricted by considerable roadways and development (i.e. Florida panther) or that occupy urban areas (i.e. black bears) that we assessed in our study. Our results support previous research on smaller datasets that even with serially correlated GPS locations, KDE with h_{ref} over-estimates size of home range compared to $h_{\text{plug-in}}$ (Table 3).

All isopleths of home ranges were only 1 to 16 times larger for KDE with h_{ref} than BBMM. The smaller difference in size of home range between KDE with h_{ref} and BBMM than KDE with h_{ref} and $h_{\text{plug-in}}$ is likely from the inherent nature of BBMM to identify pathways with Brownian bridges. Creating Brownian bridges across sequential GPS locations would be expected to result in larger size of home range than KDE with $h_{\text{plug-in}}$ that conservatively predicts a utilization distribution based on density of locations. Being that KDE has been known to over-smooth utilization distributions with h_{ref} and under-smooth with $h_{\text{plug-in}}$ (Gitzen et al., 2006), we expected BBMM to be in between the 2 bandwidth selections for KDE in size of home range.

Estimates of home range were more comparable for all species and isopleths between KDE with $h_{\text{plug-in}}$ and BBMM but $h_{\text{plug-in}}$ estimates were always smaller than BBMM with only one exception (Table 3). The minimal differences in size of home range between KDE with $h_{\text{plug-in}}$ and BBMM is likely only a reflection of identification of exploratory movements with BBMM. Similar to KDE with $h_{\text{plug-in}}$, BBMM conservatively creates a utilization distribution around areas of concentrated use but, unlike KDE with $h_{\text{plug-in}}$, also connects multiple areas of concentrated use. For example, a yearling black bear in an urban area of central Colorado, USA, exhibited exploratory movements that were identified with BBMM but not with KDE with $h_{\text{plug-in}}$ (Fig. 6). Actual size of home range for defining available habitats for analysis of resource selection may be more accurately depicted using KDE with $h_{\text{plug-in}}$ because it identified concentrated areas of use and not exploratory pathways that were not visited and are not necessary to an animal's fitness.

Across several avian and mammalian species, we identified similar general patterns of size and shape of home range for KDE with h_{ref} and $h_{\text{plug-in}}$ and BBMM. For example, 95% KDEs with h_{ref} (Fig. 7a) and KDE with $h_{\text{plug-in}}$ (Fig. 7b) bandwidths either over-smoothed or under-smoothed, respectively, size of home range of a Florida panther around agricultural habitats while BBMM (Fig 7c) identified a path around agricultural patches. Regardless of estimation method used, tradeoffs between depicting areas traversed or habitats occupied need to be considered in choosing KDE or BBMM. Use of KDE with h_{ref} or $h_{\text{plug-in}}$ may be alternatives to minimum convex polygon for resource selection studies to determine available resources under Type II or Type III study designs (Manly et al., 2002). Assessment of migration routes or commonly used travel corridors would be better represented by BBMM because bridges identify the pathways used by animals as they traverse their home range or explore new territories (Fig. 7c).

Wildlife derived GPS datasets require dedicated software and analysis tools for researchers to understand an animal's movements, behavior, and habitat use. The most well known program

to calculate KDE (ArcView version 3.x) is not directly compatible with 64-bit computer operating systems and current extensions in the newer versions of ArcMap 9.x do not offer the flexibility in several components (i.e. batch-processing, bandwidth selection) afforded by earlier versions of ArcView 3.x, are unable to handle thousands of locations and overlapping coordinates (e.g. Home Range Tools), or were incorporated into the Geospatial Modelling Environment that requires ArcMap 10.x (i.e. Animal Movement Extension, Hawth's Tools; www.spatialecology.com). Furthermore, several studies have indicated that size of home range calculated with KDE differed with each program by as much as 20% for 95% contours (Lawson & Rodgers 1997; Mitchell 2006). Most home range programs require various input parameters or are programmed with defaults that should be considered prior to selecting the program that best suits the needs of the researcher (Lawson & Rodgers 1997; Mitchell 2006; Gitzen et al., 2006). Many new programs to estimate home range are comparable to the graphical user interface of ArcMap (e.g. Quantum GIS, www.qgis.org), require ArcMap and R (e.g. Geospatial Modelling Environment, www.spatialecology.com/gme), or considerably under-estimate home range and require further evaluation (BIOTA, www.ecostats.com; Mitchell 2006). To evaluate every program available would have been beyond the scope of our objectives, so we presented home range estimators in R that is freely available to all researchers.

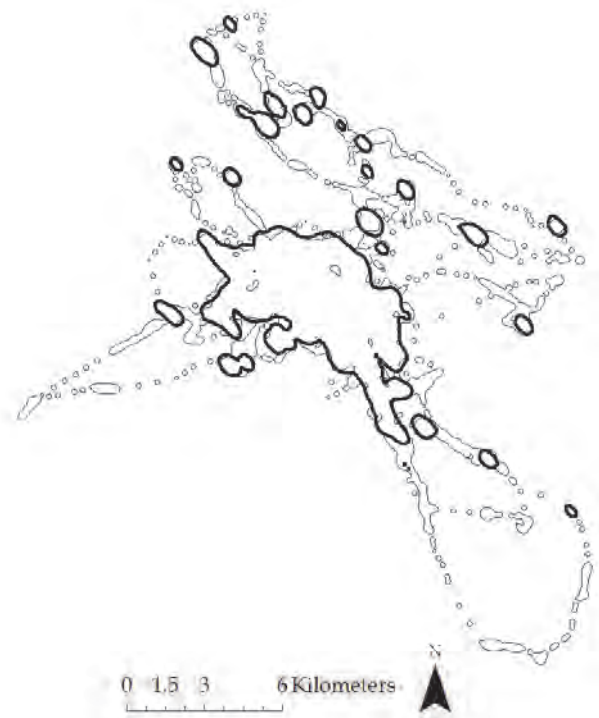


Fig. 6. Home range of a yearling black bear using 95% plug-in with kernel density estimation (thick line) and exploratory movements with 95% BBMM (thin line) prior to dispersal in year 2.

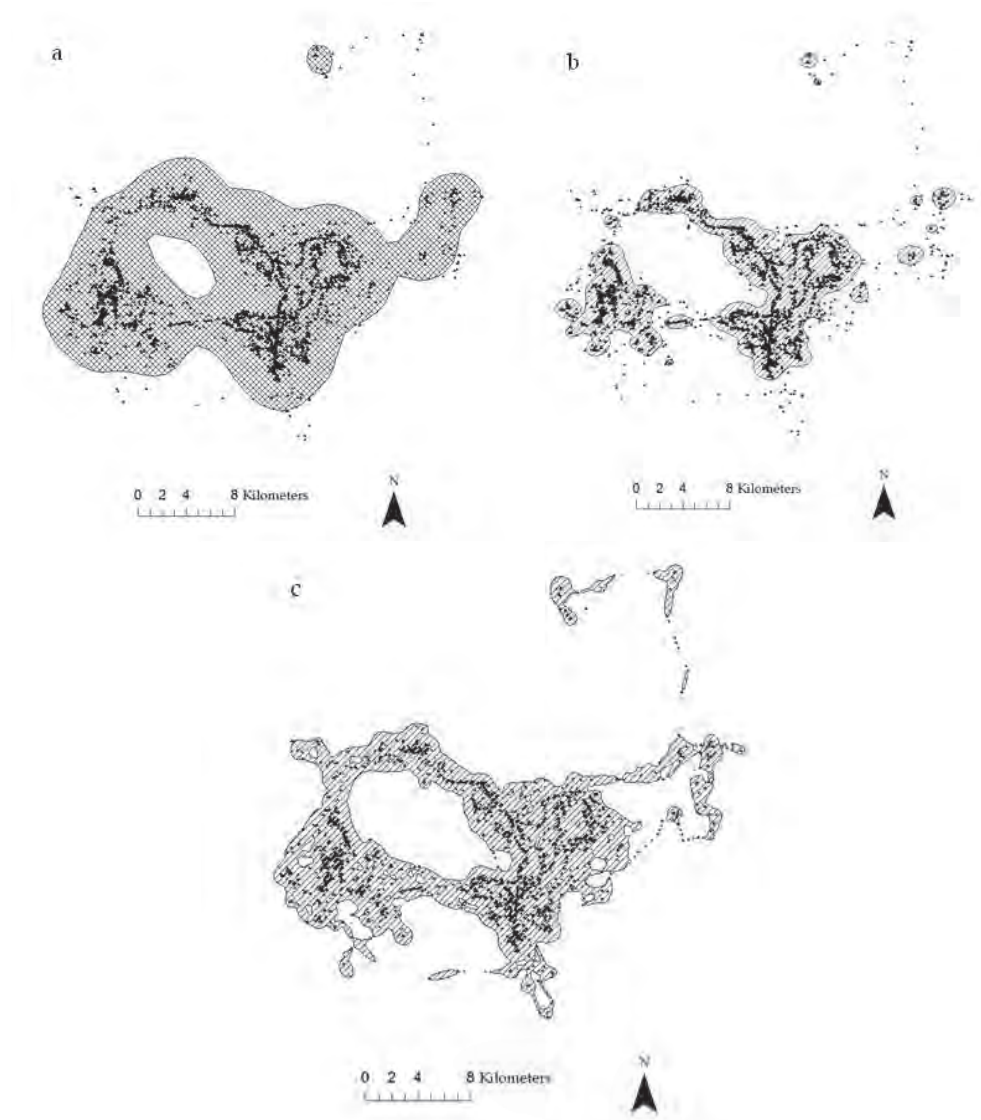


Fig. 7. Comparison of 95% estimates of panther home range derived from kernel density estimation with a) h_{ref} bandwidth selection and b) h_{plugin} bandwidth selection as well as c) a Brownian bridge movement model with GPS locations (•) in background.

6. Conclusions

Our goal was to assist researchers in determining the appropriate methods to assess size and shape of home range with a variety of species and movement vectors. Although we did not set out to assess the accuracy of methods, our results suggested that BBMM and h_{plugin} are

more appropriate for today's GPS datasets that can have >1,000 locations seasonally and up to 10,000 locations annually over a 2–3 year collection period. Of equal importance, we were not able to generate KDE with h_{scv} in Home Range Tools for ArcMap and, to our knowledge, no other software was suitable or reported to determine size of home range for both KDE with $h_{\text{plug-in}}$ and BBMM other than R. The next step of research should focus on alternate software that can be used to estimate size of home range with actual animal GPS datasets. Although all software would likely produce inconsistent home range sizes as previously indicated for earlier programs with VHF datasets (Lawson & Rodgers 1997; Mitchell 2006), the magnitude and reason for differences needs to be understood. Finally, continued assessment of accuracy of estimates of home range is necessary with simulated datasets that range from several thousand to 10,000 serial locations that have defined true utilization distributions to determine proper estimator for size of home range based on study objectives and to verify software reliability.

Further assessment of third generation methods (i.e. mechanistic home-range models, movement-based kernel density estimators) and development of user-friendly packages would be beneficial. As most third generation methods are in their infancy stages of development and evaluation, we are confident that home range estimation will continue to grow and evolve to offer researchers multiple choices for each study species. Undoubtedly, the debate over the proper technique to use should continue but we caution that ecology of the study animal, research objectives, software limitations, and home range estimators should be critically evaluated from the inception of a study (i.e. prior to ordering of GPS technology) to final estimation of size of home range.

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