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Ad hoc smoothing parameter performance in kernel estimates of GPS-derived home ranges

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Accuracy of home-range estimates in animals is influenced by a variety of factors, such as method of analysis and number of locations, but animal space use is less often considered and frequently over-generalized through simulations. Our objective was to assess effect of an ad hoc (*h_ad hoc*) smoothing parameter in kernel analysis from two species that were predicted to have different patterns of utilization distributions across a range of sample sizes. We evaluated variation in home-range estimates with location data collected from GPS collars on two species: mule deer *Odocoileus hemionus* and coyotes *Canis latrans*. We calculated home ranges using 95% and 50% kernel contours using reference (*h_ref*) and *h_ad hoc* smoothing parameters. To evaluate the influence of sample size, we calculated home ranges using both smoothing parameters for random subsamples of 5, 10, 25 and 50% of GPS locations and compared area estimates to estimates for 100% of GPS locations. On mule deer, we also conducted visual relocations using conventional radiotelemetry, which resulted in fewer locations than GPS collars. Area was overestimated at smaller sample sizes, but an interesting pattern was noted with higher relative bias at 60–100 locations than at sample sizes < 50 locations. Relative bias was most likely due to increased smoothing of outer data points. Subsampling allowed us to examine relative bias across a range of samples sizes for the two smoothing parameters. Minimum number of points to obtain a consistent home range estimates varied by smoothing method, species, study duration, and volume contour (95% or 50%). While *h_ad hoc* performed consistently better over most sample sizes, there may not be a universal recommendation for all studies and species. Behavioral traits resulting in concentrated or disparate space use complicates comparisons among and between species. We suggest researchers examine their point distribution, justify their choice of smoothing parameter, and report their choices for home-range analysis based on their study objectives.

Under ideal conditions, space use by animals would be defined by direct, continuous observations; advances in technology have yielded global positioning system (GPS) collars capable of automatically collecting copious amount of data to study animal behavior and ecology (Tomkiewicz et al. 2010), primarily via animal locations. Historic issues arise over the biological concept of home range, statistical calculations and biases resulting from estimators. The mechanisms derived to examine home range have been simulated through various functions assuming a static landscape, but the home range size and shape depends entirely on choices made by the individual animal and therefore, is likely to vary by individual, species, and environmental conditions (Börger et al. 2008, Moorcroft 2012). Our interest is the dynamic nature of home range, particularly associated with large volume GPS data. Therefore, we will quantify variation in home range area estimates for consistent individuals of two different species likely to have disparate space use using a traditional smoothing parameter and one established using a contiguous home range procedure over a range of sample sizes. Our objective in generating these home ranges is to produce consistent spatial representations of areas used by our study animals with a smoothing parameter appropriate for our data. The premise of this study was to look for a consistent home range across smoothing parameters over different sample sizes, species, and distribution contours.

Field studies and computer simulations employing various smoothing parameters and sample sizes on utilization distributions are not new exercises. Kernel analyses are popular because they are nonparametric (Silverman 1986) and produce consistent results (Worton 1989). Bandwidth or smoothing parameter (*h*) has been implicated as the critical choice in kernel density estimation (Kernohan et al. 2001, Hemson et al. 2005) because it determines the width of the kernel, yet there is no method of choosing the best *h* value (Silverman 1986, Worton 1989, White and Garrott 1990). Small values of *h* can cause the estimated kernel density function to break into constituent kernels or 'islands' (i.e. undersmooth) while large smoothing parameters overly expand estimates (i.e. oversmooth, Kernohan et al. 2001). Post hoc methods of choosing *h* may be warranted, particularly with large sample sizes generated by GPS data. The reference (*h_ref)* smoothing parameter is calculated from the distribution of points, but it tends to oversmooth multimodal distributions from clumped locations resulting in overestimated home-range sizes (Kernohan et al. 2001). Use of a smoothing parameter that minimizes a least-squares cross-validation score (*h_lscv*) has been advocated (Seaman et al. 1999, Kernohan et al. 2001, Girard et al. 2002, Gitzen and Millspaugh 2003), but problems result in undersmoothing GPS data because locations often occur at or near the same point (Hemson et al. 2005, Gitzen et al. 2006). An ad hoc (*h_ad hoc*) smoothing parameter (not to be confused with *h_opt* as described in Worton 1989) may be useful as an alternative to the reference bandwidth to reduce oversmoothing that requires investigators to visually inspect home ranges and manually adjust *h* values. Use of the *h_ad hoc* smoothing parameter incorporates researcher examination applied under a consistent and replicable rule (Berger and Gese 2007, Klaver et al. 2008, Jacques et al. 2009, Grovenburg et al. 2011).

In addition to searching for an efficient and unbiased smoothing parameter, we chose to examine the resulting influence of sample size on area distributions (Harris et al. 1990, Powell 2000) to achieve consistent estimates. There has been no universal method to determine necessary sample size, as evidenced by various recommendations, which range from 20 or 30 locations (Silverman 1986, Gese et al. 1990, Seaman et al. 1999, Pellerin et al. 2008) to 200 (Laundré and Keller 1984, Harris et al. 1990, Garton et al. 2001) or more (Gautestad and Mysterud 1995, Girard et al. 2002) depending on methodology. Larger sample sizes that can be acquired with GPS technology may render this argument irrelevant (Walter et al. 2011), although use of subsampling or incremental analysis for comparison studies revives the issue (Börger et al. 2006, Pellerin et al. 2008), especially in studies that deploy both VHF and GPS collars (Hebblewhite and Haydon 2010) such as ours.

Contour area is most commonly estimated for outer boundaries of animal use or for core areas that usually are an inner contour, which demonstrates multiple centers of activity (Harris et al. 1990). Consequently, bias in one contour area may not be equivalent to biases in other estimates (Seaman et al. 1999) across different smoothing parameters. Oversmoothing and undersmoothing were determined by comparing derived area to our largest sample size to obtain a relative bias value assuming that home range estimates reach an asymptote with adequate sample size (McLoughlin and Ferguson 2000).

We evaluated GPS data from coyotes *Canis latrans*, as well as GPS and VHF-telemetry data from mule deer *Odocoileus hemionus* in South Dakota, USA. Locations for mule deer were collected throughout the year whereas those for coyotes were collected around the period when adults were rearing pups. We visually observed these species to have divergent generalized behaviors and foraging patterns (scattered patch searches by mule deer or foraging around a den site by coyotes). Behavioral characteristics of species that vary by season, sex, and available resources resulting in different usage distributions (Gitzen et al. 2006) are rarely considered when making inferences about shared space (Powell and Mitchell 2012).

Material and methods

For all animal captures, we used standard techniques approved by the American Society of Mammalogists (1998), National Park Service (Badlands National Park 2000), and South Dakota State University (Institutional Animal Care and Use Committee Approval no. 02-A036 [mule deer] and no. 02-A042 [coyotes]). In February 2002, we captured and fitted 20 non-migratory adult mule deer (8 males, 12 females) within the Wind Cave National Park, South Dakota, USA with GPS collars (Table 1). Eighteen had data suitable for this study; two deer mortalities resulted in durations < 3 months and were not included. All collars were recovered by November after mortality or remote-release mechanism deployment with an average of 623 locations/deer. An additional 20 mule deer (6 males, 14 females) were GPS collared in the park in January 2003. We released the GPS collars in May 2004 and obtained an average of 1130 locations per deer, 18 had data suitable for this study. GPS collars also were equipped with very high frequency (VHF) radiotransmitters; visual relocations were obtained on mule deer 1–3 times week^{-1}. We recorded deer locations using a handheld GPS unit.

For coyotes, we captured and collared coyotes at Badlands National Park, South Dakota, USA from 2003–2005 in winter and/or early spring (Table 1). Collars were programmed to drop off animals during August after > 6 months of operation. We attempted to catch at least one adult per family unit. Thirty-eight coyotes were fitted with GPS collars during the three years of this project. Data from 14 adult, breeding coyotes (six males, eight females) were used for this analysis. Juveniles and non-breeding adults were not included in this study because data were truncated to only include locations taken during pup-rearing, 1 May to 31 July (Smith et al. 1981).

We analyzed data using Home Range Tools for ArcGIS 9.1 (Rodgers et al. 2007) with default resolution grids and percent volume contours. Locations were converted to shapefiles and mapped. Analyzing GPS and VHF radiotelemetry (from deer) data separately, we calculated 95% and 50% volume contours simultaneously with adaptive kernel analysis (ADK) using two smoothing parameters: 1) reference bandwidth (*h_ref*) and 2) ad hoc bandwidth (*h_ad hoc*) were created by reducing *h_ref* by 10% in successive steps until the 95% contour fractured into two or more polygons (Berger and Gese 2007, Jacques et al. 2009). Adaptive kernel was chosen over fixed kernel based on better performance at the tails of distributions (Worton 1989). Because the researcher chose the *h_ad hoc* bandwidth as the bandwidth applied just prior to fracturing of the outer contour, this process required visual inspection and was not automated. Both contours (95% and 50%) for our home-range estimates were determined using the same smoothing parameter. We did not evaluate *h_lscv* because initial analysis showed that it fractured home ranges into multiple polygons with GPS data because of undersmoothing (Blundell et al. 2001, Seaman and Powell 1996). If *h_lscv* fails, *h_ref* is often used as a default depending on the home-range software (Hemson et al. 2005, Rodgers et al. 2007). We also compared home ranges against 100% minimum convex polygon (MCP) area estimates for 100% of points for *h_ref* and *h_ad hoc*.

To evaluate sample size effects, we created a random subsample without restrictions for 5, 10, 25 and 50% of available locations for each mule deer and coyote (Create Random Selection Tool in ArcGIS 9.1; Hemson et al. 2005, Girard et al. 2006). We assumed the estimate with all the data points was closest to the true value (Girard et al. 2002, Pellerin et al. 2008). To determine relative bias, we divided area generated from each subsample by area calculated from 100% of available locations (Horne et al. 2007). Relative bias was estimated for each individual deer by:

Relative bias = [Area estimate
(subsample) − area estimate (all locations)]/
area estimate (all locations)

We tested the influence on relative bias (arcsine-transformed dependent variable) for 95% (Y_1) and 50% (Y_2) contours from the following independent factors (main effects): individual animals (X_1), smoothing parameter (X_2, *h_ref* or *h_ad hoc*), species (X_3, mule deer or coyote), and number of locations (X_4) using a general linear model with repeated measures (GLM, Systat software 2002, Hemson et al. 2005). We also tested for interactions between all independent factors with GLM. The general linear model presents advantages over multiple regression by allowing linear combinations of multiple correlated variables and ability to analyze effects of repeated measures. Home range area estimates for 100% of GPS data were assessed by adjusted least-square means (LSM, Systat software 2002) for each smoothing parameter. We evaluated subsampled data by 95% confidence intervals (CI) for relative bias estimates to determine if there was overlap with zero, which indicated no difference in relative bias from 100% of GPS locations (Johnson 1999). We also compared 100% of GPS data to VHF radiotelemetry locations of mule deer to determine smoothing parameter performance between methods of data collection (Pellerin et al. 2008). We randomly subsampled GPS data to compare GPS to VHF radiotelemetry with an equal number of locations and generated home range estimates using *h_ad hoc* and *h_ref*. We compared the relative bias and used 95% CI to determine if there was overlap with zero, indicating no difference between VHF and 100% of GPS locations (Johnson 1999), as well as comparison with the subsampled GPS derived home range estimates.

Results

Animal space use and resulting home-range estimates using *h_ref* and *h_ad hoc* smoothing parameters often demonstrated different patterns (Fig. 1, 2). Relative bias for 95% contours (Y_1) was influenced by only individual animal (X_1, $F_{47,339} = 2.326$, $p < 0.001$); the interaction term of smoothing parameter (X_2) and number of locations (X_4) was significant ($F_{1,339} = 4.660$, $p = 0.032$) indicating that the impact of number of locations may depend on the smoothing parameter used. Relative bias estimates for 50% contours (Y_2) were influenced by individual animal (X_1, $F_{47,330} = 1.551$, $p = 0.016$), smoothing parameter (X_2, $F_{1,330} = 10.063$, $p = 0.002$), and number of locations

Table 1. Geographic positioning system (GPS) collar information for animal movement studies in Wind Cave National Park and Badlands National Park, South Dakota, USA. Both studies used GPS collar that stored information and had very high frequency (VHF) transmitters. Collar weight was less than 5% of the animal body weight. Release mechanism and fix schedules were different for each species, but fix success was > 90% for both. Some coyote collars were not recoverable because of release while in dens.

Species	Collar type	Manufacturer	Collar weight (g)	Release mechanism	Fix schedule	Fix success	Recovery success
White-tailed deer	GPS store-on-board	ATS, Isanti, MN, USA	1100	Remote-release	2–3 locations day^{-1}	> 90%	100%
Coyote	GPS 3300	LOTEK, Newmarket, ONT, CAN	< 300	Timed-release (6 months)	1 location every 4 h (06:00–18:00), every hour (18:00–06:00)	> 95%	76%

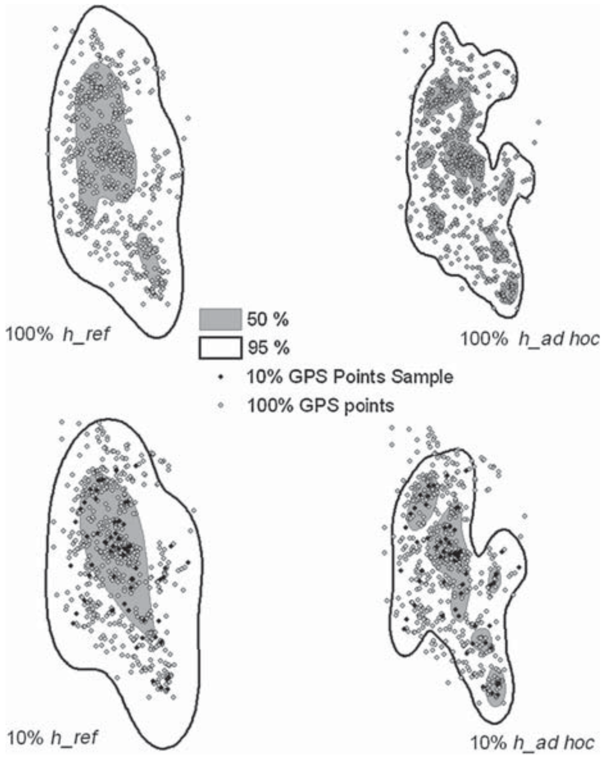

Figure 1. 95% and 50% home-range contours and GPS locations for a female mule deer in Wind Cave National Park, South Dakota in 2003. For home ranges created from 100% GPS locations ($n = 610$, top row), the *h_ref* smoothing parameter (left column) resulted in oversmoothing of the point distribution for both 95% and 50% contours. The *h_ad hoc* smoothing parameter (right column) had a tighter boundary for the 95% contour to the point distribution. For home ranges created from 10% randomly subsampled locations ($n = 58$, bottom row), *h_ref* resulted in oversmoothing and incorporated areas not used by deer; whereas, *h_ad hoc* demonstrated multiple 50% contour areas similar to that with 100% of GPS locations. Multiple core use areas were not included using the *h_ref* smoothing parameter, especially at low sample sizes.

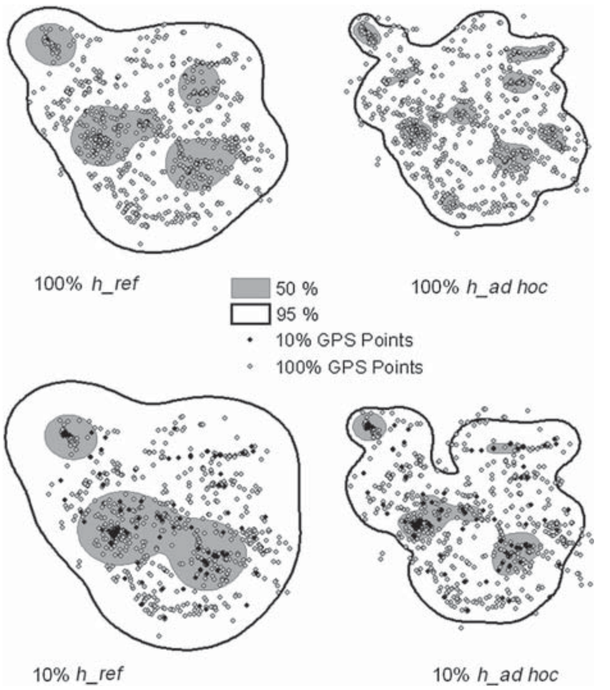

Figure 2. Coyote GPS data ($n = 1011$) for 95% and 50% contours for a female coyote in Badlands National Park, South Dakota in 2004. Home ranges created using 100% of GPS points (top row) had higher oversmoothing and fewer defined core areas with *h_ref* than *h_ad hoc*. Random subsampling for 10% of GPS locations ($n = 101$, black squares) produced home ranges that were considerably oversmoothed for *h_ref*. The *h_ad hoc* smoothing parameter demonstrated a similar boundary pattern for 10% as 100% GPS and delineated similar core use areas.

(X_4, $F_{1,330} = 47.249$, $p < 0.001$); interaction of smoothing parameter (X_2) and number of locations (X_4) was not significant ($F_{1,330} = 1.713$, $p = 0.191$). Species (X_3) did not affect relative bias estimates for either contour (95%: $F_{1,339} = 0.008$, $p = 0.928$; 50%: $F_{1,330} = 1.714$, $p = 0.191$).

Overall, home range area estimates using 100% of the data were two and a half to three times higher for *h_ref* (adjusted LSM: 95% contour = 0.152, 50% contour = 0.117) than *h_ad hoc* (adjusted LSM: 95% contour = 0.048, 50% contour = 0.045) for both contours. Estimates for 100% MCP (adjusted LSM = 0.16) were also consistently higher than 95% contour *h_ad hoc*. Relative bias estimates for the two smoothing parameters were not congruent and varied by number of points; as number of points increased, bias decreased (Fig. 3, 4B). Biases for *h_ad hoc* smoothing parameter decreased to < 10% between 100–125 points and at about 200 points for *h_ref* for both the 95% and 50% contours.

In some analyses, we saw a new trend in relative bias that did not decay as expected. We expected an asymptotic decrease in estimate bias with increasing number of points as is typically seen in area-observation curves (McLoughlin and Ferguson 2000). For deer GPS data, relative bias actually increased for home ranges in the 60 to 100 point range compared with lower sample sizes (< 50 points). With the exception of this range (60–100 points), most 95% confidence intervals for point estimates overlapped zero bias for the 95% contour (Fig. 3A, 4A) indicating bias did not differ significantly between subsamples and the full data-set. Confidence intervals overlapped zero bias at higher point values (> 150–250) for the 50% contour than the 95% contour using *h_ad hoc; h_ref* had fewer instances where relative bias CI overlapped zero (Fig. 3B, 4B). Because these point values were derived from subsamples, they should not be subject to autocorrelation. The coyote data exemplified some of the issues with home-range calculations. We found a similar peak in relative bias for both *h_ref* and *h_ad hoc* at 125 points for the 95% contour (Fig. 4A). Relative bias decreased beyond 125 points with increasing number of points for *h_ad hoc*. Relative bias was < 10% for *h_ref* for 200 points. Confidence intervals for all 95% contour estimates overlapped 0 for *h_ad hoc*, and at highest (CI: 0.00, 0.04) and lowest number of locations (CI: –0.06, 0.26) for coyote home ranges. For the 50% contour, both parameters provided relative bias values that were similar (Fig. 4B). Relative bias values did not decrease to < 10% until about 300 points for both smoothing parameters.

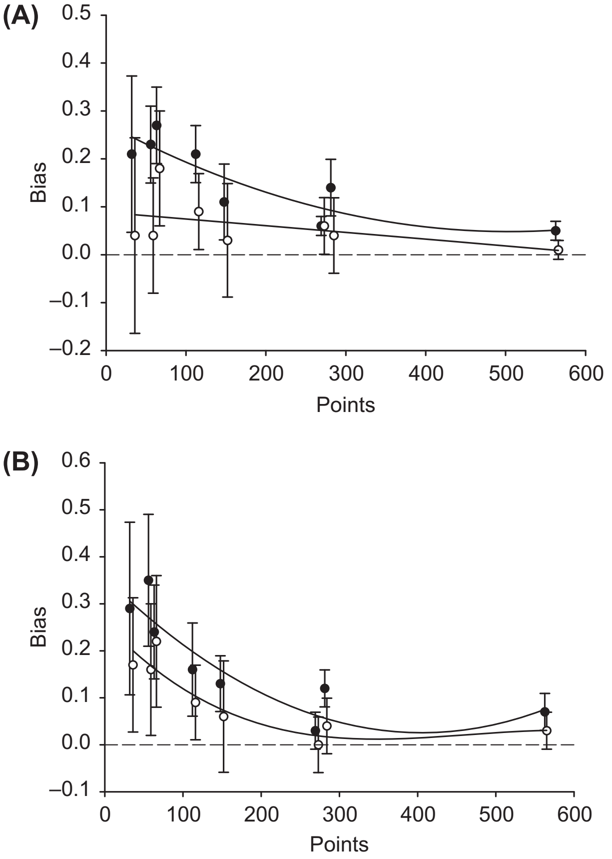

Figure 3. Overestimation values for 95% contours (± 95% confidence interval, (A) and 50% contours (± 95% CI, (B) for GPS random subsamples (averaged by subsample group) from mule deer collared in Wind Cave National Park, South Dakota. Home ranges were calculated using two smoothing parameters: *h_ref* (●) and *h_ad hoc* (○). Smoothing parameters were calculated simultaneously for 95% and 50% contours. The 95% contour (A) had consistently higher relative bias estimates for *h_ref* than *h_ad hoc;* none of the *h_ref* CI overlapped 0 bias so home range area derived from subsamples were not similar to those from the full data set. Depending on the smoothing parameter used, fewer than 100 points are necessary for < 10% overestimation bias using *h_ad hoc* and about 200–300 points for *h_ref*. The 50% contour (B) relative biases in area estimation were higher for *h_ref* than for *h_ad hoc,* but 95% CI did not overlap 0 until ˜300 points. For overestimation bias < 10%, between 100–130 points are necessary for *h_ad hoc* and a wider range of points from 180 to 400 appear adequate for *h_ref*.

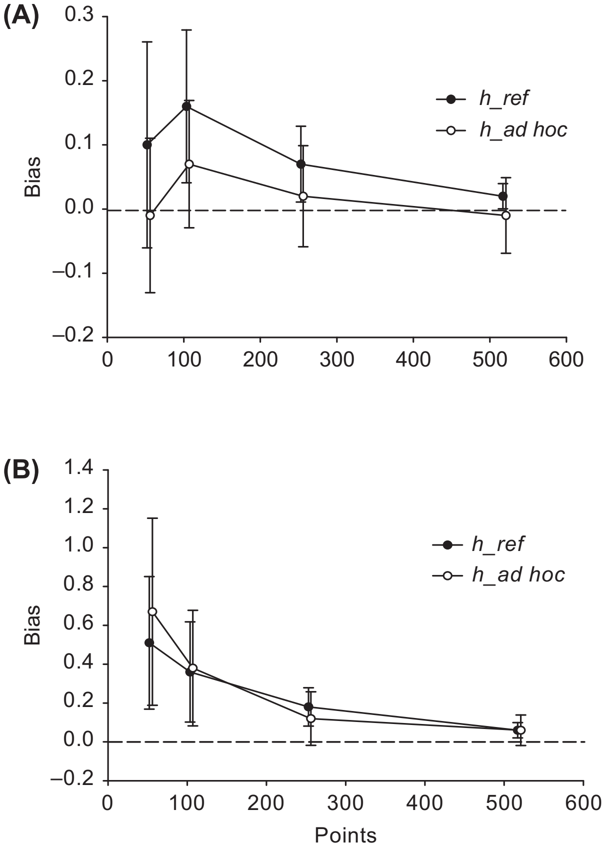

Figure 4. Relative bias plots for 95% (A) and 50% (B) contours (± 95% CI) for coyote GPS data from Badlands National Park, South Dakota. For 95% contours, *h_ad hoc*(○) smoothing parameter provided estimates with less bias than *h_ref* (●) and more CI overlapping zero. For 50% contours, there was no difference between smoothing parameters at higher sample sizes.

Traditional VHF radiotelemetry for mule deer resulted in fewer locations (mean = 55.7 ± 7.2 deer^{-1}) than GPS data and overestimated home range area when compared with estimates derived from all GPS locations at both contours, which was variable across smoothing parameter. The 95% CI for relative bias from the *h_ref* smoothing parameter did not overlap zero for either 95% contour (95% CI for 2002: 0.21, 0.76; 2003: 0.05, 0.39) or 50% contour (95% CI for 2002: 0.05, 0.55; 2003: 0.01, 0.47); in contrast, the *h_ad hoc* smoothing parameter did overlap zero for both 95% contour (95% CI for 2002: –0.26, 0.38; 2003: –0.19, 0.11) and 50% contour (95% CI for 2002: –0.31, 0.33; 2003: –0.15, 0.03). We compared VHF-telemetry data to a comparable sample size derived from a random sample of GPS locations and found that 95% CI included zero for both smoothing parameters at 95% contour (95% CI for *h_ref*, 2002: –0.30, 0.16; 2003: –0.20, 0.34. *h_ad hoc,* 2002: –0.21, 0.23; 2003: –0.27, 0.13) or 50% contour (95% CI for *h_ref*, 2002: –0.1, 0.48; 2003: –0.07, 0.27. *h_ad hoc,* 2002: –0.88, 0.64; 2003: –0.10, 0.30), indicating correspondence between area estimates for both smoothing methods.

Discussion

Kernel estimators combined with technological advances, such as GPS collars, require evaluation of performance with larger datasets (Kie et al. 2010, Tomkiewicz et al. 2010, Walter et al. 2011). Our analysis focused on issues field investigators are capable of manipulating after data collection, such as smoothing parameters, that may be influenced by number of locations, species behavior, and resources. Current recommendations also include evaluation of sampling regime (intensity and duration) to ensure temporal standardization (Börger et al. 2006, Fieberg 2007), beginning before collar deployment. In many situations, visual inspection of GPS data indicated a grouped abundance of locations (Fig. 1, 2). However, we did not know the true home range of the animals for our bias calculations (Seaman and Powell 1996, Blundell et al. 2001); rather, we chose to use a best-estimate home range that was based on the largest number of locations (Girard et al. 2002, Horne et al. 2007, Pellerin et al. 2008) and look for consistency with that measurement (Börger et al. 2008). Using locations from real animals eliminates the artificial environment and distributions created by simulated data that may not accurate reflect animal space use in a dynamic environment.

Variability among individual animals, however, may have resulted in unimodal and multimodal distributions within the same species (Boulanger and White 1990, Börger et al. 2006, Horne and Garton 2006, Moorcroft 2012). Because *h_ref* uses a unimodal normal distribution, it attributed too much variance to multimodal distributions, which resulted in oversmoothing of the data. For example, mule deer data demonstrated larger biases in *h_ref* than coyote GPS data that was collected during pup rearing, when activity likely focused around a central location or multiple centers (i.e. ≥ 1 natal dens, Smith et al. 1981, Boulanger and White 1990). Investigators using *h_ad hoc* can recognize situations where an animal has multiple centers of activity and decrease the smoothing parameter to account for those areas.

As a tradeoff between smoothing parameters produced by reference and least-squares cross-validation algorithms, we modified the reference bandwidth and then used the smallest value of *h* that resulted in a contiguous polygon (*h_ad hoc*, Berger and Gese 2007, Jacques et al. 2009), rather than a set reduction to the *h* value (Pellerin et al. 2008). This method was a consistent rule that eliminated excess area not used by the study animal. Hemson et al. (2005) concluded this type of modification to a smaller multiple of *h_ref* lacked a stable relationship with sample size and was an unsuitable substitute for *h_lscv* failure. We found that *h_ref* was inconsistent and did not have a stable relationship with sample size across species with variable distributions. Generally, less smoothing at large sample sizes reduces bias produced by kernel methods (Fieberg 2007, Downs and Horner 2008); however, we found home range area estimates produced by *h_ref* using 100% of GPS locations was slightly lower than those produced by 100% MCP, but consistently larger than *h_ad hoc.* Across a range of sample sizes, *h_ad hoc* minimized oversmoothing as evidenced by confidence intervals overlapping zero for relative bias more often than *h_ref* in both species for the outer contour.

Without a standardized methodology for home-range generation, justification of analyses chosen should be an integral part of studies using home-range methods (Harris et al. 1990). While fixed kernel with *h_lscv* has been recommended because it minimizes the mean integrated square error (Seaman and Powell 1996, Seaman et al. 1999, Gitzen and Millspaugh 2003), we did not evaluate GPS data with *h_lscv* because it resulted in a highly fractured home range that was not suitable for our study goals. Other studies using GPS collars also indicated that *h_lscv* with fixed kernel failed at higher sample sizes with identical or highly clustered locations typically obtained with GPS data (Gallerani Lawson and Rodgers 1997, Hemson et al. 2005) or linear home ranges (de Solla et al. 1999, Blundell et al. 2001). Other studies used different contour values suitable to their purpose (Marzluff et al. 2004, Kie et al. 2010). Inner contours (defined core areas) are often calculated using the same smoothing parameter as the outer contour. In this analysis, we did not stipulate that the 50% polygon must not fracture, which resulted in multiple use centers. As such, we did not see the consistency across a range of sample sizes in the 50% contour that was evident with the outer 95% contour.

Along with choice of smoothing parameter, investigators must decide on use of global or local bandwidth (Gitzen and Millspaugh 2003, Kernohan et al. 2001). Choice of fixed versus adaptive kernel bandwidth does not affect *h_ref* (Seaman et al. 1999) or *h_ad hoc* smoothing parameters. Our study employed a local bandwidth (adaptive kernel) that assigns more uncertainty to the outer edges of the home range where there are fewer points. This algorithm resulted in higher bias in the 50% contour than the 95% contour, which was similar to findings of Seaman et al. (1999) for fixed kernel analyses.

Given that animals had variable distributions not only between species but during the course of a year and in different habitats (Girard et al. 2002, Börger et al. 2006, Moorcroft 2012), a single standard for minimum number of points is difficult to establish. Examination of chronological location data may provide more insight as to locations that are actually included in a home range versus outliers or occasional sallies as defined by Burt (1943, Powell and Mitchell 2012). There did not appear to be a universal minimum number of locations for home-range estimation for either smoothing parameter. Relative bias increased with number of points for *h_ad hoc* in a range between 60–100 points compared with lower bias at smaller sample sizes (< 50) which was unexpected, although Gautestad and Mysterud (1995) stated that area-observations curves are only valid for unimodal distributions. This increase in bias likely resulted from multimodal distributions that required oversmoothing (i.e. larger value of *h_ad hoc*) because more subsampled points were from the periphery of the distribution; the point distribution was not dense enough near the edges of the home range to prevent fracture of the 95% contour. This was not as apparent for the 50% contour because fracture of the core area contour was permitted. A similar pattern was evident for *h_ref*, but not as consistently. In the range of 60–100 points, both smoothing parameters were likely to oversmooth, but *h_ad hoc* typically had lower relative bias than *h_ref*. This area of increased bias could present serious complications at a point range commonly found in VHF-telemetry data.

Our VHF-telemetry data had substantially fewer locations than GPS data, but *h_ad hoc* produced comparable estimates despite sample differences, akin to the findings of Kochanny et al. (2009), in quantifying home range overlap. Because comparison between animals should employ equivalent sample sizes (de Solla et al. 1999), subsampling can modify sample sizes or timeframe to appropriate levels (Girard et al. 2002, Börger et al. 2006) if necessary, particularly for studies that deploy both GPS and VHF collars (Hebblewhite and Haydon 2010). Reducing the number of GPS locations gave home-range area estimates that were equivalent when compared with VHF-telemetry data using both smoothing parameters. Comparisons by time period also can be achieved via subsampling (de Solla et al. 1999, Pellerin et al. 2008).

Sample size is a consideration in all location studies. Similar to Garton et al. (2001), we found relative bias decreased below 5% around 200 locations/animal for 95% contours with *h_ad hoc* (Fig. 3, 4). However, it was impossible to recommend a minimum sample size due to variability between smoothing parameters. Seaman et al. (1999) suggested a minimum of 30 with a preference for >50 locations for ADK. Pellerin et al (2008) reported obtaining reliable estimates with 40 locations/month for GPS data with *h_ref*. Above a threshold of 10 fixes month^{-1}, Börger et al. (2006) found that *h_ref* was unbiased; however, larger sample sizes (>1000 locations seasonally) suffered oversmoothing by *h_ref* regardless of species and point distribution (Walter et al. 2011). From our data, home ranges area estimates were highly variable based on not only the number of locations, but study animal and the method of data collection (GPS or VHF-telemetry) as well (Girard et al. 2002). While there was no optimum number of locations, more locations generally reduced bias and the researcher must determine satisfactory sample sizes. Thus in kernel analyses of animal home ranges, sample size should be reported along with software used (Gallerani Lawson and Rodgers 1997), bandwidth or smoothing parameter, and method of data collection.

Study sample size was dictated by project budget. Intensive monitoring of fewer animals may not be appropriate for certain study objectives or capture variability within the species (Otis and White 1999, Girard et al. 2006, Hebblewhite and Haydon 2010). While GPS collars were an expensive addition to our project, there was a tradeoff between the associated large samples generated versus radiotelemetry technician wages, smaller number of locations (Girard et al. 2002), and biased sampling by time periods (Kochanny et al. 2009, Kie et al. 2010, Hebblewhite and Haydon 2010). For instance on the mule deer project, no nocturnal radiotelemetry locations were collected due to hazards in the field (e.g. animal encounters, steep and rugged terrain). Variable landforms and habitats present challenges for fix rate, but in this study we had a fix rate with $>90\%$ success indicating few locations where fixes were not successful, except when coyotes were in natal dens. Overhead canopy cover was only available in Wind Cave and was generally $<50\%$. Overlap of telemetry data indicates that GPS functioned in all areas of home range, but our results supported previous findings (Hemson et al. 2005) that indicated that GPS data consistently collected the most location data for home-range estimates.

Conclusions

There may not be a single best recommendation given the variety of data collection hardware, home-range software, analysis methods, and smoothing parameter choices (Gallerani Lawson and Rodgers 1997, Laver and Kelly 2008). The questions posed may require different bandwidth methods when appropriate for study components (Gitzen et al. 2006) and estimating consistent bias for inference may be more important that precise area estimates (Fieberg and Börger 2012). Using maximum likelihood estimators may be an objective way to choose the best home-range model in some cases; however, kernel estimators cannot be evaluated by these methods (Horne and Garton 2006). Researchers can chose a method a priori, but should consider how that method reacts when applied to their study questions and consider additional sensitivity analyses for variance or relative bias (Fieberg and Börger 2012). In this instance for both coyote and mule deer data, *h_ad hoc* was less sensitive to changes in sample size than *h_ref*. However, there were issues at certain ranges of locations with increased bias due to oversmoothing at moderate sample sizes. Least-squares cross-validation may be an option with small sample sizes (<100 locations), but it quickly becomes negatively biased with increasing sample size and was not appropriate for our GPS data (Hemson et al. 2005, Gitzen et. al. 2006). The best home-range model was the one that has the most support from the data (Horne and Garton 2006). By examining 95% and 50% contours for two species, we noted differences even when using similar numbers of locations and smoothing parameters. Mule deer had greater bias in 95% contours whereas coyotes had more bias in 50% contours. These differences were likely tied to how the animals were using resources in their home range. Thus, behavior can impact home-range estimates and is a necessary component of researcher considerations. As a result, care must be taken not only when comparing between animals of the same species with regard to sample size, smoothing parameter, software, time of year, age, and sex, but also between species for area overlap (Berger and Gese 2007) because they are likely to have variable distributions on the landscape due to their ecological needs (Moorcroft 2012).

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