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Source: Copeia, 2006(4) : 797-802

Published By: The American Society of Ichthyologists and Herpetologists

URL: https://doi.org/10.1643/0045-8511(2006)6[797:KANAEO]2.0.CO;2

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Copeia, 2006(4), pp. 797–802

Kernels Are Not Accurate Estimators of Home-Range Size for Herpetofauna

JEFFREY R. ROW AND GABRIEL BLOUIN-DEMERS

Kernel home-range estimators are becoming more widely used to determine the home-range size for herpetofauna, despite the problems associated with selecting the appropriate smoothing factor. We used simulations to demonstrate the inconsistency of kernel estimators at determining the home-range size of random distributions. Furthermore, we used the positions of ten adult male *Lampropeltis triangulum* radio-tracked over two full active seasons (2003 and 2004) to demonstrate that the size of the home range increases significantly with an increase in the smoothing factor. The degree of increase, however, was not consistent between individuals. In addition, using least-squares cross-validation to select the smoothing factor produced a wide range of values for different individuals. Because of these inconsistencies, we suggest using the minimum convex polygon (MCP) method to calculate home-range size in studies of herpetofauna. When studying habitat use, however, we suggest using the MCP as the area of the home range and adjusting the smoothing factor until the area of the 95% kernel equals the area of the MCP. This provides an objective method for selecting the smoothing factor.

ALTHOUGH the exact definition of home range is still debated, a home range is generally accepted to be the area in which an individual performs its normal activities (Burt, 1943). There is little agreement, however, on how to quantify home-range size and, consequently, numerous methods have been employed (Powell, 2000).

One of the most commonly used home-range estimators is the minimum convex polygon (MCP), which is the smallest possible convex polygon that encompasses all the known locations of a given individual (Hayne, 1949). The minimum convex polygon is widely used because it is simple to conceptualize and does not rely on the data having some underlying statistical distribution (Powell, 2000). Despite its wide use and simplicity, however, MCP only provides a crude outline of an individual's home range. It often includes large areas never used by the animal and ignores patterns of selection within the home range (Powell, 2000; Taulman and Seaman, 2000).

To examine habitat selection within a home range, it is useful to employ estimators that quantify the intensity of use. Kernel home-range estimators are the most widely used for quantifying intensity of use because they are the most consistent and accurate of the methods available (Worton, 1989; Seaman and Powell, 1996). The kernel estimator is a non-parametric method that produces a distribution estimating the likelihood of finding the animal at any particular location within its home range (Worton, 1989), but it, like MCP, also includes areas never used by the animal. One drawback of this method is that the user must set numerous parameters, and the values of those parameters have a large effect on the size of the home range (Kazmaier et al., 2002). In particular, choosing the smoothing factor (h) of the kernel is the most important and difficult aspect of using kernels (Worton, 1989). Low values of h give nearby locations the greatest influence on the shape of the kernel, revealing small-scale detail, while large values allow more influence from distant locations, which reveals the outlying shape of the distribution (Seaman and Powell, 1996). Simulations have shown that even small changes in h can have a large effect on the size of the home range (Worton, 1995) and has led some researchers to the conclusion that kernels are more suited to analysis of use, rather than to the estimation of home-range size (Harris et al., 1990; Kazmaier et al., 2002). Other problems associated with the number of locations and the patterns of space use by individuals can also lead to variable estimates of home-range size when using kernels (Seaman et al., 1999; Blundell et al., 2001; Hemson et al., 2005). Despite the problems associated with estimating home-range size using kernel estimators, the issue is rarely addressed in studies of herpetofauna. To our knowledge, none of the studies using kernel estimators on reptiles or amphibians mentioned the problems associated with selecting the appropriate h (Rodriguez-Robles, 2003; Diffendorfer et al., 2005; Taylor et al., 2005), and some studies did not mention the method used to select h (Morrow et al., 2001; Tucker et al., 2001; Muths, 2003), which would prevent comparative studies.

Methods for choosing h have been developed, and least-squares cross-validation (LSCV) is the

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most common and accurate for most situations (Worton, 1989; Seaman and Powell, 1996; Stevens and Barry, 2002; Morzillo et al., 2003). This method varies h and identifies the value of h that produces the minimum estimated error (Seaman and Powell, 1996). Although LSCV works relatively well for most types of data, it does not perform well when the data are highly autocorrelated, which arises, for example, when animals use the same location multiple times (Worton, 1987; Seaman and Powell, 1996). When the data are autocorrelated, it has been suggested to subsample the data to eliminate the autocorrelation (Swihart and Slade, 1985; Worton, 1987).

Herpetofauna do not move frequently and often use locations or areas (e.g., favorite retreat sites) multiple times throughout the course of an active season. This renders radio-tracking data highly autocorrelated even when one uses a consistent sampling scheme that allows the animal ample time to reach a new location between telemetry positioning. Subsampling may eliminate autocorrelation in this case, but it would reduce the biological significance of the home-range estimate (De Solla et al., 1999).

In this study, we used simulations and a radiotelemetry dataset typical of most studies on herpetofauna to establish if kernels are accurate home-range estimators for reptiles and amphibians. Using simulations, we first determined the consistency of kernel home-range estimators when using LSCV to select the smoothing factor (h). Secondly, we determined the accuracy and precision of kernels at estimating the home-range size for *Lampropeltis triangulum*. We suggest an objective and biologically relevant method for selecting h when biological autocorrelation restricts the use of LSCV.

Materials and Methods

Simulations.—Previous studies have used complex simulations to test the accuracy of different home-range estimators (Worton, 1989, 1995; Seaman and Powell, 1996). These studies have determined that fixed kernel estimators with LSCV are the most accurate of the methods available. Here, we tested the consistency of fixed kernel estimators and LSCV at determining the size of a home range. We used home-range sizes and sample sizes typical of studies on herpetofauna. We generated 30, 60, or 100 random locations 20 times within a 28-ha and within a 6.5-ha polygon. For each distribution, we computed the MCP area and the 95% kernel area (with LSCV to select h). These simulations allowed us to determine how consistent kernel estimators were at generating home-range sizes for random distributions of similar size and shape.

Study area and study species.—We collected data on *Lampropeltis triangulum* at the Queen's University Biology Station, 100 km south of Ottawa, Ontario (44°34′ N, 76°19′ W) from April 2003 to November 2004 as part of a larger study on habitat use and thermoregulation (Row and Blouin-Demers, 2006). We captured Milksnakes opportunistically and at hibernacula of Ratsnakes.

We implanted radio-transmitters (Model SB-2T, battery life of 12 months at 20 C, Holohil Systems Inc., Carp, Ontario) in ten males (mean SVL ± SE = 832 ± 16.43 mm, mean mass ± SE = 165 ± 8.99 g). The transmitter weighted 5.5 g and never exceeded 5% of the snakes' mass. Transmitters were implanted under sterile conditions and isoflurane anaesthesia (Blouin-Demers et al., 2000; Weatherhead and Blouin-Demers, 2004).

We released the snakes at their point of capture one day after implantation and located them every 2–3 days using a telemetry receiver and a directional antenna. At each location, we recorded the UTM coordinates with a GPSmap76 (Garmin International Inc., Olathe, KS). Based on their observed movement patterns, Milksnakes could easily traverse their entire home range in two days. Thus, when they were relocated in the same site, we believe it was the snake's choice to stay, not an impossibility to reach a new location in the time interval between relocations.

Home ranges.—The home ranges used in this study were from individuals that were tracked for at least 75% of an active season, which spanned from early May until early October. For each individual, we calculated the MCP home-range size after successive relocations to ensure that a plateau was reached, indicating that we had estimated the complete home range. Two snakes were tracked both years, and we included both years independently in the analysis.

We used LSCV to determine h, and we calculated the 95% kernel home-range size for all snakes to establish the range of h that would be relevant for this population. For each individual, we also calculated the size of the kernel home range generated with h = 15, 30, 50, and 100 (biologically relevant values for Milksnakes) to determine how home-range size varied with h and if the trend was consistent across individuals.

Statistical analysis.—We used the Animal Movement Analysis extension 1.1 (Hooge and Eichenlaub, Anchorage, AK) in Arc View 3.2 (ESRI,

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TABLE 1. MEAN HOME-RANGE AREA FOR 20 SETS OF LOCATIONS RANDOMLY DISTRIBUTED WITHIN THE SAME 28.0-HA AND 6.5-HA POLYGONS. The home-range estimates were larger and more variable for the 95% fixed kernel method than for the minimum convex polygon (MCP) method.

	Size = 28.0 ha				Size = 6.5 ha			
Type	*n*	Mean area (ha)	SE	Range	*n*	Mean area (ha)	SE	Range
MCP	30	19.31	0.18	2.70	30	4.41	0.06	0.94
MCP	60	23.62	0.13	1.91	60	4.92	0.05	0.64
MCP	100	24.05	0.13	1.96	100	5.27	0.03	0.43
Kernel	30	44.00	0.84	12.51	30	16.29	0.43	7.27
Kernel	60	45.55	0.56	12.72	60	15.22	0.30	4.54
Kernel	100	43.15	0.49	8.69	100	14.29	0.22	4.12

Redlands, CA) to calculate home-range sizes and smoothing factors (h). We used JMP version 5.0 (SAS Institute, Cary, NC) to conduct all statistical analyses. We reported all means ± 1 SE.

RESULTS

Simulations.—Within the 28.0-ha polygon (Table 1) and for $n = 30$, the MCP range spanned 2.70 ha (12.92% of the maximum value). For $n = 60$, the range spanned 1.91 ha (7.66% of the maximum value), and for $n = 100$, the range spanned 1.96 ha (7.85% of the maximum value). Thus, MCP generated moderately precise estimates of the home-range area. Within the 28.0-ha polygon (Table 1, Fig. 1) and for $n = 30$, the kernel home ranges spanned 12.51 ha (24.86% of the maximum value). For $n = 60$, the range spanned 12.72 ha (23.83% of the maximum value), and for $n = 100$, the range spanned 8.69 ha (18.79% of the maximum value). The kernel home ranges were much larger than the polygon within which the random locations were generated. The distribution and range of home-range sizes (Fig. 1) indicated that kernel estimators become more precise as sample size increases. The range, however, was still large relative to the size of the home range, even with large sample sizes, indicating that kernels give imprecise estimates of the home-range area.

Within the 6.5-ha polygon (Table 1) and for $n = 30$, the MCP range spanned 0.94 ha (19.03% of the maximum value). For $n = 60$, the range spanned 0.64 ha (12.19% of the maximum value), and for $n = 100$, the range spanned 0.43 ha (7.85% of the maximum value). Within the 6.5-ha polygon (Table 1, Fig. 2) and for $n = 30$, the kernel home ranges spanned 7.27 (36.74% of the maximum value). For $n = 60$, the range spanned 4.54 ha (26.54% of the maximum value), and for $n = 100$, the range spanned 4.12 ha (26.25% of the maximum value). When considering absolute values, the precision of the kernel estimate was better with the smaller polygon. When considering the range of sizes in relation to the size of the home range, however, kernel estimators performed just as poorly with smaller home ranges.

Home ranges.—We used LSCV to calculate h for ten adult male Milksnakes. The h values ranged from 28 to 110, which produced home-range sizes that spanned 55.93 ha (3.04–58.97 ha). Home-range size increased with h for all individuals (Fig. 3). An ANCOVA revealed a significant interaction between individual and h ($R^2 = 0.11$, $F_{9,39} = 68.38$, $P < 0.001$), indicating that the change in home range size with h varied among individuals.

The MCP method produced a size range that spanned 24.04 ha (5.01–29.05 ha), which was less than half the range produced by the kernel method. We also determined that there was no significant difference between kernel home-range size and MCP home-range size ($d = 0.39$, paired $t_9 = 1.29$, $P = 0.22$).

DISCUSSION

When using kernel home-range estimators, choosing the appropriate smoothing factor (h) is the most important and difficult decision (Seaman and Powell, 1996; Powell, 2000). The most common and recommended method for choosing the smoothing factor is LSCV (Seaman and Powell, 1996; Powell, 2000). When using LSCV to select the smoothing factor, sample size, and data structure have a significant effect on the level of smoothing, which in turn affects the size of the home range (Seaman and Powell, 1996; Hemson et al., 2005). Using simulations, we demonstrated that, even under ideal situations for reptiles and amphibians, kernels are inconsistent and produce a wide range of areas for randomly distributed sets of locations that have approximately the same size and shape.

In real datasets, individuals exhibit diverse selection patterns and site fidelity. This increased

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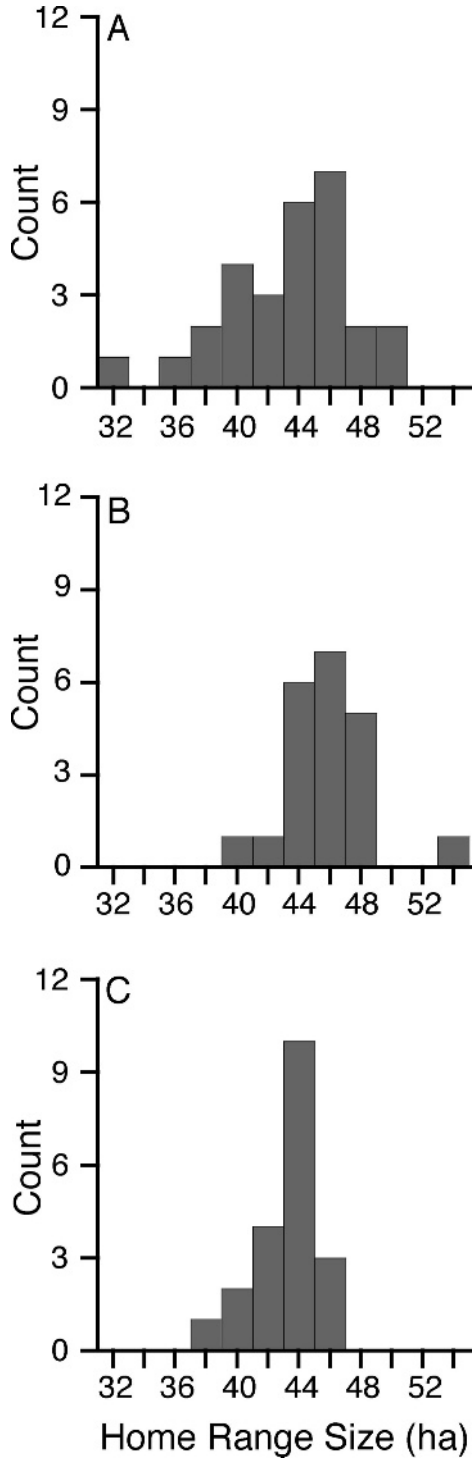


Fig. 1. Kernel home-range size varies widely when generated from 20 random distributions that had approximately the same size and shape. (A) 30, (B) 60, and (C) 100 random points were generated within a 28-ha polygon.

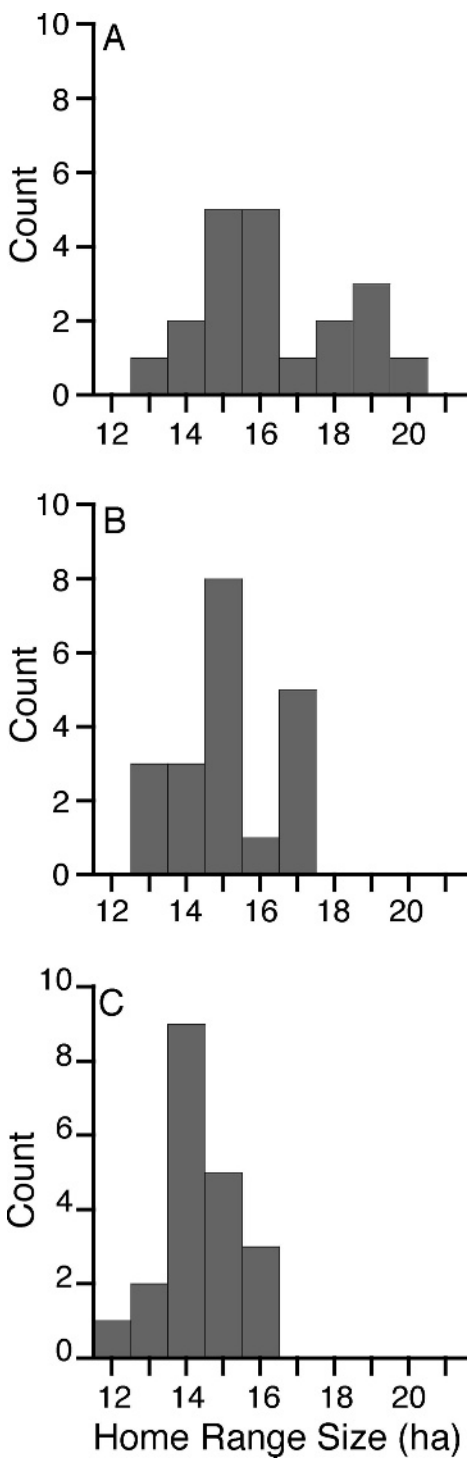


Fig. 2. Kernel home-range size varies widely when generated from 20 random distributions that had approximately the same size and shape. (A) 30, (B) 60, and (C) 100 random points were generated within a 6.5-ha polygon.

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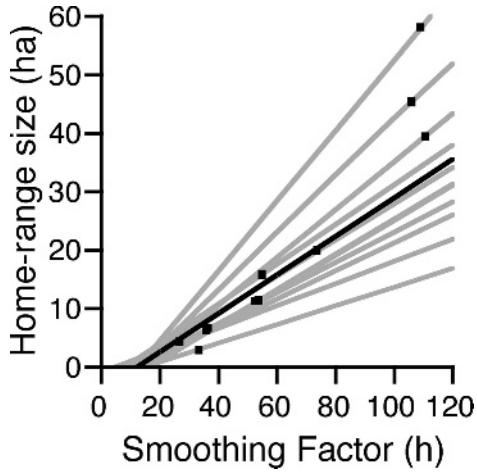


Fig. 3. Kernel home-range size increases significantly with the smoothing factor (h = 15, 30, 50, and 100) used for ten adult male *Lampropeltis triangulum* radio-tracked in eastern Ontario in 2003 and 2004. The mean slope (dark line), the slopes of all individuals (gray lines), and the smoothing factor chosen with LSCV (black squares) are shown.

variation would cause the range of the smoothing factor, and thus the range in home-range area, to increase further. This problem will be exacerbated for herpetofauna where site fidelity leads to autocorrelation. Using data from ten adult male Milksnakes, we demonstrated that LSCV selected a wide range of h and that home-range size increased significantly with h for all individuals. The increase in home-range size, however, was not the same for all individuals. Using kernel methods to estimate home-range area would have led to inconsistent home-range estimates across individuals. When we used kernels to estimate home-range size, the range of sizes was twice the range produced from MCP. We believe this situation would be typical of most datasets from herpetofauna. Despite these inconsistencies, many studies on amphibians and reptiles use kernel estimates to compare home-range sizes between groups or between time periods and fail to mention the problems associated with choosing the appropriate smoothing factor (Rodriguez-Robles, 2003; Diffendorfer et al., 2005; Taylor et al., 2005).

Reptiles and amphibians offer unique opportunities for studying movements. First, unlike mammals and birds that are easily disturbed, they can often be located within a few meters without disruption and, therefore, they can be located without triangulation. Triangulation leads to large positional errors (Rettie and McLoughlin, 1999). Second, reptiles and amphibians do not move far during the active season and use the same location many times and for extended periods of time. Therefore, consistent sampling every few days throughout the active season is usually sufficient to ensure that the entire home range is estimated. Because of these characteristics, we believe MCPs would accurately represent the maximum home-range area for most herpetofauna and should be used for size comparisons between groups or across time periods (Kazmaier et al., 2002).

For analyzing habitat selection at the home range scale, however, we propose combining the MCP and kernel methods. Because a probability of 100% is extremely unlikely, the 95% kernel is most often used to estimate the total home-range area of an individual (Powell, 2000). Therefore, for each individual we suggest using the MCP as the area of the home range and adjusting h until the area of the 95% kernel equals the area of the MCP. This provides an objective method for choosing h that will allow kernel home ranges to be used in habitat selection studies of herpetofauna. Although the areas of the two home-range estimates are the same, kernels provide a more biologically relevant home range by placing a probability distribution around locations, which puts more emphasis on areas with higher use, whereas MCPs simply encompass all the locations. Furthermore, this method will allow for analysis of core areas inside the 95% kernels, which is not possible with MCPs.

Acknowledgments

We thank G. Bulté and S. Duchesneau for their able help with data collection. We also thank the staff at the Queen's University Biological Station for logistical support. Our work was conducted under protocol BL-179 of the University of Ottawa's Animal Care Committee. Funding for this research was provided by an NSERC discovery grant to GBD.

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