

An individual-based quantitative approach for delineating core areas of animal space use

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ABSTRACT

Core areas are often employed in space-use studies to emphasize sections of a home range where an animal supposedly concentrates its time spent (i.e., areas of intense use). The area designated as the core is often subjectively selected based on aggregations of animal locations, thus not quantitatively repeatable, or selected based on arbitrary areas from a home range estimator, thus not biologically significant. We present an explicit ecological model of space use for objectively delineating areas of intense use, or core areas, based on further refining the definition of core area as the *area within which an animal spends a maximum amount of time*. Core areas were delineated using a time-maximizing function derived from kernel analyses. Essentially, we plotted utilization distribution area against volume and determined the point at which the slope of the line fitted to the data is equal to 1; this point represents a threshold where the proportional home range area begins to increase at a greater rate than the probability of use and the corresponding isopleth value defines the boundary of the core area; an animal's time spent within this area is maximized relative to the periphery. We used summer locations from 60 adult female moose (*Alces alces*) to demonstrate our method. Moose core areas were bounded by the $\bar{x} = 58\%$ (SD = 0.60) isopleth and comprised $\bar{x} = 77\%$ (SD = 6.09) of animal relocations. Core areas represented $\bar{x} = 27\%$ (SD = 1.99) of the home range ($\bar{x} = 3837$ ha, SD = 4336.15; 95% utilization distribution) and were used an average of 2.16 (SD = 0.20) times more intensely than home range peripheries. Proportions of intensively used areas, as defined by isopleth values, were not related to home range size. Our technique reflects a biological understanding of a core area and provides a repeatable, quantitative method that enables statistical testing of hypotheses related to the effects of environmental factors on home range and core area size and usage. Adopting our approach will greatly improve our capacity to understand and ability to compare spatial dynamics of resource selection within home ranges of wildlife.

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1. Introduction

Multi-scale approaches are imperative in capturing the hierarchical manner in which animals perceive their environment: from core, or usual area, to the overall perception of a familiar area, or home range (Bissonette et al., 1997; Hodder and Kenward, 1998). Burt (1943) first described a home range as the area traversed by an individual in its normal activities, including refugia for protection, feeding, mating and other life history requisites. Since its conception, home range has been a main focus and useful tool in animal ecology. Hierarchically, home range is considered to be the second order spatial scale of selection (Johnson, 1980). Between

second order selection and patch selection (third order selection) is a dynamic category termed the core area (Kaufman, 1962). Core area has been defined as an area of intensive (Samuel et al., 1985) or most concentrated (Seaman and Powell, 1990) use. The utility of studying animals at the core area scale has been demonstrated in examples such as the conservation of a threatened species (e.g., woodland caribou [*Rangifer tarandus caribou*; Schindler et al., 2007]), management of harvested species (e.g., pronghorn antelope [*Antilocapra Americana*; Jacques et al., 2009], white-tailed deer [*Odocoileus virginiana*; Walter et al., 2009]), or basic ecology (e.g., iguanas [Christian et al., 1986; Pasinelli et al., 2001]). However, core areas do not necessarily conform to any prescribed spatial scale, *per se*, and can constitute a small percentage or the majority of a home range; a core is not strictly determined by home range size (Powell, 2000). Consequently, species with different patterns of home range behaviour, such as central place foragers, territorial or non-territorial animals, may have home ranges of equal size but different proportions of concentrated use, depending on the distribution of critical resources (Powell, 2000). Indeed,

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individuals within a species may have equal home range size but different proportions of intensively used areas because resources are distributed differently within the areas they occupy. If parts of a home range with greater availability or accessibility of critical resources are more important than areas with few resources, their probability of use should be higher and animals should spend more time in these areas.

Delineating core areas has been applied in several ways, including selecting arbitrary values that qualitatively fit data, to semi-quantitative delineation of core areas (Chamberlain et al., 2000; Kitchen et al., 2000; Kilpatrick et al., 2001). Often subjective isopleth values are used, ranging from 30% to 50% of the volume under individual utilization distributions or a 50% minimum convex polygon to describe core areas (Heikkila et al., 1996; Chamberlain et al., 2000; Kitchen et al., 2000; Kilpatrick et al., 2001; Koen et al., 2007). Arbitrary assignment of core area is perhaps a suitable method for some studies but there are inherent problems with replication and comparability. These methods do not facilitate statistical testing of hypotheses related to core size (Seaman and Powell, 1990). In addition, arbitrary selection of isopleths that are not correlated to a specific behaviour or a pattern of space use may result in a loss of biological significance.

Several authors have appreciated the drawbacks related to arbitrary methods of designating core areas (Samuel et al., 1985; Seaman and Powell, 1990; Powell, 2000; Glenn et al., 2004). To improve on these arbitrary methods, various quantitative approaches have been proposed that generally fall into one of two associated families of techniques: the first using variations on percent inclusion of animal locations (Hodder and Kenward, 1998; Kalmer et al., 2003) and the second using probability density functions (Samuel et al., 1985; Christian et al., 1986; Wray et al., 1992; Glenn et al., 2004). Hodder and Kenward (1998) concede that the percent inclusion technique, though quantitative, produces a smooth curvilinear representation of space use, the interpretation of which often remains subjective. In contrast, probability density functions, or utilization distributions, are used by Samuel et al. (1985) and Seaman and Powell (1990) to describe the core area within the home range as the area where the probability of occurrence is greater than would be expected with uniform use. Seaman and Powell (1990) were the first to propose an objective threshold for designating cores as the area of “most concentrated [or intensive] use”. The remainder of the home range is termed periphery (Seaman and Powell, 1990; Powell, 2000). The Seaman and Powell (1990) and Powell (2000) method plots percent maximum relative frequency of use against percent of home range; they defined the point at which the plot is maximally distant from a straight line with a slope of -1 (i.e., the slope of a distribution describing random use) as the threshold between areas of high and low probability of use: at this point the percent of home range area increases more rapidly than the relative frequency of use and the intensity of use declines from core to periphery.

Following from Seaman and Powell (1990) and Powell (2000), we aim to further refine the definition of a core area and introduce kernel density functions as the means of designating probability of use. Areas of “most concentrated” use (i.e., core areas) comply with a repeatable mathematical function: where a core area is the *area within which an animal spends a maximum amount of time*. The boundary around the core represents the threshold where the distance an animal travels in the periphery represents more area per unit effort than movements within the core area. Hence, the area of the periphery increases at a much greater rate per unit time than the core area and the probability of use declines. Consequently, time spent in the core area is maximized relative to the periphery. The objective is thus to determine the point at which home range area increases at a greater rate than probability of use. We show the results of applying our model to location data of moose (*Alces alces*);

a non-territorial species in which habitat and resource selection occur at multiple spatial scales (Johnson, 1980; Voigt et al., 2000; Vander Wal, 2004) and result in non-uniform use of home ranges (Heikkila et al., 1996).

2. Methods

2.1. Home range data

Relocation data were obtained from 60 free-ranging adult female moose that were fitted with Global Positioning System (GPS) collars (GPS 1000, LOTEK Engineering Inc., Newmarket, Ontario) between 1995 and 2000 in Northwestern Ontario (Crouse, 2003). The study area has been described by Rodgers et al. (1995) and Rempel et al. (1997). GPS collars recorded animal locations every 4 h from deployment in February of capture until February the following year. All locations used in our analyses were taken during the ‘summer’ (Vander Wal and Rodgers, 2009). Only 3-dimensional, differentially corrected locations were included in the analysis, resulting in a location error of 3–7 m (Rempel and Rodgers, 1997). The mean number of relocations per animal during the summer was 466 (range: 48–1225).

2.2. Core area designation

Kernel analysis was applied to calculate utilization distributions for individual female moose using the Home Range Extension (HRE) software package (Rodgers and Carr, 1998) in conjunction with ArcView 3.2a (ESRI, Redlands, CA, USA). Core areas are a study of internal range configuration; thus, a fixed kernel was used as it best describes the ‘inner anatomy’ of a home range (c.f., adaptive kernel; Worton, 1989; Kernohan et al., 2001). For simplicity, we used the reference bandwidth (h_{ref}), which determines the width of individual kernels placed over animal locations assuming an underlying bivariate normal distribution in the data, and controls the smoothing in the utilization distribution (Silverman, 1986; Worton, 1989; Kernohan et al., 2001). The 95% isopleth value was selected from each animal’s utilization distribution to delineate its home range.

A plot of utilization distribution area by utilization distribution volume from fixed kernel analysis of individual relocation data results in an exponential relationship (Fig. 1) from which a core area can be derived. The area is the 2-dimensional coverage of the animals’ utilization distribution and the volume under the utilization distribution (i.e., the third dimension) – delineated by isopleths – is indicative of the likelihood of the animal spending time within different portions of its home range: the greater the volume, the greater the amount of time spent. To interpret the curve, the axes must be congruent; thus, home range area is standardized proportional to the total area covered by the utilization distribution and displayed as a percentage ($0 \leq \text{total area} \leq 1$; similar to $0 < \text{distribution volume} < 1$) (Fig. 1).

From a theoretical perspective, it would appear that a line fitted to the data should go through the origin and take the form of a quadratic relationship. However, that would be unrealistic. By its existence, an animal must occupy some minimal space and is likely to use some minimal patch size to meet its basic biological requirements, so a curve fitted to the data may intercept the y axis near zero but will not go through the origin. At the other extreme, because the utilization distribution is constructed from unbounded bivariate normal (i.e., Gaussian) kernels, a curve fitted to the data will be asymptotic. Moreover, given the cumulative nature of the relationship between utilization distribution area and volume, a line fitted to the data must be monotonic increasing and a quadratic form that may include segments with both positive and negative slope would be unrealistic. Consequently, the relationship of utilization

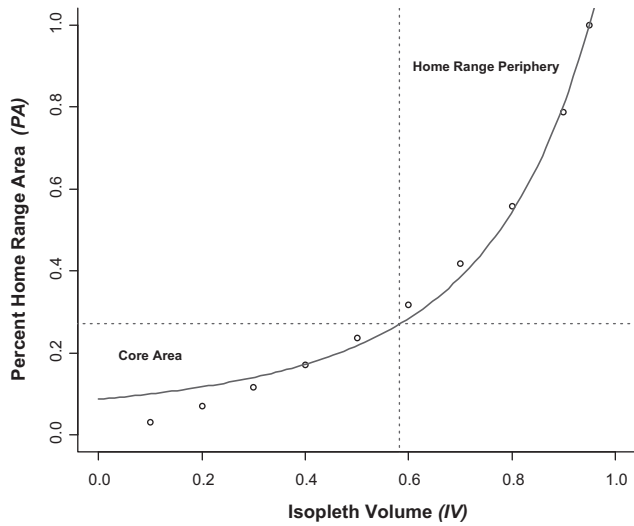


Fig. 1. Open circles represent the mean Percent Home Range Area (PA) bounded by each Isoleth Volume (IV). The solid curve is fitted to the data according to Eq. (1). The intersection of the dashed lines indicates the threshold (slope = 1) where area under the curve in the lower left quadrant is core area and area under the curve in the top and bottom right quadrants delineate home range periphery.

distribution volume to area is better approximated with an exponential regression (e.g., Fig. 1):

$$\ln(PA) = \ln(b_0) + (b_1 * IV) \tag{1}$$

where PA is the Percent Home Range Area (y axis), IV is the Isoleth Volume (on the abscissa); b_0 is the y-intercept; and b_1 is the exponential regression equation constant, both of which can be determined from statistical curve-fitting procedures.

Consistent with the utilization distribution, a fitted exponential regression curve will be monotonic increasing and asymptotic; when differentiated, the point at which the slope is equal to 1 reflects the vertex where the proportional home range area begins to increase at a greater rate than the probability of use and the corresponding isopleth value defines the boundary of the core area; an animal's time spent within this area is maximized relative to the periphery. Therefore, generating an exponential regression equation with statistical software (R Development Core Team, 2010) and subsequently setting the first derivative (2) equal to 1 (3), the threshold for the core area on the curve can be identified (4):

Where the first derivative is:

$$\frac{\partial PA}{\partial IV} = b_0 b_1 e^{b_1 * IV}, \tag{2}$$

and time is maximized when the first derivative (2) equals 1:

$$\frac{\partial PA}{\partial IV} = 1, \tag{3}$$

such that substituting Eq. (3) into Eq. (2) and solving for IV determines the isopleth value that constitutes the outer boundary of the core area:

$$IV = \frac{-\ln(b_0 b_1)}{b_1}. \tag{4}$$

To understand inter-individual variation among female moose, we calculated the isopleth value designating the core area for each animal, the area defined by the core, number of relocations in the core, and the proportion of the total home range enclosed by the core. To demonstrate the efficacy of our approach and verify the existence of a core area within the home range of individual

animals, we calculated relative intensity of use using the method of Samuel et al. (1985):

$$I = \frac{\%Use}{\%HomeRange} \tag{5}$$

where I is intensity of core area use, %Use is the isopleth value (or probability of use) associated with the boundary of the core area, and %HomeRange is the proportion of the total home range occupied by the core area. Values >1 indicate that the core area is being used more intensely than the remainder of the home range, whereas values ≤1 indicate the contrary. If an area is not being used with greater intensity than the remaining home range it deviates from the definition of core area and the individual may be presumed to use its home range more uniformly than other animals.

Seaman and Powell (1990) and Powell (2000) suggest that the proportion of the home range designated as a core area should be independent of home range size. We used general linear models with R software (R Development Core Team, 2010) to test this requirement.

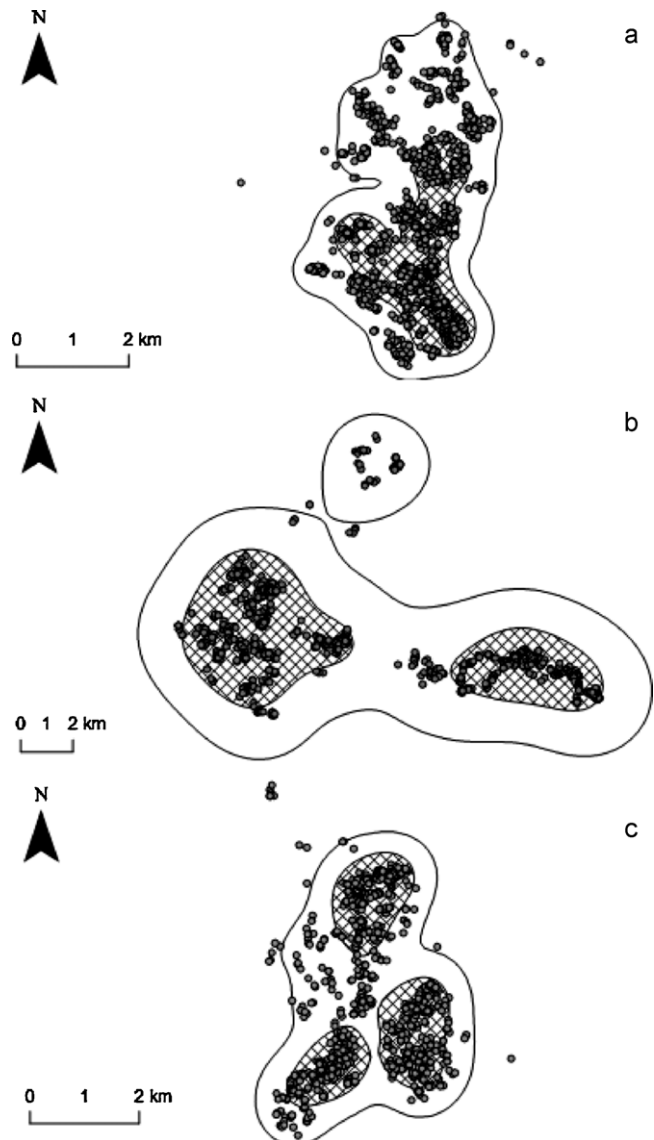


Fig. 2. Examples of core areas (hatched) nested within home ranges (95% utilization distribution) of GPS-collared adult female moose. Points are relocations from which the home range was derived. Number of spatially discrete cores and the relative intensity of use values (I) vary among the 3 individuals: one core, 2.0 (a); two cores, 1.9 (b); and three cores, 2.9 (c), respectively.

Table 1
Summary statistics for subsets and dividers of home ranges (HR) for female moose ($n = 60$) in northwestern Ontario, 1995–2000.

Measure	\bar{x}	SD	Range	
			Min	Max
Total home range area ^a (ha)	3837.06	4336.15	583.19	27884.89
Core area (ha)	1038.16	1185.79	168.00	7849.53
Home range periphery (ha)	2798.90	3154.34	415.18	20035.36
Proportion core (%)	27.11	1.99	20.83	30.35
Proportion home range periphery (%)	72.89	1.99	69.64	79.16
Isopleth Volume (%)	58.25	6.02	57.33	60.15
% Relocations in the core	76.90	6.09	65.14	90.87
R^2 ^b	0.98	0.01	0.97	0.99
Relative intensity of use	2.16	0.20	1.89	2.89

^a Home range based on 95% isopleth value of a utilization distribution determined by fixed kernel analysis using the reference bandwidth.

^b Coefficient of determination from regressions of the exponential curve fit.

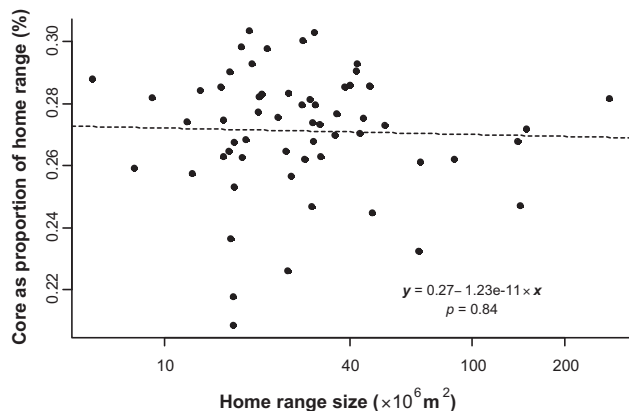


Fig. 3. Relationship between isopleth values used to define the boundary of the core area (i.e., proportion of the home range where the animal spends a maximum amount of time) and home range size.

3. Results

Moose home ranges (95% fixed kernel) clearly had areas of intense use (Fig. 2); i.e., core areas, based on our method. Relative intensity of use, however, varied within the home range of individual animals ranging from 1.89 to 2.89 ($\bar{x} = 2.16$, $n = 60$; $SD = 0.20$) times more use of core areas than the remainder of home ranges (Table 1). Home ranges of moose in Fig. 2 represented typical examples of concentrated patch use, showing differences in intensity of use and the possibility of individual home ranges including multiple discrete centres of activity (i.e., “multiple cores”).

The mean isopleth value that designated the core area for female moose was 58.25% ($n = 60$; $SD = 6.02\%$ Table 1). Isopleth values were well fit with an exponential curve (mean $R^2 = 0.98$; $n = 60$, $SD = 0.01$). Proportions of intensively used areas, as defined by isopleth values, were not related to home range size ($p = 0.83$, Fig. 3). Mean core area size was 1038.16 ha ($n = 60$; $SD = 1185.79$ ha) and included 76.90% of relocations ($n = 60$; $SD = 6.09\%$). Proportionally, this represented a mean of 27.11% ($n = 60$; $SD = 1.99\%$) of the over-all home range (area within the 95% isopleths; $\bar{x} = 3837.06$ ha $n = 60$; $SD = 4336.15$ ha).

4. Discussion

“Core areas are those areas used more frequently than any other areas and probably contain the home-sites, refuges and [the] most dependable resources” (Samuel et al., 1985). We submit that the definition of core area can be further refined: cores are areas of intense use that can be described as the *area within which an animal spends a maximum amount of time*. The method we proposed identified areas that were used more intensively by adult female moose than home range peripheries and proportions of intensively

used areas were not related to home range size. Thus, our technique reflects a biological understanding of a core area, as suggested by Seaman and Powell (1990) and Powell (2000). Looking at core areas as a maximizing function related to probability of use adds several advantages: conceptual framework founded in mathematics, quantitative repeatability, probability of occurrence that implies time, and it captures the variation in areas used by individual animals. Biologically, individual variation is critical to understanding how animals relate to their environments and the resulting implications, e.g., genetic structure (Porlier et al., 2009), social behaviours (Silk, 2007), reproduction and survival (McLoughlin et al., 2006). As such, our method enables statistical testing of hypotheses related to the effects of environmental factors on home range and core area size and usage that are not otherwise possible.

Though the method of bandwidth selection used in kernel analyses remains subjective (e.g., h_{ref} versus LSCV), our core area designation is objective beyond that point. Once the maximizing function (Eq. (1)) is accepted, the researcher no longer has control of the outcome. This strength ensures repeatability and provides for individual variation; for moose, core areas were delineated that had large spatial variation (one order of magnitude) which corresponds to variation found in home range size. In this study, the mean isopleth value that delineated the core area for moose was 58%; i.e., on average, there was a 58% probability of finding an animal within a core area that comprised an average 27% of its overall home range (95% isopleths). Isopleth values for individual adult female moose can thus be used to distinguish core areas within overall home ranges for subsequent determination and comparison of functional relationships such as habitat characteristics.

Samuel et al. (1985) and Seaman and Powell (1990) suggest methods that incorporate probability of use and detail internal range configurations represent animal space use patterns more realistically than subjective techniques. The technique described herein incorporates these strengths, including the possible existence of multiple centres of activity (i.e., “multiple cores”). Conversely, Samuel et al. (1985) expressed concern in using a technique, based on unbounded utilization distributions (e.g., kernel analysis), where selecting different maximum isopleth values to designate the home range will alter the results of core delineation. Kernel analysis is a continuous asymptotic technique which uses probabilities rather than certainties (utilization distributions are not true home ranges, *sensu* Burt, 1943; also see Kie et al., 2010). The maximum isopleth chosen for the technique is inconsequential, as the approximation of the curve (Fig. 1) simulates the asymptotic (i.e., infinite) nature of kernel analysis. Theoretically, the 100% isopleth of the utilization distribution from a kernel analysis equals infinity. This is analogous to the upper limit of an exponential function, such that the equation for the exponential regression curve (which ultimately equals infinity) simulates the probabilities of the outer isopleths of a utilization distribution formed by kernel analysis. Thus, whether the home range is bounded, for example, by the

90% isopleth or the 95% isopleth, it will have little influence on the area designated as core.

The main limitation of our approach is the need to meet minimum sample size requirements for kernel analysis (Seaman et al., 1999; Girard et al., 2002). However, this is easily overcome with the use of GPS technology for collection of animal locations (Rodgers, 2001). Of particular concern is the debate surrounding bandwidth selection methods for kernel analysis (Worton, 1989; Kernohan et al., 2001; Gitzen and Millsaugh, 2003), which has yet to be resolved. Additionally, it is important to understand the scale at which questions are posed, and determine whether it would be more appropriate to look at finer scale patch level (third order) processes, or fourth order feeding site selection (Johnson, 1980), which could have less spatial variation than a core area.

5. Conclusion

Based on our positive findings and the clear benefits of our approach (e.g., ease of application, logical extension, repeatability) over existing methods, we suggest that our technique be tested on other taxa to see if it can isolate areas of intense use as it can for moose. Schindler et al. (2007) have already used our method described here (based on Vander Wal, 2004) to test the differences in habitat suitability between core and range periphery for woodland caribou (*Rangifer tarandus caribou*). In particular, it would be beneficial to investigate animals that have different foraging strategies than ungulates: e.g., central place foragers, predators, highly mobile or migratory animals. Adopting our approach will greatly improve our capacity to understand and ability to compare spatial dynamics of resource selection within home ranges of wildlife.

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