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IDENTIFYING PATTERNS AND INTENSITY OF HOME RANGE USE

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Abstract: Assessing patterns of concentrated and diffuse use of an animal’s home range is an important component of understanding ecological and behavioral processes. We present the Area Independent Method (AIM), a graphical and quantitative technique for identifying the pattern of home range use (i.e., clumped or even) and for distinguishing between heavily and lightly used parts of an individual’s home range when clumping is present. This technique does not require that the data have any specified statistical distribution. The results of the AIM are compared with those from Samuel et al. (1985) when both methods are applied to radio-telemetry locations of 18 black bears (Ursus americanus). Total home range size has a lesser effect on the size of the core area identified by the AIM than by Samuel et al.’s (1985) method. Both methods result in core area usage that is little affected by total home range size. This technique provides an objective method for comparing areas of concentrated and peripheral use among individuals.

Home ranges reveal the ecological requirements of animals since they include all of the resources that are used by a resident. Home ranges and the movements within them are the behavioral manifestations of basic biological requirements such as finding sufficient food, shelter, and mates.

Knowledge about home ranges contributes to both management and ecological theory. Direct management applications include assessing how much space and what kind of habitat are necessary (e.g., Poelker and Hartwell 1973). Our theoretical understanding may benefit from learning the effect of various factors (e.g., food supply and breeding requirements) on spacing behavior and movements (Simon 1975, Carpenter and MacMillan 1976, Gass et al. 1976).

Management efforts may suffer if their data lack detail; simple outlines of home ranges may include unused habitat and resources, and thus give distorted pictures of what animals use (Dixon and Chapman 1980). Of course, concentration of use by an animal does not imply that heavily used areas or resources are more important than others. The importance of different areas must be decided by studies of the activities associated with the areas of different levels of use (e.g., Belovsky 1978).

From a theoretical standpoint, an ecological factor that changes the pattern of concentrated use (but does not change the perimeter of the range) may have a real and important effect. Realizing this can help us progress to a more thorough understanding of behavioral ecology.

To perform detailed studies of home range we need a technique for identifying the core of a home range. The core is the area of most concentrated use, and the technique for identifying the core must reflect our understanding of the biological meaning of a core. Two factors are of primary importance in this concept. First, the core area is used much more heavily than other areas of the home range (this will be defined explicitly in the methods to follow). This is important because an area that is used only slightly more than average could result from random use. The requirement that the core be used much more than other areas may be considered vaguely analogous to the statistical requirement for a number to be far above (or below) the mean before we say that it is significantly different from the mean. Second, the core size must not be strictly determined by total home range size. The result of this condition is that animals with equal sized home ranges but different use patterns (e.g., central place foragers, strongly territorial animals, and extensive wanderers) can have different core sizes.

Several methods exist for identifying core areas (e.g., Ford and Krumme 1979, Dixon and Chapman 1980, Samuel et al. 1985). Dixon and Chapman (1980) outline a subjective procedure in which the core is delineated by eye, which cannot form a legitimate basis for studies that involve statistical testing of hypotheses concerning core size, so we will only discuss objective procedures. Ford and Krumme (1979) developed a method called MAP (minimum area vs. probability) that designated any arbitrary constant amount of use as the core. In other words, the researcher is free to decide that the highest x percent of use represents the core of the home range for all individuals in the study. A crucial drawback to such a method is that the core is not strictly tied to intensity of use, and will almost certainly include areas of low use or exclude areas of high use. Samuel et al. (1985) presented a method for objectively identifying the maximum possible core area. This method defined the core as being all areas used more heavily than would result from the even distribution of use by the resident. The core area defined in this way is responsive to the patterns of use of different individuals, and cannot include areas used with frequency lower than the mean.

This paper will present the Area Independent Method (AIM) for identifying areas of concentrated use, compare
it with the method of Samuel et al. (1985), and show the results of applying the 2 techniques to radio-location data from 18 black bears.

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METHODS

Home Range Data

Bears were outfitted with radio transmitters (Telonics, Mesa, AZ) and their locations estimated by tracking from a truck with a single 8-element Yagi antenna mounted through the roof. Receiving locations were located precisely (±10 m) on U.S. Geological Survey (USGS) 1:24,000 scale topographic maps, and their coordinates stored in a computer file for triangulation. Location data were recorded directly into a laptop computer, then transferred to a personal computer for triangulation.

We grouped the locations into 25-ha grid cells. Cell size was chosen to be approximately ± median telemetry error. The number of locations in a cell gives the height of the utilization distribution at that point. The utilization distribution is representative of the duration of use of grid cells in the home range because we used an unbiased data collection scheme (Powell 1987). Telemetry locations of animals are an incomplete sample of the animals' locations. To estimate the complete utilization distribution we interpolated between the observations (Powell 1987). We used the SAS procedure G3GRID that generates a surface that “can be thought of as the one that would be formed if a stiff, thin metal plate were forced through the given data points” (SAS Institute Inc. 1985:414). This may generate unrealistically high interpolated values when data points are widely spaced, and may generate values far beyond the range of observations if the outermost data points are relatively high. To control the second of these problems, we arbitrarily set a boundary 2 km beyond the extreme locations, then eliminated the tails of the distribution by keeping only the most heavily used 95% of the interpolated distribution. Worton (1989) presents a smoothing method that may avoid both of the problems with interpolation.

Concentration of Use

The Area Independent Method is illustrated with a simple artificial data set (Fig. 1, Table 1). The goal is to identify a criterion for locating a dividing point between areas of high and low use in the home range. The following example is based on using 95% of the interpolated utilization distribution.

For each bear (Table 1), we divided the number of interpolated observations (OBS) in each grid cell by the total number of interpolated observations; this gave a relative frequency of interpolated observations (PROB). The relative frequencies summed across cells equals 1.0 if all cells are included, or equals 0.95 if only 95% of the distribution is used.

Each relative frequency value was divided by the highest individual cell value to determine the percent of the maximum relative frequency for that cell (PCTPROB). We ranked the cells (AREA) from highest to lowest

<table>
<thead>
<tr>
<th>AREA</th>
<th>PROB</th>
<th>PCTPROB</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>14</td>
<td>1.000</td>
</tr>
<tr>
<td>3</td>
<td>12</td>
<td>0.968</td>
</tr>
<tr>
<td>4</td>
<td>10</td>
<td>0.926</td>
</tr>
<tr>
<td>5</td>
<td>6</td>
<td>0.750</td>
</tr>
<tr>
<td>7</td>
<td>2</td>
<td>0.583</td>
</tr>
<tr>
<td>9</td>
<td>1</td>
<td>0.200</td>
</tr>
</tbody>
</table>

Fig. 1. Grid with interpolated numbers of observations in grid cells. Grid lines represent X, Y map coordinates. Integers in large typeface print are "actual" numbers of observations for this artificial data set, numbers with decimals are interpolated or "expected" numbers of observations for neighboring cells. Integers in small typeface indicate the rank of the cell from highest to lowest number of observations.
Table 1. Simple artificial data set, showing the scaling of values for determining core by the AIM.

<table>
<thead>
<tr>
<th>OBS</th>
<th>PROB</th>
<th>Area no.</th>
<th>PCTPROB</th>
<th>PCTRANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.000</td>
<td>0.021209</td>
<td>14</td>
<td>10.000</td>
<td>100.000</td>
</tr>
<tr>
<td>2.009</td>
<td>0.021305</td>
<td>13</td>
<td>10.045</td>
<td>92.857</td>
</tr>
<tr>
<td>3.000</td>
<td>0.031814</td>
<td>12</td>
<td>15.000</td>
<td>85.714</td>
</tr>
<tr>
<td>3.041</td>
<td>0.032249</td>
<td>11</td>
<td>15.205</td>
<td>78.571</td>
</tr>
<tr>
<td>3.063</td>
<td>0.032482</td>
<td>10</td>
<td>15.315</td>
<td>71.429</td>
</tr>
<tr>
<td>4.000</td>
<td>0.042419</td>
<td>9</td>
<td>20.000</td>
<td>64.286</td>
</tr>
<tr>
<td>4.685</td>
<td>0.049683</td>
<td>8</td>
<td>23.425</td>
<td>57.143</td>
</tr>
<tr>
<td>5.000</td>
<td>0.053023</td>
<td>7</td>
<td>25.000</td>
<td>50.000</td>
</tr>
<tr>
<td>7.000</td>
<td>0.074233</td>
<td>6</td>
<td>35.000</td>
<td>42.857</td>
</tr>
<tr>
<td>7.272</td>
<td>0.077117</td>
<td>5</td>
<td>36.360</td>
<td>35.714</td>
</tr>
<tr>
<td>8.128</td>
<td>0.086195</td>
<td>4</td>
<td>40.640</td>
<td>28.571</td>
</tr>
<tr>
<td>11.710</td>
<td>0.124181</td>
<td>3</td>
<td>58.550</td>
<td>21.429</td>
</tr>
<tr>
<td>13.390</td>
<td>0.141997</td>
<td>2</td>
<td>66.950</td>
<td>14.286</td>
</tr>
<tr>
<td>20.000</td>
<td>0.212094</td>
<td>1</td>
<td>100.000</td>
<td>7.143</td>
</tr>
</tbody>
</table>

Note: No. of interpolated observations
b Relative frequency of location = OBS/cell - total OBS
c Rank of cell according to OBS, from highest to lowest
d % of maximum relative frequency = PROB / maximum PROB
e % of home range represented by cell = % cells with PROB = PROB

Relative frequency. The percent of the home range (PCTRANGE) represented by each relative frequency was defined as the percent of cells having relative frequency values greater than or equal to it.

The area of the home range can be graphed in relation to its use. This plot (Fig. 2) shows the percent of the home range at or above a given relative frequency value (where the relative frequency is expressed as a percent of the maximum relative frequency). Very little of the home range (7%) is at the highest frequency value, and all of the home range (100%) is at or above the lowest. We defined the dividing point between high and low use as the point where the plot is maximally distant from a straight line with a slope of -1, the slope of a distribution that cannot be distinguished from random use. The dividing point can also be described as the point where the relative frequency values begin to change slower than the area associated with them. That is, the drop in intensity of usage from core to periphery has become more shallow. This is different from an inflection point, which is where the slope of a smooth curve changes from increasing to decreasing. The relative frequency level that is associated with the division between core and periphery is entirely independent of the size of the home range; instead, it is determined by the individual animal's utilization distribution. In our artificial data set, the core includes grid squares 1 to 3 (Table 1).

The pattern in Fig. 2 is the typical pattern that we observed for our bears, with a small area of the home range used much more heavily than the rest. However, 3 basic patterns of home range use can be described. In a 3-dimensional map of a home range (such as Fig. 3), “clumped” use consists of a small core area and much periphery. “Even” use would be represented as an elevated flat plateau, and “random” use would show roughly equal areas of peaks, valleys, and transitional areas. These patterns can be distinguished by the AIM. Clumped use results in a plot like the one shown in Fig. 2; even use results in a plot that stays above the straight line and falls to meet it; random use results in a plot that closely follows the straight line.
Fig. 3. Core areas as determined by the AIM (A) and Samuel et al.'s (1985) method (B). The core is shown with flat-topped symbols, the periphery with pyramidal symbols. Data are from an adult male bear, followed from May to December 1986.

The technique of Samuel et al. (1985) defines the dividing point between high and low use as the level of use that would occur if all use were distributed evenly over all of the occupied cells. This is algebraically equivalent to 1/(number of cells occupied). Thus the use level that divides high from low use is strictly determined by the home range size. In our artificial data set, the core defined by this method includes squares 1 to 6. The following analysis explores the extent to which the area of the core is influenced by the home range size. The core area that results from application of each method to real bear data clearly shows the difference between the 2 definitions (Fig. 3). The AIM definition of core includes only the most highly used areas, and the Samuel et al. (1985) definition includes all areas used more heavily than the mean.

Once the division between high and low use areas is established for each of the 2 methods, several variables can be calculated:

\[
\text{Total Area} = (\text{Number of cells used}) \times (\text{Area of a cell})
\]

\[
\text{Core Area} = (\text{Number of cells in core}) \times (\text{Area of cell})
\]

\[
\text{Core Use} = \text{Sum over all cells in core} (\text{Relative frequency of use})
\]

We used regressions (SAS, General Linear Models Procedure) on various pairings of these variables in an analysis exploring the characteristics of the core area resulting from the 2 definitions.

RESULTS AND DISCUSSION

Core size is influenced by total home range in both methods. However, the core size determined by the AIM is smaller than that determined by Samuel et al.'s method (Fig. 4). The influence of the total home range size is weak for the AIM; the coefficient of determination \(r^2 = 0.34\) and the slope (0.08) of the relationship are low. The low \(r^2\) is a result of a great amount of scatter, indicating much variation in core size within total home range size. But the method is not entirely independent of home range size, as the significant regression slope shows. This makes sense, since the core cannot be larger than the total home range.

The periphery (the complement of the core) must expand when the home range increases unless the core increases in direct proportion to the total home range (Fig. 5). Not surprisingly, the size of the periphery is strongly determined by home range size in both methods \((r^2 \approx 0.98\) and 0.95 for the AIM and Samuel et al. (1985) methods, respectively). The strong connection between home range size and periphery size emphasizes that these analyses (and the researchers who created them) are oriented towards an interest in the core rather than the periphery. Perhaps the use of peripheral areas warrants more research attention than it has received.

The amount of use in the core tends to decrease at larger home range sizes (Fig. 6). This trend is marginally
significant ($p = 0.04$) for the AIM, but not for Samuel et al.’s method ($p = 0.14$), however the slopes of the 2 regressions are not significantly different from each other ($p = 0.13$). Thus any conclusions from this regression will be weak. The percent of use in the core shows a large amount of scatter for both methods, indicated by their low $r^2$ values ($r^2 = 0.24$ and 0.13 for the AIM and Samuel et al. method, respectively). This highlights the difference between these methods and one such as Ford and Krumme’s (1979), which defines the core as the area containing an arbitrary constant amount of use. This relationship demonstrates the responsiveness of the AIM and Samuel et al. methods to individual patterns of use.

Constant methods fail to reflect the patterns exhibited by the animal, whereas the variable methods presented here allow the individual’s actual distribution of locations in the home range to determine the amount of use in the core. The decreasing core use in the AIM is the result of redistributing use out of the core into the periphery as the home range increases. In the Samuel et al. (1985) method this trend is not significant because the core expands with the home range and “reclaims” the use that is being spread over a larger area.

The inverse of the highest cell usage value (maximum relative frequency) (Fig. 7) strongly determines the core area of the AIM ($r^2 = 0.91$), but has a lesser influence on the core defined by the Samuel et al. method ($r^2 = 0.34$). However, the slopes of the 2 methods do not differ significantly ($p = 0.24$), showing that both are similarly influenced by this aspect of home range. We investigated this relationship because the AIM uses the maximum relative frequency as the divisor in the calculation that determines the division between core and periphery. The maximum of a distribution may be missed due to sampling error and, if the technique highly depends on the maximum, its results may be erratic. The fact that the 2 methods are similarly influenced by $1/\text{maximum relative frequency}$ indicates that there is an inherent connection between the height of the utilization distribution and the amount of area that is used intensively. That is, the
essential resource such as food, mates, or shelter. Intense usage may be restricted to an area smaller than the total home range for at least 2 reasons: 1) the resource is patchily distributed in small areas, or 2) neighbors utilize the resource and limit the individual’s use of areas outside its own core. Conversely, the home range may include peripheral areas because: 1) they are traversed while travelling between disjoint core areas, 2) they contain crucial resources that are used less intensively than those in the core, or 3) animals must continually explore for new resources.

The Area Independent Method also can be used on a population basis simply by including the analysis locations from all individuals. This would allow identification of important geographic areas for the population. It is, of course, difficult to get complete data from all individuals. Such sampling problems are inherent in any

more time an animal spends in a small part of its home range, the less time it can spend elsewhere, consequently the core is smaller.

The choice of grid size has a major influence on the results of any home range method that uses a grid. Results from the AIM will not be comparable between studies that use differing grid sizes. A large grid size may incorporate much unused area if an animal enters only a small part of it, and will artificially inflate the home range size. A large grid size will also obscure patterns of differential use if a cell includes both high and low use areas. An extremely small grid size will reduce the home range to virtually a tracing of the animal’s travel path. A small grid size will similarly obliterate patterns of differential use, few cells will be heavily used since a slight change in position will put the animal in a different cell. Intermediate grid sizes will alter the size of the home range and the resolution of the core boundary to a lesser extent.

We speculate that the core of the home range represents an area within which an individual uses a rich and
In summary, the Area Independent Method has essential differences from other measures of central tendency for animal locations. It uses objective criteria to define a heavily used area, and the criteria are primarily based on an animal's greatest concentration of use. This makes the technique well suited for studies that statistically test hypotheses concerning the effects of environmental factors on home range and core area size and usage.

LITERATURE CITED


