

Home ranges reconsidered

A reply to 'Are Home Ranges Fractals?' by A.O. Gautestad and I. Mysterud

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The authors bring to bear several criticisms (Gautestad and Mysterud 1994) of my 1990 paper on animal home ranges (Loehle 1990). Some of these criticisms are valid and are corrected here, but others are not.

The first criticism concerns my use of disks to represent the areas searched. If one is only interested in where an animal is found, then point data are clearly adequate. If however, we wish to characterize either foraging or territoriality, then point locations are inadequate. In my previous paper, I was interested in hawk foraging. At any given time a hawk can scan a large area as it is soaring, particularly with respect to observing birds in the air. Deer, on the other hand, can reach only what is in front of them. This limitation must be taken into account if we wish to know how thoroughly the deer searches its habitat for food. When wolves howl, the sound carries for miles, so that very sparse coverage of its borders is sufficient to warn away other packs. It is possible to estimate effective search areas (for a hawk) and effective howl zones (for a wolf) experimentally or by observation. For such behaviors the point observations of animal location are not the 'real' data but are only *correlated* with the real data (the area searched for food or the territory defended).

Gautestad and Mysterud next commented on my concentration index C

$$C = \frac{A}{n\pi r^2}, \quad (1)$$

where A is total projection area covered by circles, n is number of points, and r is the search radius. C will indeed be dubious if data are recorded so frequently that the animal is still standing and chewing at both t and $t + \Delta t$. For C to be useful, Δt must be sufficiently large so that successive circles do not overlap when the animal is foraging, though clearly no such condition is relevant if the predator uses a perch. The objection of Gautestad and Mysterud that ' C is a dependent variable even when the locations are non-autocorrelated. The reason is that, for large n , a new (non-autocorrelated) location has a tendency to increase the local plot density within A at a given box resolution, rather than contributing to a larger A . Thus, more overlap is generated with increasing n , making C n -dependent.'

In reply, I note first that the degree of overlap with previous circles is precisely what C is meant to measure: how much the same area is used (searched) repeatedly. It is true that C will decrease as n increases, but C should stabilize at some minimum n that is sufficiently large to be truly representative (as measured by a stable fractal measure). C is not calculated as a function of box size, will not depend on Δt if successive points are non-correlated, and is intended to vary with r , which reflects the search radius and is a biologically meaningful difference between species.

Gautestad and Mysterud proposed an alternative 'graininess' parameter C as

$$C = \frac{A}{\sqrt{n}}, \quad (2)$$

where A is the area of the average minimum convex polygon and n is reasonably large ($n > 50-100$). For their C , I note (1) that it assumes that all of the area within the minimum convex polygon is used (whereas a lake may in fact be in the middle of a bear's range), (2) that it neglects the search area, and (3) that A will tend to stabilize at large n , leading to a decrease in C with increasing n . Furthermore, the minimum convex polygon area is very sensitive to excursions (occasional long trips away from the central territory) and is meaningless for non-territorial or migrating species. A young eagle may wander over several states, but is this its territory? Both my index C and my fractal characterization work equally well for all of these cases.

Gautestad and Mysterud next pointed out that my method of calculating the fractal dimension has problems. This is true, but the problem has nothing to do with the introduction of the disks. The disks represent the area searched, and we do in fact wish to quantify this pattern. The disks only 'fill in' the area between points if one takes a map (aerial) perspective. If we lay a fine-scale grid of points over the circles, the Z value (elevation) at each grid point is the number of circles overlapping that point (Loehle 1990). This set of overlapping circles represents more of a 'utilization distribution' than just a set of animal locations.

The next step is the use Z values from above to obtain a fractal dimension. Gautestad and Mysterud are correct that my method of calculation in 1990 was in error. The proper calculation should be based on a frequency approach, as follows.

We are interested in computing the fractal dimension of the map of pseudoelevations in order to quantify the roughness. The difficulty here is that ordinary fractals require that the x , y , and z dimensions all be in the same metric (e.g., meters). This condition is not met here because the elevation dimension is in counts of circle overlap units, not planar map units. Farmer *et al.* (1983) provided a solution to this problem. They pointed out that dimension has several definitions, which fall into two general classes: (1) those that depend only on metric properties (capacity) and (2) those that depend on the frequency with which a function visits different regions of the space (including several

measures generally referred to as the dimension of natural measure). Here we use the information dimension d_I , which is of the latter type. The information dimension quantifies the degree of deviation from uniformity over space of the probabilities of occurrence of the function. The pseudoelevations must be converted into some sort of probability measure.

For a box size of one pixel, it is straightforward to convert the Z values into 'probabilities' or relative information values as follows:

$$P_i = Z_i / \sum_{i=1}^M Z_i \quad (3)$$

Here P_i measure the relative number of disks overlapping a pixel, and

$$\sum_{i=1}^M P_i = 1. \quad (4)$$

As we look at the home range at a coarser scale, we progressively lose information about the fine-scale structure because we are averaging or lumping larger areas together. This is a type of dissipation of information with change of scale. Average Z_i values within a box ϵ reflect this information dissipation or smoothing. To maintain P_i as a probability at each scale, the P value within a box ϵ must be recalculated as

$$P_\epsilon = \sum_{i \in \epsilon} Z_i / \sum_{i=1}^M Z_i, \quad (5)$$

where $K(\epsilon)$ is the total number of boxes of size ϵ . For example, for 2×2 boxes we would sum the four Z_i values within box ϵ . For computational details, refer to Loehle and Wein (1994).

Given these probabilities as a function of location and scale, we may define the information dimension d_I as follows (Sommerer and Ott 1993):

$$d_I = \lim_{\epsilon \rightarrow 0} \frac{\sum_{i=1}^{K(\epsilon)} P_i \log P_i}{\log (1/\epsilon)} \quad (6)$$

In the present context we have no reason to suspect that the limit defining d_I is well defined for a home range, because it is not necessarily self-similar (i.e., d_I is not constant across scales). We

therefore compute the information dimension discretely at a series of scales by using

$$d_I(\varepsilon) = \frac{\sum_{i=1}^{K(\varepsilon)} P_i \log P_i - \sum_{j=1}^{K(\gamma)} P_j \log P_j}{\log [1/\varepsilon] - \log [1/\gamma]}, \quad (7)$$

where γ is the box size next larger than ε . Equation 7 computes d_I as the slope of the line, at each scale, given by the information measure versus $\log (1/\varepsilon)$. This expression allows us to take advantage of a convenient nesting for computing d_I at a series of scales within a single loop, as in Loehle (1990). For details see Loehle and Wein (1994).

We can see that the information dimension d_I is based on an information theory calculation of uniformity $P_i \log (1/P_i)$; as such, d_I is related to the standard diversity indices used in ecology and is also a natural extension of the indices of O'Neill *et al.* (1988). The index d_I is also a dimension related to fractal dimensions (d_f). For a flat map where all pixels are assigned to a type (value = 1) or not (value = 0), giving a black and white image, generally $d_I = d_f$. Thus, a uniform map with a distinct linear feature such as a river will have a $d_I = d_f \approx 1$. For the case studied here, where pixels are assigned probabilities corresponding to usage intensity, however, $d_I \neq d_f$ because in fact d_f cannot be computed.

The above calculation method overcomes the difficulties pointed out by Gautestad and Mysterud for my earlier paper. In particular, above a minimum sample size \mathbf{d} , is very insensitive to n because it is probability (frequency) based. It is also insensitive to rare outlier points because they are not weighted heavily, whereas even a single long excursion by an animal will result in a huge increase in the

minimum convex polygon size. The concern that the fractal dimension is not well defined at very small box sizes, discussed by Gautestad and Mysterud, is not a real problem but merely reflects the limit of spatial resolution inherent in any set of empirical data.

In conclusion, with this revision in the calculation of the fractal dimension, I believe that my original approach remains valid and, in fact, even more successfully overcomes the limitations inherent in prior methods.

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