

# COMPLEX MOVEMENT AND SCALE-FREE HABITAT USE: TESTING THE MULTI-SCALED HOME-RANGE MODEL ON BLACK BEAR TELEMETRY DATA

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**Abstract:** Black bears (*Ursus americanus*) use the landscape over relatively coarse scales compared to many other mammals. We analyzed the way these animals relate to their habitat in general terms using a statistical approach. *A priori*, we conceived of scale-specific and scale-free types of habitat use. The scale-specific model assumes that an individual's movements are due to dynamic responses to the individual's perceptions over a limited spatial scale that reflects the circle of perception (CP) around the animal's location. Using serial processing, the animal moves to new sites, gaining new perceptions that lead to new movements, but is constrained by site fidelity (home range, HR) tendencies. This model is of a scale-specific statistical process at the scale of CP. According to the alternative model, individuals now and then use memory maps of past experiences to take strategic, relatively directed (i.e., coarse-scaled) movements beyond the CP but within the HR using principles from parallel processing. Although the former model is more traditionally used in modeling, the latter more closely resembles an ecological understanding of animal behavior. Our model, the multi-scaled random walk (MRW), assumes (1) spatially explicit memory effects, and (2) that optimization of patch use at coarse scales is as important as optimization at finer scales over the scale range from CP to HR. Mechanistically, this property makes the habitat use process scale-free, or fractal, over this range of scales. From the 2 basic MRW assumptions, the observed part of the HR area ( $A$ ) from  $n$  non-autocorrelated relocations is expected to increase proportionally with the square root of  $n$  up to  $n$  well beyond the limits of applied ecology. We verify the predictions of this model on telemetry material on black bear movements. Some implications for bear research and management are discussed.

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**Key words:** black bear, complexity, home range, Hurst exponent, memory map, movement, random walk, rescaled range analysis, telemetry, *Ursus americanus*.

Radiotracking of animals has over recent years generated large data sets on movement and habitat use. Despite extensive samples of relocations from such efforts, one is still confronted with difficulties connected to transforming the scattered coordinate plots into a quantitative variable like home-range (HR) size. Fuzzy borders and frequent outlier relocations make any line of demarcation rather dubious. Over time this has sparked the development of relatively sophisticated statistical methods for HR demarcation, but a generally accepted standard has yet to emerge. However, we have shown elsewhere (Gautestad and Mysterud 1993, 1995) that the statistical problems go deeper than methodology. Demarcating an HR size and location from a set of coordinate plots involves more than applying a statistical protocol. We question some of the basic assumptions from the classic home-range paradigm, as they follow directly or indirectly from traditional statistical protocols connected to HR descriptors (size, location, utilization distribution, overlap, occasional sallies, and so on) (Gautestad and Mysterud, unpubl. data).

For the first time, we use rescaled range analysis ( $R/SD$ ; size of range/standard deviation) to reveal the way individuals (black bears in this case) relate to their habitat in general terms. This analysis makes it possible to differentiate between animals that use their home range

habitat in a tactical manner only (model 1) and animals that use the habitat in a more complex way by mixing there-and-then tactical movements with strategic, long-range movements (still within their HR) due to local and temporal conditions as they appear from a more coarse-grained perspective (model 2). Our focus below on HR area and extreme relocation plots (range) is rooted in the potential of these descriptors to test whether an animal responds to its environment in accordance to model 1 or 2. These 2 models use very different sets of assumptions and statistical methods for analyzing HR descriptors (Gautestad and Mysterud, unpubl. data). Thus, it is of great practical importance to explore which of the 2 models is most feasible for black bears.

The material for the present test consists of >7,000 telemetry relocations from 84 black bears from Great Smoky Mountains National Park and Cherokee National Forest, both in Tennessee. The data were collected during several research projects by various graduate students under supervision of M.R. Pelton. We thank D.L. Garshelis, H.B. Quigley, P.C. Carr, C.R. Villarrubia, S.R. Garris, A.P. Clevenger, J.J. Beringer, S.G. Seibert, S.R. Reagan, and F.T. van Manen for making this telemetry material available for the present analysis. We also thank M.L. Munson-McGee and 2 anonymous referees for critical and constructive comments that spanned from

extensive corrections of style and typography to aspects of HR modeling in general.

## THEORETICAL BACKGROUND

Any statistical protocol for estimating HR descriptors is based on assumptions about how the individual in question relates to its environment during movement which results in a given scatter of coordinate plots (relocations) from radio telemetry. For example, a traditional assumption from the classic HR paradigm (which we refer to as the classic model, or model 1, below), is to expect an area asymptote to emerge when the demarcated area ( $A$ ) is graphed as a function of number of non-autocorrelated relocations ( $n$ ). This assumption has just recently been questioned and shown not to be valid (Gautestad and Mysterud 1993, 1995). To understand this paradox, we have to consider some theory from statistical physics.

The assumption about an asymptote would be valid if individuals used their habitat in a scale-specific manner: in statistical mechanics terms this is the Brownian motion of particles (random walk) in physics. We first describe this process in its general form, under the condition of free dispersal. Next, we define how this process is modified in a HR context, where site fidelity limits free dispersal.

In Brownian motion, particles collide resulting in new directions and speeds from each collision. Each collision is deterministic from there-and-then conditions, as described by Newton's laws of motion. In an ecological context, the individual replaces the particle and the collisions are analogs for movement-influencing events. However, when the path for a given particle or individual is observed at time intervals ( $t$ ) that are large enough for many independent collisions or events to occur during the interval, the successive observed displacements become *de facto* random in direction and length. Further, the distribution of observed displacements become unimodal and normal when sample size is large, due to the central limit theorem. From statistical mechanics theory we can also forecast that the mean square displacement (MSD) from a chosen initial location of the particle or individual on average can be expected to increase proportionally with time (i.e., the distance is expected to increase with the square root of time). For example, if we repeatedly measure the displacement distance at  $t$  and calculate the mean displacement, we can expect that this mean would have increased by a factor of square root of 10 if we had increased  $t$  by a factor of 10. At very fine time scales, each movement-influencing event for an animal can be considered biologically

and ecologically deterministic. However, from the randomness that appears in the displacement pattern at larger time intervals, a new kind of order will emerge, the statistical mechanics law of diffusion-like expansion of MSD as a function of time. Thus, by studying MSD over intervals which are large enough to ensure randomness in successive displacement lengths and directions, we can test whether an individual over the total observation period related to its environment in a purely tactical and sequential, and thus scale-specific, manner. If MSD increases proportionally with time, this is verified.

If such a random walk particle or individual shows site fidelity by expressing a stronger tendency to move toward a center the farther it is from this center, we can eventually translate the scatter of particle or individual relocations as an HR. From such a scale-specific process (where the characteristic scale is the mean distance between each collision), several statistical properties will emerge. For example, if we graph the area ( $A$ ) from the minimum convex polygon (MCP) embedding a sample of  $n$  non-autocorrelated relocations (by choosing  $t$  large enough to expect at least 1 return towards the center during  $t$ ) as a function of  $n$  we expect the rate of increase of  $A$  to decrease with increasing  $n$ . Typically, an asymptotic approach towards what can be called the particle's or individual's true HR can be expected to emerge from  $n$  of magnitude 100–150 and upwards (Gautestad and Mysterud 1995).

It may surprise many ecologists to learn that the RW paradigm above is automatically invoked if one assumes that such an area asymptote can be estimated realistically from a set of 100–150 or less relocations. An RW process excludes any historic influence on successive displacements from 1 relocation to the next when  $t$  is of the magnitude of 10–20 scale units of the characteristic time scale (mean time interval between successive, independent movement-influencing events) or larger. RW also excludes any influence from habitat patterns as they appear at coarser scales than the characteristic spatial scale (mean distance between movement-influencing events) beyond the influence predicted from simply summing embedded local influences at the characteristic scale. In other words, the random walk paradigm demands that the model animal has no cognitive relationship to its environment at scales coarser than the characteristic scale.

Obviously, the RW model does not seem to resemble an ecological understanding of animal behavior in a HR context. A reevaluation of real data from many taxonomic groups of vertebrates has shown that the RW assumption is not valid in general terms (Gautestad and Mysterud 1993, 1995). In this respect, there is a deep-

rooted discrepancy between empirical data and theoretical models. Thus, an alternative hypothesis for animal area use is needed. Herein, we supplement our previously published tests on predictions from such an alternative model for space use, the multi-scaled home-range (MHR) model (Gautestad and Mysterud 1993, 1994, 1995, unpubl. data) on black bear data. An MHR is represented by the spatial pattern that emerge from  $n$  non-autocorrelated relocations when  $n$  is very large. The process that generates this MHR pattern is the multiscaled random walk (MRW).

## THE MRW–MHR MODEL

MHR is an overall pattern of space use that is expected to emerge from a set of non-autocorrelated relocations if an individual performs a multi-scaled random walk (MRW). MRW is based on the assumption that information at coarse resolutions in the long run influences successive displacement steps to the same magnitude as information at finer resolutions. This means that the product of scale (measured as, for example,  $\text{km}^2$ ) and number of deterministic movements on this scale can be expected to be constant from 1 scale to another (up to the scale of the HR itself). In the long run, many short-distance movements should be intermingled with fewer displacements on coarser scales. If so, optimization of habitat use within an HR is uniform over scales up to the size of the HR. In other words, MRW is based on an assumption that the rules for patch choice should be applied by the animal to (ideally) all patches at all spatial resolutions (scales) within its HR, and not on fine scales only. The number of patches within a given demarcated HR is larger for finer resolution patches. Thus, more local movements to and from neighbor patches have to be performed on a fine spatial scale relative to (fewer but larger) displacements on a coarse scale when an animal seeks to equalize its optimizing effort over a range of scales.

The MRW model involves testable rules about how an animal over time uses its experiences in local habitat, by assuming the use of memory map information, over a range of spatial scales (grid resolutions). It simply represents a generalization of the classic and scale-specific RW model to a scale-free RW model.

We now need to define the ecological analog to this characteristic scale for a scale-specific process (the classic HR paradigm). The individual's circle of perception (CP) is a feasible choice. CP is defined as the (idealized) average area around the individual's location within which it can obtain information about local conditions

and new events directly by its senses. Even if a bear reacts to smell from a long distance, the typical HR is orders of magnitude larger than this distance (if CP was of the magnitude of HR, the MRW would be simplified to classic RW). The CP for a bumblebee would be small relative to the CP of a black bear. However, bears relate their activities to a vastly larger HR than a bumblebee during a time span like a season. Consequently, the CP in both cases can be considered small relative to the extent of the respective HRs. Thus, a large RW/CP ratio is a second general assumption for the idealized MRW model.

To summarize, while an RW process involves tactical and sequential movements due to events at the scale of CP or finer, MRW includes more strategic influences due to environmental conditions as they appear on resolutions between CP and HR. In practice, we will sometimes see large and relatively directed movements which appear inexplicable from current local conditions. However, from a coarser perspective in space and time the movement can be explained, demonstrating the complexities of parallel processing. The MRW involves 2 assumptions which are not valid for the classic RW assumption under HR constraints on free dispersal. First, optimization of habitat use is expected to take place with equal effort on all scales from CP to HR, and second, the HR/CP ratio is assumed to be relatively large.

## MHR Defined

Consider a set of imaginary grids superimposed on an idealized HR as a multilayered chessboard of  $m$  discrete levels (Fig. 1). The discrete levels represent slices from a continuous range, like when we are studying the pattern from a process over (continuous) time at discrete points in time with interval  $t$ . In this picture, the characteristic scale for the movement process in a classic HR model would be limited to 1, the bottom slice, of magnitude CP. However, for MRW we assume that parallel dynamics over a range of scales beyond CP contribute to the observed movement. The next larger chessboard layer has  $k$  times larger grid cells. We use  $m$  discrete levels with cell sizes scaling as  $k^0, k^1, k^2, \dots, k^m$ , where  $k$  is a parameter  $>1$ . The highest level on this 3-dimensional chessboard has only 1 cell, the true HR, with size  $k^m$ . The choice of the magnitude of  $k$  is not central. It simply expresses how coarsely we divide a continuous scale axis. We define the size of the chessboard as the true home-range, knowing that this is an idealized demarcation of a complex object with fuzzy borders. If a given displacement during  $t$  is very large due to conditions that the individual reacted to (indirectly, via the memory map)

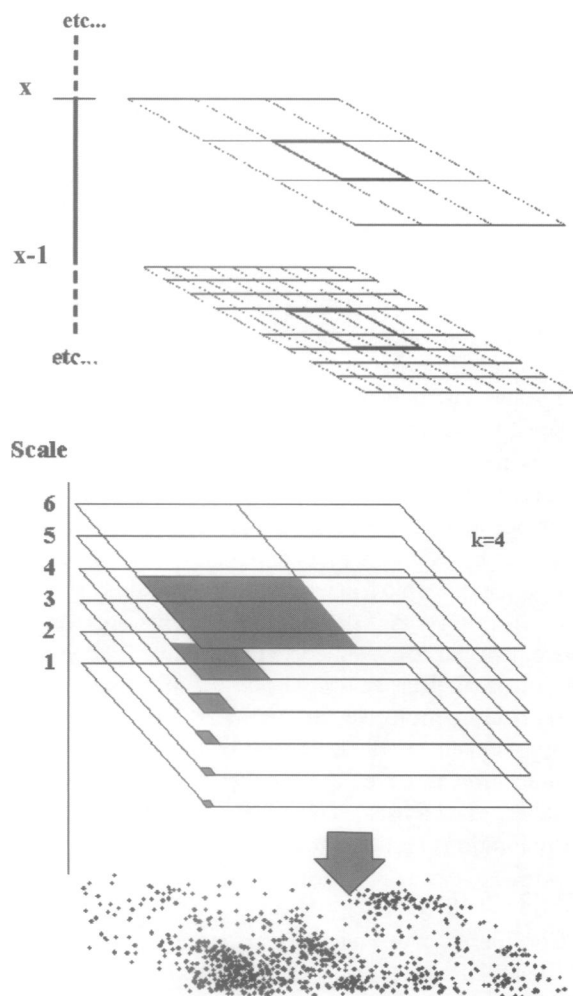


Fig. 1. The multi-scaled home range (MHR) geometry can be visualized as a multi-layered chessboard where the next layer ( $x$ ) has  $k$  times larger grid cells than the lower layer ( $x-1$ ). The 6 grids of a geometrically scaling home range (HR) structure is superimposed over a set of animal relocations (dots below the grids) in this example. A smaller  $k$  gives more layers for a given HR.

as they appeared from a coarse scale's perspective, this displacement is defined as a strategic step to a neighbor cell on a higher scale level (Fig. 1). Conversely, a large step could also appear from a sequence of events to which the animal reacts only tactically, at a low scale level, as could happen if the animal were being chased. In that case, displacement is not strategic, but tactical.

A strategic move (relative to the scale of CP) is different mechanically than the movement of the classic approach, where relatively large steps (from point A to B on the map when  $t$  is small) has to be initiated by a strong

movement-influencing event (or by several milder influences in succession) at the scale of CP or below. MRW dynamics has to be invoked to understand the move as strategic, which can be defined as displacement from A to B not being explained by summing the effects from a sequence of events at a local scale up to CP during  $t$ . In other words, the mechanics become functionally non-linear from this scaling perspective; the system cannot be understood or modelled without including the true emergent properties of the system. We must study specific statistical properties from a large set of displacements to conclude what process influenced the movements in general terms when seen as a whole.

The advantage of geometric scaling (i.e., log-linear [Fig. 1]) is that the number of grid cells increases inversely proportional with scale level. Choosing  $k$  times as large grid cells gives  $1/k$  fewer grid cells within a given area. This satisfies our model assumption that individuals, in the long run, tend to equalize their effort to optimize patch use and movements over all scales within the home range (with the help from their memory map). To optimize use of area and collect information at all levels in the mental HR memory map, coarse-scale movements between neighbor cells at high levels in the memory map scaling hierarchy should be less frequent than fine-scale movements. A magnitude of  $k$  times as many local displacements are needed to respond optimally to local conditions at the next lower level, where grid cells are  $k$  times as numerous. Similarly,  $1/k$  fewer displacements are needed to visit the  $k$  times larger (but  $1/k$  as frequent) grid cells at the next larger level, regardless of our focal scale in the range from 2 to  $m-1$ , where level 1 is the (idealized) level for CP and  $m$  is the HR level.

If the inter-relocation interval  $t$  is sufficiently large, successive relocations of an animal performing MRW (RW horizontally, on a given level in Fig. 1, mixed with RW vertically, by shifting scale level) will be non-autocorrelated. In this respect, it is similar to classic models (Swihart and Slade 1985). MRW, with its mixture of tactical (within-CP scale) and strategic (memory-based) movements, can have a large effect on statistics like HR size estimates.

### Observed HR Area as a Function of Sample Size

In HR analyses it is traditionally assumed that, from a set of non-autocorrelated successive relocations, the observed area ( $A$ ) from a sample of  $n$  relocations should approach the true HR area asymptotically as  $n$  is increased (e.g., Andreassen et al. 1993). Normally, one also assume a stationary HR center for the observation period

(a fairly stable moving average of successive  $x$ - or  $y$ -coordinate values over a series of relocations). For small  $n$ , one can then expect to observe a relatively small part of the true HR, but for a sufficiently large  $n$  (typically,  $n$  of magnitude 150–200 if non-autocorrelated relocations are used), relatively little net increase in  $A$  is expected as  $n$  increases.

The classic assumption about an area asymptote when we deal with non-autocorrelated relocations can be defined as

$$A = KQ(n), \quad (1)$$

where  $K$  (the true HR) is a function of the area-defining method that we apply ( $A$  from the minimum convex polygon method will give a different  $K$  than, say,  $A$  defined from the harmonic mean method).  $Q(n)$  is a function which can be used as a rule-of-thumb to estimate the expected relative underestimate of  $A$  when  $n$  is small and the MCP method is used (Gautestad and Myrsetrud 1993):

$$Q(n) = \exp(6/n^{0.7}) \quad n > 5 \quad (2)$$

When  $n$  is small,  $Q(n)$  is relatively large ( $>1$ ), but  $Q(n)$  approaches 1 asymptotically with increasing  $n$ . To find a realistic estimate of  $K$  (the true, idealized HR area) is then a matter of using the correct  $Q(n)$  function or collecting a sufficiently large sample size (for which  $Q(n)$  becomes a constant and  $K$  is found directly).  $Q(n)$  will change with different patterns of the local intensity of use (i.e., different utility distribution topography) within the true HR. However, eq. (2) is a fairly good approximation for the average form of observed utilization distributions (Gautestad and Myrsetrud 1995).

## Defining Area from Autocorrelated Relocations

If the HR center is not stationary through the total observation period  $T$ , the magnitude of autocorrelation in the series will obviously increase. The observed  $A$  from  $n$  relocations can be expected to be larger the larger we make the interval  $t$ . Thus, autocorrelation has to be present, since 2 relocations separated by a small  $t$  tend to be closer in space than 2 relocations that are separated by a larger  $t$ . Thus, whether we confirm non-autocorrelated relocations from statistical analysis, or we simply assume them to be so, this premise implies that the HR center was stable during the total observation period  $T$ , at resolution (temporal scale) of  $t$  to  $T$ . This is an important point. From the traditional RW-based paradigm,  $A$  can expand *non*-asymptotically for large  $n$  if

successive relocations are autocorrelated. In that case,  $A$  from a given  $n$  should be smaller when  $t'$  is relatively small within the interval  $t < t' < T$ , and  $t' = T/t$ . If we deal with autocorrelated relocations, we do not expect to find a proper and stable HR area estimate even for relatively large  $n$ .

For the classic paradigm the area asymptote will also be difficult or impossible to estimate if the HR utility distribution is very long-tailed; that is, if most of the individual's activities are very concentrated about 1 (or a few) sites within its true HR and the major part of its HR is used very sparsely. In that case a statistical autocorrelation analysis (ACF) will reveal a pattern of autocorrelated plots, even when time lag ( $t$ ) is very large. The reason for this is that the ACF method not only assumes the RW paradigm, but also assumes a fairly unimodal normal distribution for the utility distribution. If the activity is extremely concentrated to 1 or a few core areas, this is clearly violated and the ACF scores become inflated. A spurious verification of autocorrelation then emerges.

To summarize, from the traditional statistical mechanics assumptions, we always expect to find a fairly good estimate for the asymptote  $K$  in eq. (1) if the sample consists of a fairly large set of non-autocorrelated relocations. For smaller  $n$ ,  $K$  can be estimated (less precisely, though) by using  $Q(n)$  as an adjustment factor for the expected magnitude of missing HR area (eq. 2).

## Non-autocorrelated Data Sets: The MRW Model

MRW gives a different function for  $A$  as a function of  $n$ . If we assume a set of non-autocorrelated relocations and we define  $A$  as the minimum convex polygon (MCP) around the  $n$  relocations,  $A$  should expand as a function of  $n$  in a non-trivial way and in accordance with (Gautestad and Myrsetrud 1993)

$$A = CQ(n)\sqrt{n} \quad (3)$$

$C$  is the ecological and biological parameter area per square root of relocation, expressing how coarse-grained the individual has perceived its HR on average over the observation period. The choice of MCP is convenient, since it is a non-parametric method and its area can be expected to change proportionally with the mean square deviation (MSD) for a given data set. We can see from eq. (3) that  $C$  is much smaller than  $K$  in the classic model in eq. (1). However, the variation of  $C$  expresses to some degree the same ecological aspect as we seek to quantify classically by using  $A$  as the dependent variable. The

major difference is that  $C$  estimates the average magnitude for fine-scale habitat use within the HR, while  $A$  expresses the more coarse-scaled perspective of habitat use for the HR as a whole (large vs. small HR).  $C$  is expected to be larger when conditions are severe, and it is larger for a bear than for a mouse.  $C$  is positively correlated with the average step length between successive (non-autocorrelated) relocations,  $L_{av}$ . The relationship is  $L_{av} = z\sqrt{C}$  (since  $L$  is 1-dimensional, and  $C$  is 2-dimensional), where  $z$  is a scaling parameter that depends on how  $A$  is defined.

Eq. (3) implies that  $\sqrt{n}$  of the relocations disappear from the expansion function for  $A$  as a function of  $n$ . It takes  $\sqrt{n}$  more relocations to reveal a given percent of the true HR relative to the situation we expect if the RW model applies. For example, if we collect 100 non-autocorrelated relocations from an individual and expect to reveal about 60–80% of the true HR from this sample, we are fooled if the individual has used its habitat more in accordance with the MRW model. In that case we would need up to  $(100)^2$  (10,000) relocations to reveal 60–80% of the true HR. However, the magnitude of the scale interval from CP to the true HR will influence the necessary sample size. A smaller HR/CP ratio will reduce the number of relocations needed to define a given percent of the true HR size, with the classic RW paradigm appearing as a special case of MRW when CP and the HR is of equal magnitude (and the  $n$  relocations are non-autocorrelated). Since the HR/CP ratio can be expected to be orders of magnitude larger than CP even for bears with their well-developed senses of smell and hearing (i.e., a large CP), we can still expect eq. (3) to hold for sample sizes well beyond practical limits for field research.

For example, consider a situation where the true HR is of the magnitude of 10,000 times larger than CP. In black bear terms, consider an HR that is 100 x 100 km<sup>2</sup> and an idealized CP to approximately 1 km<sup>2</sup> (due to its well-developed olfactory organs). We can imagine this as a grid with 10,000 cells of size one km<sup>2</sup> each, where the total grid area represents the HR area. First, we consider the classical assumptions. Let us say we have 20 non-autocorrelated relocations available for analysis. Since the relocations are non-autocorrelated, they are probably located in 20 different cells on the grid (each location is randomized among the 10,000 cells). If we increase the number of (still non-autocorrelated) relocations to 200, we still expect nearly all of them to be located in separate cells. Thus, the aggregated area of the cells with  $\geq 1$  relocations (i.e., calculating  $A$  from counting boxes) tends to increase proportionally with  $n$  so long as the probabili-

ty of overlap (frequency of  $>1$  location per cell) is small. If we use the MCP method instead of counting boxes, we expect to see area increasing less than proportionally with  $n$  as  $n$  grows larger toward  $n = 200$  (but  $A$  increases proportionally with  $n$  for smaller  $n$ ), due to the asymptotic influence (see eq. [1]). Next, let us consider the same grid under MRW conditions. We expect to see  $A$  to be 3.3 times larger from 10 times larger sample size  $n$ , when we count boxes (Gautestad and Mysterud, unpubl. data) and 3.3 times larger if we apply MCP and adjust with  $Q(n)$  (Eq. [3]). In other words, we reveal no more area from 200 relocations than we expect to reveal from  $20 \times 3.3 = 66$  relocations under the classic paradigm. The missing area from 134 relocations (200–66) is due to a larger probability for an MRW to revisit previously visited cells compared to revisitation probability under classic assumptions. Thus, if we try to estimate  $K$ , the true HR size, from  $n = 200$  in this case (using eq. [1] and [2]), we will underestimate  $K$  substantially, relative to the true  $K$  of 10,000 km<sup>2</sup>.

To summarize, the MRW model predicts that the estimated HR area after the  $Q(n)$  adjustment of  $A$  (increasing observed  $A$  with a factor of  $Q$ , where  $Q$  is a function of  $n$ ) will expand proportionally with  $\sqrt{n}$  for all practical magnitudes of  $n$ . Thus, the defined area from, say, 200 non-autocorrelated relocations should reveal a much smaller part of the true HR than expected from the classic paradigm. *Contrary to the classic paradigm, this non-trivial expansion is not due to autocorrelation.* We assume non-autocorrelated relocations in eq. (3), so the expansion is neither time dependent nor a spurious result from an extremely multimodal or long-tailed utility distribution for the HR. The expansion is due to model animals that use their habitat in a parallel fashion, considering options for intra-HR movement and habitat choice from a multiscaled point of view, where the intensity of use is equalized over the scale range from CP to the true HR. One particular aspect of this model is expressed in eq. (3), where the non-trivial area expansion is a true emergent property from a scale-free process. The expansion is non-trivial, since the area asymptote,  $K$  (in eq. 1), can be expected to be absent even for large  $n$  and series of non-autocorrelated relocations. The expansion is scale-free, since  $A$  for a given  $n$  is not influenced by the time scale  $t$  beyond the critical limit for autocorrelation. We can change the magnitude of  $t'$  within the interval  $t < t' < T$ , and we still expect to find the same estimate for  $A$  for a given  $n$ . Paradoxically (from the classic paradigm),  $A$  will expand with the square root of  $n$ , and we find the same magnitude of  $C$  whether we use a large or a small  $t'$  within a given  $T$ .

The MRW–MHR theory is not metaphysics, but rather an unfamiliar aspect of a special branch of statistical mechanics. Because of this theoretical expansion of the classic RW theory in an ecological context, we can test whether an individual (or a set of individuals) relate to the environment in a scale-specific and RW-like manner or in a more complex (but ecologically more feasible) manner by using many scale resolutions in parallel. Further, we now have protocols to test whether the multi-scaled habitat use is scale-free, by estimating the necessary statistics to compare with eq. (3) with eq. (1) as the null hypothesis.

### Proper Data Sets for a Test of the MHR Hypothesis

As we explained above, this test depends on non-autocorrelated relocations. Thus, we must ensure that 2 central conditions are satisfied. First, the inter-relocation interval,  $t$ , must be large enough to satisfy the criterion that  $A$  from  $n$  relocations will, on average, give the same  $A$  whether we choose  $t'$  large or small within a given range  $t < t' < T$ . Second, we must remove data sets which give spurious autocorrelation signals (i.e., an inflated ACF) due to, for example, very long-tailed utility distributions (UDs) or inclusion of very extreme outliers in the data set. For extremely non-normal and non-unimodal UD, ACF will be inflated for small lags in the series, even when no true time-dependency remains between successive relocations.

The presence of autocorrelation does not indicate whether an RW or MRW model is confirmed by the data. It simply makes the test spurious, since the expansion of  $A$  in eq. (3) could then be due to, for example, a time-dependent drift or an extremely non-normal UD (whether the underlying process is RW-like or MRW-like).

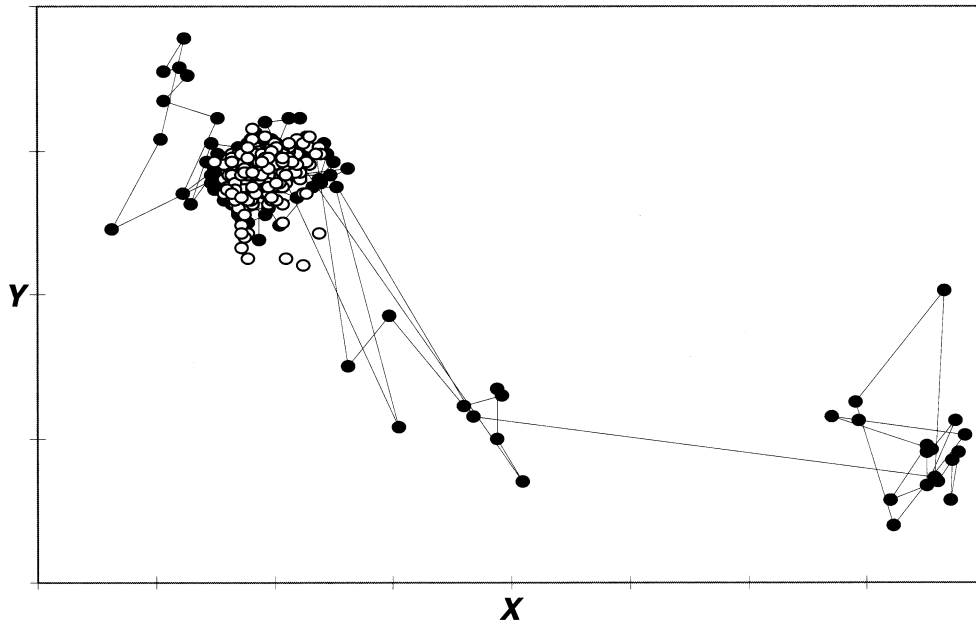
## METHODS

The material for this test of the MRW–MHR hypothesis consisted of 6,487 radio fixes from 84 black bears collected with a time interval of 1 day or more during 1976–83. The bears lived in Tennessee, in Great Smoky Mountain National Park and Cherokee National Forest, with 42 bears trapped in each region. We found no significant differences in space use and movement patterns between the 2 regions with respect to factors that were relevant for the present analysis, so we pooled the 2 data sets. Statistics for males and females, however, were computed separately. The average time between relocations

was 6 days; average observation period was 1.2 years/bear (Appendix).

Nine relocations (0.1% of all the relocations) with very large distance from the other plots were removed, to exclude extremely non-normal UD with very inflated over-all mean square deviations (i.e., the presence or absence of these extreme outlier relocations would strongly influence the variance for the given series and spuriously inflate the autocorrelation scores for small lags). The critical level for *a priori* removal of a location was set to a distance  $>2$  times the diameter of the smallest circle covering all other relocations for a given series. Thus, for all 9 outliers the plot pattern was a single dot (the outlier) far from a relatively compact swarm (the other relocation plots). More or less extreme outliers are expected to occur in a sample of relocations of an animal performing MRW within a MHR. However, for small series ( $n = 77$  on average for the present material) the presence of very infrequent large steps at high scale levels (Fig. 1) will appear to be separated by a long distance from the rest of the coordinate plots in a small set of relocations. With a long range of medium-sized outlier distances missing as they were in the 9 cases here (due to what we expect from relatively small sample sizes), an extreme outlier in a small sample will have a disproportionate effect on estimates of the HR center and the level of (spurious) autocorrelation. The removal of the 9 relocations is conservative and statistically sound, because its effect should tend to support the null hypothesis (area asymptote) rather than the MRW hypothesis (no area asymptote within practical limits of  $n$ ).

Some bears had an unstable and drifting HR center (calculated as the moving average location in the  $x$ - and  $y$ -direction over the last 20 relocations in a series; Fig. 2). A time interval of 6 days on average was obviously too short to give non-autocorrelated coordinate plots for the relatively large area used by the male bear, although it was sufficient for the smaller area used by the female bear (Fig. 2). A test of MRW using non-autocorrelated plots demands a reasonably stable HR center, since a drifting HR center, whether it is due to an extremely non-normal UD or a true time-dependency in the series, will inflate the ACF. Thus, before testing the MRW model from eq. (3), we separated all series with average correlation coefficient ( $r$ ) scores larger than 0.5 in a linear correlation between the coordinate plots for successive relocations (i.e., lag 1 in an ACF analysis). These series were categorized as autocorrelated; all others were categorized as non-autocorrelated. The  $r$ -score was calculated from both the  $x$ - and  $y$ -coordinates for a



**Fig. 2.** Two relocation series, one for a male (M185; filled dots, drifting HR center) and one for a female (F201; open dots, stable HR center).

given bear's data set. To illuminate the close relationship between spurious autocorrelation (as measured here by  $r$ ) and drift of the HR center, we graphed series with  $n \geq 100$  and compared the drifting tendencies between series from the 2 categories of  $r$ . The observed area expansion as a function of  $n$  (eq. [1] and [2] above) was tested separately for the 2 categories of autocorrelation (below and above  $r = 0.5$ ). In addition, we tested males and females separately for the series with  $r < 0.5$ .

We have previously used the average minimum convex polygon (MCP) from  $n$  relocations as a measure of observed HR area for sample size  $n$ . In the present test we use rescaled range analysis ( $R/SD$ ), where  $R$  is range and  $SD$  is standard deviation.  $R/SD$  is easier to apply on large as well as on small data sets. It is also superior to MCP due to simpler computations and the well-explored (but still not fully understood) nature of complex, multiscaled phenomena in general (Hurst 1951, Mandelbrot 1983:247–255). With  $R/SD$  we compute how the range of values (the dependent variable) in a series expands with series length (the independent variable,  $n$ ) as follows. First, we computed the average of the  $x$ - or  $y$ -coordinates up to relocation  $n$ , estimating the HR center's  $x$ - or  $y$ -projection as they appeared from  $n$  relocations. Second, we computed the series' ( $n - 1$ ) successive deviations from this average, which alternated randomly

between positive and negative values (due to non-autocorrelated relocations). On average, 50% of the deviations can be expected to be positive and 50% negative. Third, we calculated  $R$  as the range (maximum distance) between the maximum and the minimum value from the series where the ( $n - 1$ ) deviations were successively added. Fourth, we divided  $R$  with the same series' standard deviation ( $SD$ ) over the  $n$  values. Dividing by  $SD$  standardizes  $R$  so that  $R$  as a function of  $n$  can be compared over series with different magnitudes of  $R$  for a given  $n$  (i.e., large and small  $C$  in eq. [2]). Finally, we computed  $R/SD$  (i.e., the rescaled range,  $R$  divided by  $SD$ ) as a function of  $n$ .

For an RW,  $R/SD$  is expected to increase proportionally with  $\sqrt{n}$  (Feder 1988:149–162). Thus, with log-transformed  $R/SD$  and  $n$ , we expect a slope 0.5 in a  $\log(n) - \log(R/SD)$  plot. However, for an RW with HR constraints on free dispersal (i.e., the classic HR paradigm) we expect that  $R/SD$  should be constant (i.e., independent of  $n$ ), after an asymptotic approach toward this constant  $R/SD$  ratio with increasing  $n$ . This asymptote is analogous to the square root of  $K$  in eq. (1).

However, because  $R$  was divided by  $SD$ , the asymptotic approach toward a constant (the  $R/SD$  analog to a true HR size) will appear sooner ( $n$  of magnitude 30–40) than we expect from analysis of the mean squared deviation or MCP as a function of  $n$  ( $n \approx 150$ –200). This is

verified by a simulation below. Thus, the slope of  $\log(R/SD)$  versus  $\log(n)$  is expected to be zero beyond relatively small series lengths. This property is very advantageous ecologically since we often have to work with relatively small data sets. For example, the bear data sets average 77 relocations. Since we expect the slope of  $\log(R/SD)$  versus  $\log(n)$  to reach the asymptote relatively fast, a mean series length of  $n = 77$  should be enough for testing the MRW–MHR hypothesis against the null hypothesis, the scale-specific RW with HR constraints on free dispersal.

Another advantage with the  $R/SD$  analysis of increments is that the slope becomes directly comparable to the slope from minimum convex polygon area expansion when we are studying non-autocorrelated relocation series. We explained above that  $L_{av} = z\sqrt{C}$ . For an  $R/SD$  analysis  $L_{av}$  is proportional with  $R_{av}$ , where  $R_{av}$  is the average  $R$  for a given series length  $n$ , over a set of non-autocorrelated series of  $x$  or  $y$ -coordinates. Since the 1-dimensional magnitudes  $L_{av}$  and  $R_{av}$  are proportional with the square root of the 2-dimensional  $C$ , they also change in proportion with the square root of  $A$ , which we have defined by the MCP method in eq. (3). If the slope from  $\log(R/SD)$  on a series of increments is  $b$ , and the slope from MCP is  $b'$  (after adjusting with  $Q[n]$  for MCP, as described above), we have

$$b = b'/2 \quad (4)$$

In other words, since RW predicts  $b' = 0.5$  and classic models predict  $b' = 0$ , we should test whether the slope from  $R/SD$  analysis of increments is close to 0.25, and significantly different from 0.

The intercept  $C$  in eq. (2) is not comparable with the intercept from  $R/SD$  analysis because the former is an area parameter and the latter is a unitless (non-denominated) ratio. The  $R/SD$  intercept is probably related to the degree of leptocurtosis (skewedness) of the distribution of residuals. However, in the present test we do not test variations in  $C$ . We test the overall, averaged expansion of  $R/SD$  (which is proportional to the square root of  $A$ ) as a function of  $n$ , so that the magnitude of the intercept is not important. It is the magnitude of the slope of log-transformed  $R/SD$  versus  $\log(n)$  which is used to test MRW against the classic RW models.

## RESULTS

### Autocorrelation and the Stability of the HR Center

Of the 84 bears 17 had a series length of  $\geq 100$  relocations. We used the 34  $x$ - and  $y$ -coordinate series from

these bears (7 males and 10 females) to test for autocorrelation (measured here as  $r$ ) to indicate HR center stability. The distribution of  $r$  scores from a correlation between successive displacements (lag 1 in an autocorrelation analysis) was strongly bimodal. Sixteen data sets had an averaged  $r$  score of 0.59, while the other 18 sets had an averaged  $r = 0.17$ , with very small standard error for both subsets (Fig. 3). To illustrate what this large difference means in practice, we have graphed the relative drift of the HR center (calculated as a running average over the last 20 relocations) for the  $x$ -coordinates from the 2 groups (Fig. 4). The 8 series with the largest  $r$  scores had distinctly less stable HR centers than the other 9 series in this sample. Males had a less stable HR center than the females (27% stable for males; 72% stable for females), when drifting center was defined as bears with  $r$  scores  $> 0.5$  for their  $x$ - and  $y$ -coordinates. Thus, a proper test of the MRW–MHR model should include series with stable HR centers only, since an expansion of  $A$  as a function of  $n$  for drifting series could be due to autocorrelation from small  $t$ , strongly non-normal utilization distributions (whether the underlying process was MRW or not).

### Home-range Expansion with Series Length

Data sets for 33 female black bears (Fig. 5, upper lines) and 24 males (Fig. 6) with  $n \geq 50$  per series had  $r < 0.5$  and were thus defined as non-autocorrelated. For these data sets,  $\log(R/SD)$  increased approximately linearly with slope = 0.25 for  $\log(n) > 1.5$  ( $n \approx 30$ –35). The  $\log(R/SD)$ -intercept was approximately the same for male and females, but the male data had a larger standard error for large  $n$ . The latter was due to a more variable magnitude of the  $\log(R/SD)$  scores for large  $n$  for the males.

A computer simulation of noncorrelated and approximately normally distributed increments (independent increments from an RW process, as expected from a series using large  $t$  in an HR situation) showed an asymptotic approach toward slope 0 for  $n > 50$ –100 (Fig. 5, lower lines). However, the asymptotic effect was for  $n$  as low as 30–35 ( $\log[n] = 1.5$ ). This was also the size of  $n$  from which the slope 0.25 became linear and relatively stable for the lines from the bear data (Figs. 5–6).

For  $n < 80$ –100 relocations,  $\log(R/SD)$  expanded approximately linearly with  $\log(n)$ , with slope = 0.5 for the pooled  $R/SD$  results for 16 male and 11 female bears with drifting HR centers (classified as autocorrelated series) (Fig. 7). Thus,  $R/SD$  was relatively large for  $n < 100$ , compared to the situation in Fig. 5–6. This was

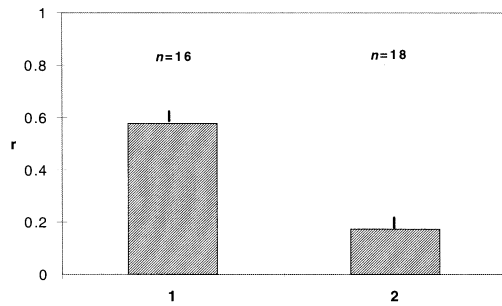


Fig. 3. Autocorrelation for lag one (average  $r$  scores for linear correlation for  $x$ - and  $y$ -coordinate location  $n$  vs. location  $n+1$ ,  $\pm 1$  SE) for all series with  $n \geq 100$ : 8 black bears had a drifting home-range center (1) and 9 bears had a relatively stable HR center (2), according to a classification to 2 groups with  $r$  below and above 0.5 for black bears in Tennessee, 1978–83.

due to a small  $SD$ , rather than a large  $R$ , for these sample sizes. Above  $n = 100$ ,  $R/SD$  approached the trend from Figures 5 and 6 (reference line).

In Figures 5–6 the positive slope of  $\log(R/SD)$  versus  $\log(n)$  was not a function of time but of sample size ( $n$ ). We considered a practical example from this property, the minimum convex polygon area for 3 of the female bears with non-drifting HR centers (Fig. 8). The accumulated MCP area from 5 independent samples of 10 relocations was practically identical, whether the 10 re-

locations were approximately uniformly distributed over 1 month or over 2–4 years. If autocorrelation from a drifting HR center explains why area expands with the square root of  $n$ , the latter samples should give a 5–7 (i.e.,  $\sqrt{24-48}$ ) times larger observed HR area on average from 10 relocations. Instead, the area is the same. Also, the area from relocations collected hourly give a smaller HR area from 10 relocations than the other sets (Fig. 8). This is what we expect from auto-correlated, short-term relocations. The paradox emerges only where we have clearly non-autocorrelated data and  $R/SD$  or  $A$  (from MCP, and after adjusting with  $Q[n]$ ) still expands with  $\sqrt[4]{n}$  and  $\sqrt{n}$ , respectively.

## DISCUSSION

We described a simple metaphor for the scale complexity of a memory map, the multi-layered chessboard, bearing in mind that a stochastic movement mechanism in model terms does not imply that the animals move randomly. MRW is a statistical mechanical (i.e., a physical) model, mimicking how a real animal uses an area in a statistical sense. One could imagine each movement-inducing event as completely deterministic and biologically explicable on a fine time and space scale. However, during the time span from 1 location of the animal to the next, a series of such deterministic events has occurred.

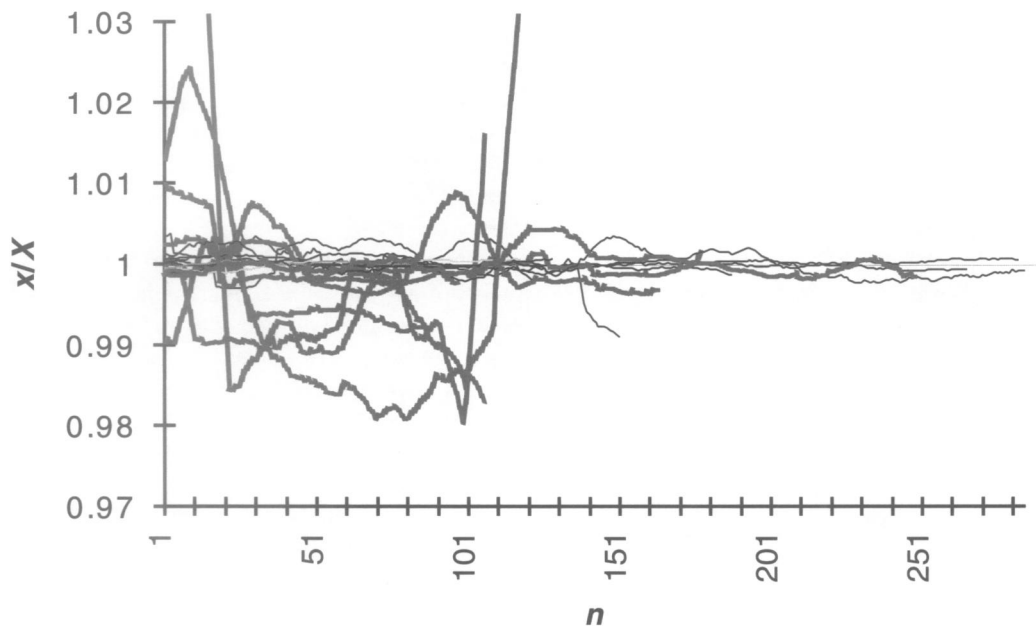


Fig. 4. The ratio of the  $x$ -coordinate and the moving average over the last 20 relocations ( $X$ ) demonstrates the degree of autocorrelation through the degree of stability of the HR center estimate ( $X$ ). Larger deviations from  $x/X = 1$  indicate center instability and autocorrelation. The thick lines are the 8  $x$ -coordinate sets defined as autocorrelated series in Fig. 3.

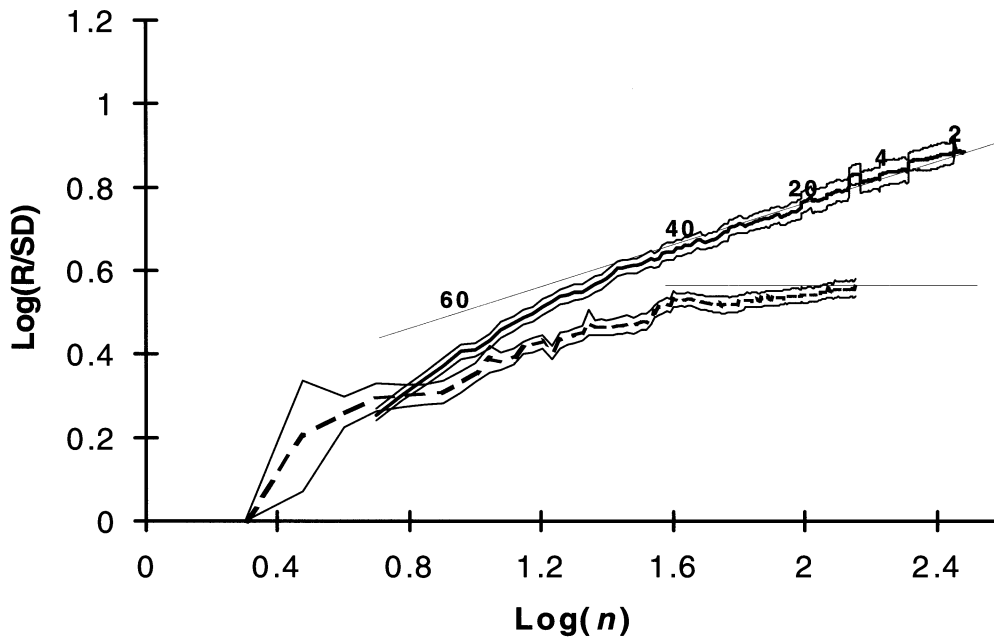


Fig. 5. Range size (R)/Standard deviation (SD) analysis of series with non-drifting HR centers for 33 female black bears (66  $x$ - and  $y$ -coordinate sets). Reference line has slope = 0.25 (MRW model prediction). Numbers above upper line are the number of series at the given size of  $n$ , and thin lines describe  $\pm 1$  SE for the mean over these series for a given  $n$ . Lower lines represent results from a simulation of non-autocorrelated random displacements with an approximately normal distribution, the prediction from the classic HR model with asymptote = 0 for reference.

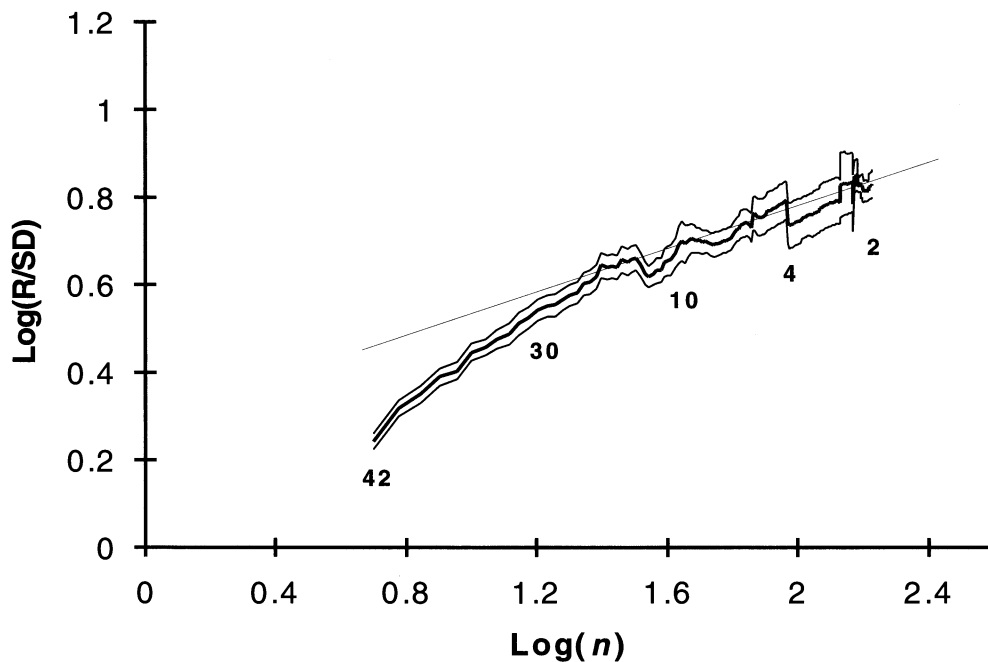


Fig. 6. Range size (R)/Standard deviation (SD) analysis for 24 male black bears (48  $x$ - and  $y$ -coordinate sets) with non-drifting HR centers. Reference line has slope = 0.25. Numbers below the lines are the number of series at the given size of  $n$ , and thin lines describe  $\pm 1$  SE for the mean over these series for a given  $n$ .

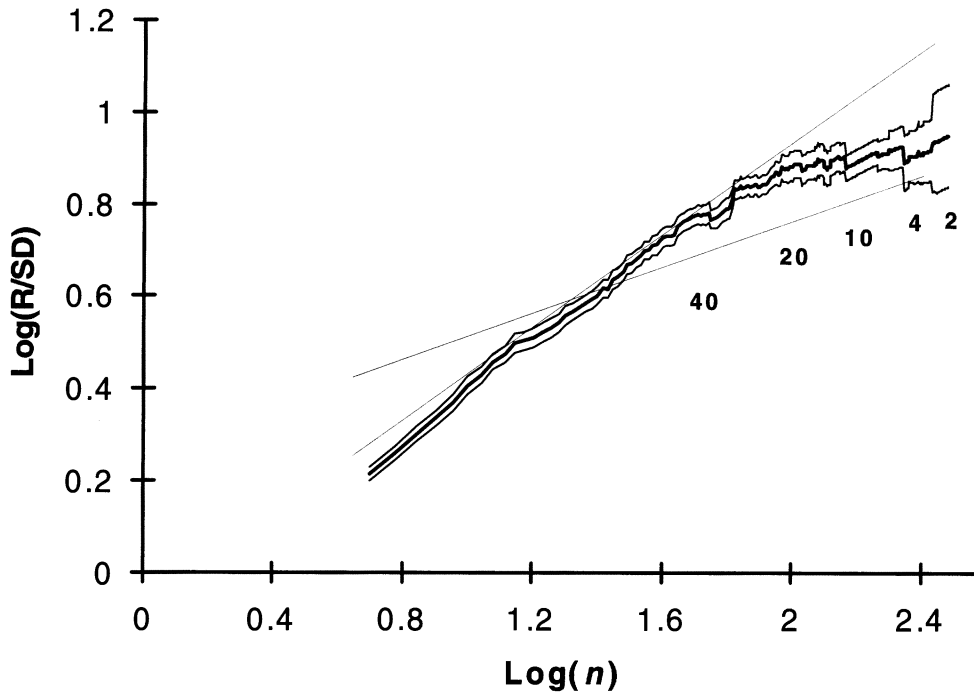


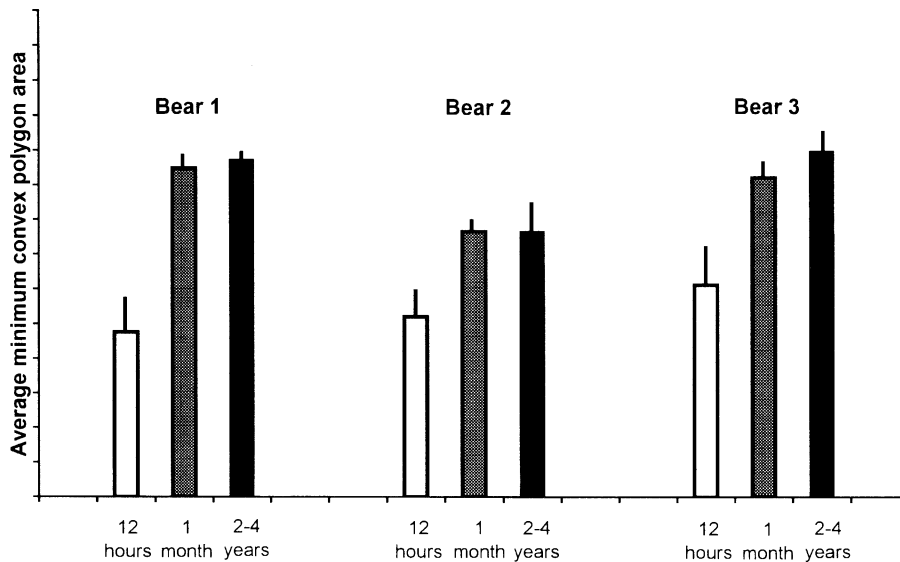
Fig. 7. Range size (R)/Standard deviation (SD) analysis for 16 male and 11 female black bears in Tennessee 1978–83 with drifting HR centers (autocorrelated series). The less steep line describes the same slope (0.25) and y-intercept as the MRW model prediction lines in Fig. 5–6. The other reference line has slope 0.5 and fits the plots up to  $n$  approx. 80–100. Beyond, the graph approaches the result from series with stable HR centers (Fig. 5–6).

Thus, we expect a transition toward statistical predictability of specific parameters describing the movement for an array of sets of such biologically deterministic events. For example, we expect 25% of a large sample of successive relocations to be directed toward each of the four cardinal directions from the previous location. This result is *not* an outcome of biology of the animal and it can *not* be explained from individual deterministic events triggering new movements. It is a purely statistical expectation from the law of large numbers. Thus, when reading the MRW model description above, we think as physicists and forget biology for a while! In a scale-free modeling context, eq. (2) is no more paradoxical or metaphysical than classic RW for a scale-specific context. It is important to understand that the slope of 0.5 for  $\log(A)$  and slope 0.25 for  $\log(R/SD)$  versus  $\log(n)$  is not determined by biology, but physics (emerging pattern from statistical mechanics for a body or particle moving in accordance with specific rules). For the classic models, a slope of zero or 0.5 (for HR-constrained RW and free dispersal RW, respectively) in  $\log(R/SD)$  as a function of  $\log(n)$  describes the physics. On the other hand, the biology of the pattern from MRW lies

in the parameter  $C$  in eq. (3), like the biology for the classic HR model lies in the magnitude of  $K$  in eq. (1).

It is also important to see that eq. (3) is a neutral model. It should be modified if, for example, the home-range drifts due to time-dependent autocorrelation or spurious autocorrelation (for which normality of the distribution of step lengths is strongly violated). It should also tend toward the classic model in eq. (1) in the limit where an animal moves according to classic statistical mechanics (no memory map effects), for example, where the environment is so variable and unpredictable that memory-based strategic moves become counter-productive. The classic model also emerges as a special case when the HR/CP ratio approaches 1. However, except for very crowded population conditions, perhaps, the latter should be rare. Thus, it is crucial to test over a large range of species and individuals the generality of the MRW model compared to the classic models.

Eq. (3) represents an alternative hypothesis to be tested against the null hypothesis in eq. (1) using non-autocorrelated relocations. In short, do black bears, with their large home ranges, optimize habitat use on the scale of magnitude CP only (even if it is large), or do they tend to equalize their effort over the scale range



**Fig. 8.** Illustration of expansion in estimated home range size as a consequence of time-independent and location frequency-dependent relationships. If the estimated home range size for a given number of locations ( $n$ ) increases with longer intervals between locations ( $t$ ), then the home range size for this number of locations is time-dependent (successive relocations are autocorrelated). Conversely, if the estimated home range size for a given number of locations does not change significantly when  $t$  is increased, then it can be concluded that the values of  $t$  in this range produced non-autocorrelated fixes for this individual animal. This point is illustrated in this figure using 5 independent samples of relocation points for each of 3 female black bears. Each sample consisted of 10 successive locations for an individual. For each sample, the area of the average minimum convex polygon (MCP) was calculated for a set value of  $t$ . The 5-sample mean MCP and SE were calculated for each of the 3 female bears. This same procedure was repeated for 3 different set values for  $t$ . The set values for  $t$  were selected by assuming that the 10 locations per sample had been collected over a 12 hour period, over a 1 month period, and over a 2-4 year period ( $t = 1.2$  hours, 3 days, and 73-146 days, respectively). For the 2 longest periods, the locations were treated as non-successive. On average, 10 relocations from a 1 month period (grey bars) and 10 relocations from a 2-4 year period (black bars) provided equivalent mean MCP home range size estimates (1 SE with 4 degrees of freedom is given on top of each bar). The mean MCP estimate using 10 locations over a 12 hour period for the 3 bears (white bars) show the autocorrelation effect for a given  $n$  when  $t$  is very small. The white bars are significantly smaller than the grey and black bars for each of the 3 bears. Since  $n$  is constant, this difference must be due to differences in the set value of  $t$ . Spreading a fixed number of non-autocorrelated relocations over 2-4 years rather than over a period of a few months would appear to gain nothing if the purpose of obtaining the data was to quantify home range size based on a given number of total locations.

from CP to the true HR area? If the latter is verified it should have practical and theoretical consequences for black bear research and management. In practical terms, we can not assume even a relatively large sample of, for example, 200 non-autocorrelated relocations to be close to the true HR area for a given bear. For example, if we increased  $n$  to 2,000 for the same total period of observation, we could expect the observed HR area to be  $\approx 3.16 (\sqrt{10})$  times as large (the upper limit for this expansion is discussed below). Thus, instead of estimating HR size as such, we should estimate  $C$  instead. The ecological interpretation of variation of  $C$  should be analogous to variations in  $A$ , or estimates of  $K$  from the observed  $A$ . Further, we should not be so worried about differentiating between outlier relocations and HR relocations. From eq. (3) we expect most or all the present outliers to be incorporated in the ob-

served HR area (from harmonic mean, kernel, or some other method) simply by increasing  $n$ . When we removed the 9 extreme outliers above, this was just a cautionary procedure to prevent spurious autocorrelations to emerge due to extremely non-normal UD. In short, from the MRW-MHR perspective, we should be less concerned with distinguishing between true HR movements and occasional sallies outside the HR.

We confirmed the MRW hypothesis and reject the classic model through an extensive reevaluation of 45 published graphs and tables for various birds and mammals (Gautestad and Myrsterud 1995), an analysis of roughly 1,400 relocations of free-ranging domestic sheep (Gautestad and Myrsterud 1993), and the present analysis on 84 black bears. The most detailed earlier test, on domestic sheep, was criticized for using non-

wild animals. However, the present result for black bears shows that the MRW model applies to other species. We confirmed that the slopes in Figures 5–6 satisfy MRW and are inconsistent with the classic models. Further, we showed that the seemingly paradoxical area and  $R/SD$  expansion rate is time-independent (Fig. 8). Thus, it can neither be due to a drifting HR over time, nor a true HR expanding over time.

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## APPENDIX

Telemetry data for 84 black bears from Great Smoky Mountains and Cherokee National Forest, both in Tennessee, 1976–83. ID: identification number, F = female, M = male. TRP: Initials of the student responsible for trapping the bear (DG = D.L. Garshelis, HQ = H.B. Quigley, PC = P.C. Carr, CV = C.R. Villarrubia, SG = S.R. Garris, TC = A.P. Clevenger).  $X_{ini}$ ,  $Y_{ini}$ ,  $X_{end}$ ,  $Y_{end}$  are initial and terminal x- and y- UTM coordinate, respectively.  $D_{ini}$ ,  $M_{ini}$ ,  $YR_{ini}$ ,  $D_{end}$ ,  $M_{end}$ ,  $YR_{end}$ : Initial and terminal day, month, and year of observation, respectively. Birth: Year of birth.  $n$ : number of relocations with inter-relocation interval of one day or larger.  $D$ : days from first to last location in the set of  $n$  relocations.  $D/n$ : average number of days between relocations. A dash (-) indicates data are missing.

Great Smoky Mountains															
ID	TRP	$X_{ini}$	$Y_{ini}$	$D_{ini}$	$M_{ini}$	$YR_{ini}$	$X_{end}$	$Y_{end}$	$D_{end}$	$M_{end}$	$YR_{end}$	Birth	$n$	$D$	$D/n$
F040	DG	2541	39409	4	9	76	2519	39419	17	9	77	67	62	378	6
F045	DG	2548	39418	19	8	76	2539	39429	9	12	76	67	39	110	2
F060	HQ	2378	39366	22	5	78	2320	39319	13	11	78	71	53	171	3
F097	DG	2697	39469	5	4	77	2696	39468	22	9	77	69	18	167	9
F111	DG	2551	39442	29	7	76	2539	39452	30	11	76	68	27	121	4
F112	DG	2547	39430	27	7	76	2514	39435	13	9	76	60	9	46	5
F131	DG	2577	39441	23	7	76	2575	39447	13	5	77	63	54	295	5
F136	DG	2527	39426	23	6	76	2524	39413	17	9	77	74	78	449	5
F151	PC	2365	39362	26	7	80	2361	39356	14	12	80	71	36	138	3
F165	DG	2525	39406	8	9	76	2519	39385	27	8	77	75	48	354	7
F170	DG	2574	39449	18	3	77	2580	39447	21	6	77	76	32	93	2
F176	DG	2536	39416	19	8	77	2461	39445	2	9	77	69	3	13	4
F182	HQ	2341	39352	17	8	78	2353	39360	20	4	82	71	168	1343	7
F201	HQ	2369	39360	23	6	78	2356	39357	27	4	82	75	304	1404	4
F243	HQ	2375	39370	29	6	78	2382	39364	24	4	82	75	268	1395	5
F244	HQ	2384	39351	2	7	78	2376	39360	14	7	78	75	3	12	4
F269	HQ	2368	39360	5	9	78	2348	39347	11	9	81	76	183	1101	6
F303	HQ	2362	39360	22	7	79	2364	39353	30	8	80	77	70	403	5
F309	HQ	2374	39373	10	8	79	2386	39370	24	4	82	72	84	989	11
F310	HQ	2370	39374	13	8	79	2367	39373	20	7	80	77	32	342	10
F312	HQ	2372	39372	14	8	79	2365	39373	20	7	80	76	37	341	9
F336	PC	2374	39363	22	6	80	2391	39362	19	5	81	72	62	332	5
M005	DG	2526	39421	20	8	76	2529	39400	13	6	77	69	52	298	5
M012	DG	2540	39432	27	7	76	2507	39451	19	12	76	70	37	142	3
M068	DG	2390	39364	21	4	77	2397	39351	21	5	77	70	5	30	6
M161	DG	2380	39365	13	4	77	2372	39359	18	6	77	71	17	65	3
M168	DG	2527	39402	11	9	76	2544	39423	11	9	77	75	33	365	11
M185	HQ	2349	39358	12	8	78	2591	39276	28	1	81	75	145	901	6
M226	HQ	2372	39362	28	6	78	2699	39379	5	11	79	75	76	492	6
M227	HQ	2380	39361	8	7	78	2382	39374	10	9	79	74	29	427	14
M255	HQ	2341	39352	13	8	78	2305	39242	20	10	80	77	125	797	6
M257	HQ	2337	39357	17	8	78	2353	39367	20	4	82	75	220	1343	6
M263	HQ	2337	39357	25	8	78	2334	39033	30	10	78	76	12	65	5
M264	HQ	2369	39360	1	9	78	2378	39346	18	7	79	74	30	322	10
M294	HQ	2376	39370	13	6	79	2829	39363	15	4	81	72	55	672	12
M301	HQ	2337	39357	15	7	79	2323	39410	24	4	82	74	85	1014	11
M334	PC	2341	39351	16	6	80	2385	39300	1	12	80	78	43	165	3
M338	PC	2360	39360	8	7	80	2337	39410	15	4	82	76	88	647	7
M350	PC	2374	39363	7	7	81	2349	39430	24	4	82	80	58	292	5
M362	HQ	2376	39360	20	6	79	2376	39393	16	3	82	78	93	1001	10
M373	PC	2373	39361	4	6	81	2347	39386	12	11	81	79	39	158	4
M453	PC	2378	39367	6	7	81	2381	39364	24	4	82	80	52	293	5

## Appendix. Continued.

Cherokee National Forest															
ID	TRP	$X_{ini}$	$Y_{ini}$	$D_{ini}$	$M_{ini}$	$YR_{ini}$	$X_{end}$	$Y_{end}$	$D_{end}$	$M_{end}$	$YR_{end}$	Birth	$n$	$D$	$D/n$
F719	CV	7669	39295	–	–	–	7687	39288	23	11	80	70	95	–	–
F724	CV	7664	39271	–	–	–	7660	39260	5	12	83	72	285	–	–
F725	CV	7653	39243	29	6	78	7643	39243	25	12	82	75	207	1636	7
F726	CV	7648	39252	–	–	–	7665	39259	3	10	79	76	66	–	–
F728	CV	7660	39240	–	–	–	7654	39255	9	12	78	75	15	–	–
F731	CV	7635	39264	–	–	–	7638	39259	5	12	80	76	95	–	–
F734	CV	7668	39258	15	6	79	7661	39268	14	7	79	76	8	29	3
F738	CV	7638	39291	14	7	79	7635	39294	3	12	79	77	12	139	11
F739	CV	7630	39279	18	7	79	7634	39278	3	11	79	76	8	105	13
F842	SG	7671	39262	27	6	80	7679	39267	2	12	83	78	302	1250	4
F846	SG	7672	39263	23	7	80	7682	39292	29	12	80	79	51	156	3
F847	SG	7693	39263	8	8	80	7764	39169	2	12	83	76	197	1209	6
F850	SG	7680	39269	19	8	80	7698	39268	13	5	83	77	169	999	5
F852	SG	7693	39263	18	8	80	7696	39264	26	11	80	78	36	98	2
F853	SG	7644	39269	19	8	80	7645	39284	29	12	80	75	36	130	3
F855	SG	7648	39250	14	8	81	7663	39288	2	12	83	80	139	838	6
F857	SG	7671	39262	10	8	81	7674	39256	28	11	81	80	55	108	2
F859	TC	7672	39263	15	7	82	7677	39251	5	12	83	79	137	505	3
F864	TC	7643	39243	12	2	83	7660	39264	5	12	83	82	148	293	2
F868	TC	7667	39265	27	6	–	7678	39279	2	12	83	–	92	–	–
F870	TC	7671	39262	5	6	83	7675	39268	2	12	83	–	98	177	2
F871	TC	7643	39243	12	2	83	7651	39246	5	12	83	–	105	293	2
M723	CV	–	39253	23	6	78	7651	39249	13	8	78	72	4	50	12
M727	CV	7311	39176	–	–	–	7646	39231	12	11	79	76	56	–	–
M729	CV	7657	39279	26	6	79	7631	39285	12	8	79	76	9	46	5
M730	SG	7647	39250	29	6	80	7615	39297	28	11	82	76	106	879	8
M732	CV	7707	39288	20	9	78	7666	39213	13	8	81	77	93	1058	11
M735	CV	7646	39263	20	6	79	7678	39285	20	11	79	76	34	150	4
M736	SG	7688	39258	–	–	–	7631	39311	6	12	82	76	170	–	–
M737	TC	7666	39254	3	8	83	7705	39196	28	11	83	77	47	115	2
M854	SG	7672	39263	18	7	81	7730	39300	3	12	81	77	35	135	3
M865	TC	7672	39263	20	8	82	7625	39318	24	9	82	79	16	34	2
M866	TC	7658	39251	20	8	82	7624	39271	2	12	83	79	90	467	5
M867	TC	7676	39278	25	6	83	7780	39205	8	11	83	82	57	133	2
M869	TC	7669	39263	5	6	83	7743	39214	2	12	83	82	97	177	2
M877	TC	7672	39263	4	8	83	7722	39172	2	12	83	79	37	118	3
M885	CV	7655	39260	5	6	79	7683	39245	15	11	81	75	117	890	7
M886	CV	7700	39325	28	7	79	7677	39315	3	8	79	76	3	5	2
M887	CV	7671	39260	5	6	79	7608	39220	12	9	79	76	9	97	10
M889	CV	7669	39266	11	6	79	7699	39201	3	12	81	75	149	902	6
M890	CV	7657	39245	3	3	79	7678	39264	4	12	79	78	22	271	12
M891	CV	7655	39244	21	4	79	7625	39287	21	11	79	78	16	210	13