

Animal movement rates as behavioural bouts

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Summary

Johnson *et al.* (*Journal of Animal Ecology*, 2002, **71**, 225–235) have proposed a new technique for identifying scales of movement in animals. Animals are located at certain time intervals, and movement rates between successive animal relocations are calculated. The null model of a nonscalar response predicts a decreasing linear relationship between $\log(\text{frequency})$ vs. movement rate, while a scalar response predicts a monotonically decreasing curve with an inflection point at the separation between the processes. I tested this technique using three types of simulated movement paths: correlated random walks, directed walks, and movements in patchy habitat. None of the simulations showed the results expected by the technique. This occurs because the technique assumes that movement rates are exponentially distributed, which is highly unlikely. Thus before this technique can be applied to animal movement data we need to understand how spatial and temporal scale, as well as sampling interval, affect the frequency histogram of animal movement rates.

Key-words: correlated random walk, exponential, fractal, spatial scale.

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Introduction

In the last two decades the importance of spatial scale has been emphasized in the study of animal ecology. However, while biologists have realized that animals may respond to their environment at different spatial scales, it has proven difficult to measure the scales at which they respond. Johnson *et al.* (2002) proposed a new technique for identifying scales of movement in animals. Animal movement is the glue that links individual behaviour to population dynamics, and being able to measure the scale of spatial response could have major implications in behavioural ecology. Thus we need to ensure the validity of this technique before applying it to other data sets.

Johnson *et al.*'s (2002) technique adapts a method used to analyse behaviour patterns. In the original application (Sibley, Nott & Fletcher 1990) the time between some behavioural events is measured – for example, feeding pecks by birds. The analysis assumes that time between events is exponentially distributed. Thus the null hypothesis of no scalar response gives a decreasing linear relationship between $\log(\text{frequency of events of length time})$ vs. time.

When the events are grouped into bouts, then it is often useful to separate the times between events into within vs. between bouts. For example, pecks will occur more frequently within a meal than between meals, and we might wish objectively to delineate meal boundaries. In this case the $\log(\text{frequency})$ vs. time plot would show a combination of the two exponential distributions (time between pecks, and time between meals). Thus the alternate hypothesis of a scalar response gives a monotonically decreasing curve with an inflection point at the separation between the processes.

Johnson *et al.* (2002) adapted this method to animal movement data collected by radio-telemetry. Animals were located at certain time intervals, and instead of times between behavioural events, movement rates between successive animal relocations were used. The null model of a nonscalar response was assumed to give a decreasing linear relationship between $\log(\text{frequency})$ vs. movement rate, and deviations from this linear shape were assumed to be the result of scalar responses.

I tested this new method by applying it to simulated movement paths of both nonscalar and scalar responses. According to Johnson *et al.*'s (2002) model, the nonscalar paths should show a decreasing linear relationship between $\log(\text{frequency of events of length time})$ vs. time, while a scalar response should show a monotonically decreasing curve with an inflection point at the separation between the processes.

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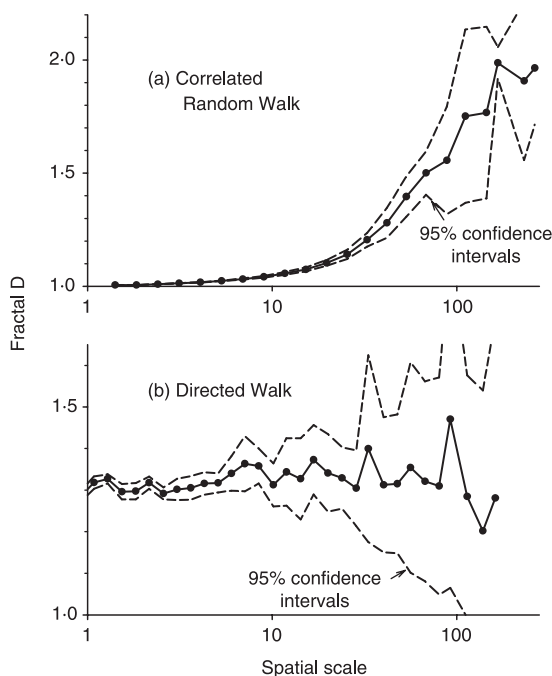


Fig. 1. Tortuosity at different spatial scales for (a) a correlated random walk, and (b) a directed walk. Fractal D was estimated using the VFractal (Nams 1996) estimator. Note that tortuosity increases with spatial scale for the correlated random walk, but is constant for the directed walk.

Methods

I tested two different kinds of nonscalar movement patterns. The first was a correlated random walk; this has been proposed as a null model for animal movements in general (Turchin 1996), and has been the basis of the movement model for a variety of animals (e.g. carabid beetles *Pterostichus* sp.; Firlie *et al.* 1998), wood mice *Apodemus sylvaticus* (Benhamou 1990) and caribou *Rangifer tarandus* (Bergman & Lutich 2000). I modelled a series of correlated random walks with fixed step lengths, and turning angles distributed with a circular normal distribution (Cain 1985). The parameter K describes the turning angle concentration, with larger K -values representing straighter movement paths.

I modelled movement paths using K -values of 20, 10, 5, 2.5 and 1, where larger values give straighter paths. The movement paths were sampled at two intervals (10 and 100 steps) to simulate two different sampling intervals for radio-telemetered animals, with path lengths of 100 000 steps. Movement rate was calculated by the Euclidean distance moved per specified unit of time.

The second nonscalar movement pattern was completely different (Nams 2005). Although a correlated random walk is nonscalar, its tortuosity does change with spatial scale (Turchin 1996) – the fractal dimension increases sigmoidally with scale to an asymptote of 2 (Fig. 1a). I modelled a directed walk in a fractal habitat, whose tortuosity does not change with scale (Fig. 1b). This model assumes that animals walk towards specific points, there are obstructions in the habitat,

these obstructions are fractally distributed in space, and the animals know or can see the main habitat features of their home range.

For example, suppose a deer is walking to a certain point. Considering first obstructions at the largest scale, the deer may have to walk around a large hill. On the way to that hill it would encounter smaller obstructions – for example, it may have to walk around a smaller hill. On the way to the smaller hill it may have to avoid even smaller obstructions – e.g. a ravine – and so on, down to the scale of individual footsteps. At the smallest scale, the deer must avoid individual shrubs.

If the obstructions the deer encounters are fractally distributed (various vegetation features have been found to be fractal; Morse *et al.* 1985; Gunnarsson 1992) – meaning that at each scale they have the same spatial distribution – then at each scale, we could represent the deviations from the intended path in a similar manner. The larger obstructions the deer remembers, while the smaller ones it sees as it walks.

I modelled this situation by first choosing starting and ending points. Then I represented the effect of the largest obstruction on the path, by randomly selecting a perpendicular deviation at the middle of the path, and splitting the path into two around this deviation. I then represented the effect of the next largest obstructions by taking each of the two path segments and repeating the above. This was repeated down to a very small scale, and then data saved at the scale of the animal's step size. The deviations were drawn from a normal distribution with a constant Coefficient of Tortuosity,

$$C_T = \frac{\sqrt{\text{var}}}{\text{segment length}}$$

which is analogous to the coefficient of variation. A lower C_T gives a straighter path. The fractal nature of the habitat is incorporated by having a constant C_T at all scales. I modelled directed walks using C_T -values of 0.1, 0.4, 0.55, 0.7 and 0.9, with path lengths of 100 000 steps and sampling intervals of 10 and 100.

For a scalar movement pattern, I simulated an animal responding to the environment at two spatial scales. At a smaller scale, the simulated animal travelled a tortuous ($K = 5$) correlated random walk inside square patches, reflecting at the boundaries until the animal had walked a certain number of steps, and then leaving when it crossed the patch boundary. After leaving a patch the animal walked in a quite straight ($K = 250$) correlated random walk for a certain distance before entering another patch. Thus there were two very distinct spatial scales – the size of small patches, and the distance between patches. I modelled five different movement paths, using combinations of path size, number of steps within a patch, and distance between patches of (25, 60, 400) (35, 100, 300) (50, 250, 200) (75, 500, 150) and (100, 1000, 100). Each path was simulated for 100 000 steps and sampled at time intervals of 10 and 100.

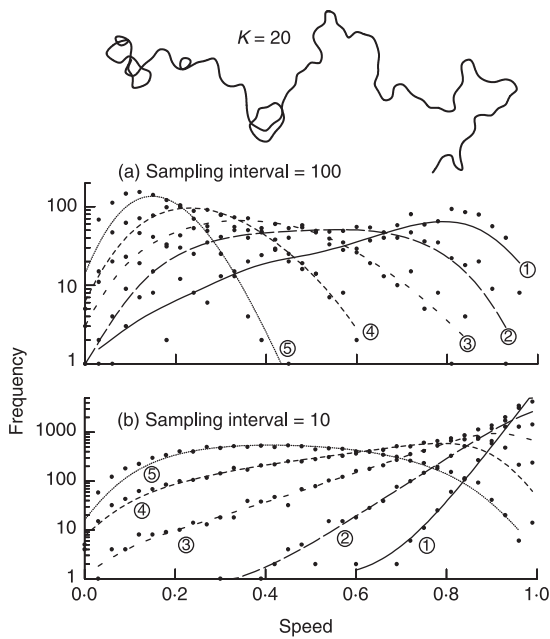


Fig. 2. Frequency histograms of movement rates from five simulated correlated random walks, sampled at two different time intervals. For paths 1–5, the concentration parameter K was 20, 10, 5, 2.5 and 1, with larger K -values giving straighter paths. For display purposes only, data were smoothed with a distance weighted least squares smoothing. None of the plots show the linear decreasing relationship expected under the null model of a nonscalar movement, and the shape of the plots changes with sampling interval.

Results

The null hypothesis of nonscalar movement predicts a decreasing linear relationship between $\log(\text{frequency})$ and movement rate (Johnson *et al.* 2002). None of the movement paths showed the expected result (Figs 2 and 3). Not only was the relationship not linear, but it was not even monotonically decreasing. Furthermore, the shape of the plots, and thus the position of potential inflection points, changed with the sampling interval (Fig. 2a vs. Figs 2b and 3a vs. Fig. 3b).

The alternate hypothesis of scalar movement predicts a curvilinear, monotonically decreasing curve (Johnson *et al.* 2002). None of the simulated paths showed this. At a sampling interval of 10 steps, the $\log(\text{frequency})$ plot shows an almost –linear increase (Fig. 4b), but in the wrong direction – up, not down. At a sampling interval of 100 steps the plot is curvilinear, but not monotonically decreasing (Fig. 4a). Neither plot shows the expected non-null decreasing pattern, and the shape of the plots also varies with sampling interval.

Discussion

The nonscalar paths that I tested did not show the expected null pattern of a linear decrease; thus deviations from the linear shape are not solely the result of scalar responses. Furthermore, none of the scalar paths showed the expected non-null pattern, and the patterns

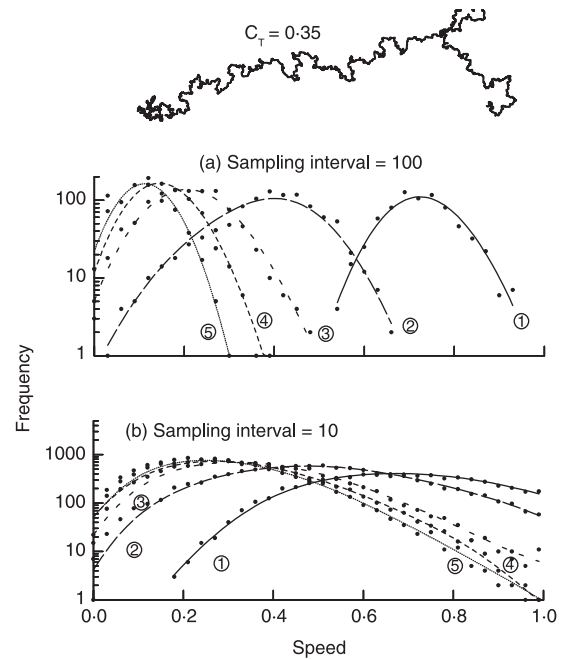


Fig. 3. Frequency histograms of movement rates from five simulated directed walks in fractally distributed habitats, sampled at two different time intervals. Fractal dimension of these movement patterns is constant with spatial scale (e.g. Fig. 1). For paths 1–5, the Coefficient of Tortuosity, C_T , was 0.1, 0.4, 0.55, 0.7 and 0.9, with smaller C_T -values giving straighter paths. For display purposes only, data were smoothed with a distance weighted least squares smoothing. None of the plots show the linear decreasing relationship expected under the null model of a nonscalar movement, and the shape of the plots changes with sampling interval.

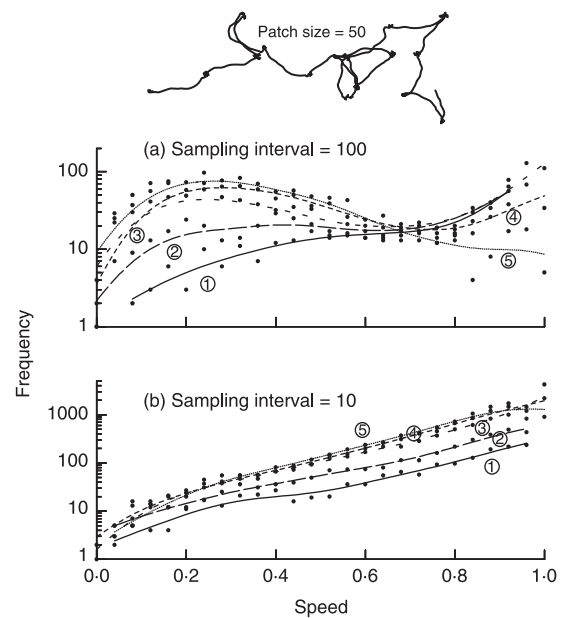


Fig. 4. Frequency histograms of five simulated correlated random walks in patches of various sizes, sampled at two different time intervals. For paths 1–5, the patch size was 25, 35, 50, 75 and 100. For display purposes only, data were smoothed with a distance weighted least squares smoothing. None of the plots shows the linear break-point plot expected for a scalar response, and the shape of the plots changes with sampling interval.

changed with sampling interval – making interpretation of the analysis difficult.

Why do the null movement paths not show the expected linear decrease? I suggest that animal movement rates do not fit the assumed statistical distribution. The original method was applied to discrete events – to animal behaviours. The events are assumed to be generated by a Poisson process (Sibley *et al.* 1990), which results in the time between events being exponentially distributed. This is the critical assumption that gives the predicted distribution of frequency of events.

It is difficult to see how to apply this model to measuring the distances that animals travel. The original model fits natural, discrete, events. Here there are no natural discrete events that occur; rather, the animal's trail is divided into segments based on fixed time intervals, and the segment lengths are measured. The segment lengths do not measure a parameter of a discrete event. It is impossible for distances to be exponentially distributed for all time periods (Appendix 1) – and the analysis crucially assumes this.

The simulations confirmed that the relationship between log(frequency) and movement rate changes with sampling interval (Figs 2 and 3). This is not surprising, as sampling at a different time interval also affects the spatial scale sampled. If the tortuosity of the movement path changes with scale (e.g. Fig. 1a) then we would expect that estimated movement rate would also change with sampling interval. However, if the shape of the plot is affected by sampling interval then it is not clear how to interpret any observed inflection points.

Why do Johnson *et al.*'s (2002) data show the expected pattern of a scalar response, when none of my simulations showed this? I did not even find any examples of a monotonically decreasing response. This is not because of inappropriate test simulations. I tested three very different models, with many parameter variations in each. None gave results that were similar to those expected. Likely those models did not completely describe caribou moving in their environment [although Bergman & Luttich (2000) did show that caribou movements follow a correlated random walk], but Johnson *et al.*'s model does not specify a specific movement type or environment. I was not simulating the caribou that Johnson *et al.* studied, but was simulating the animals assumed by Johnson *et al.*'s model. As described, it does not specify an exact form of movement.

Appendix 1: Proof that sampling time interval affects the distribution of distances travelled

Suppose x , the distance travelled by an animal over one time interval, is exponentially distributed. Then the probability distribution function of x would be given by

$$f(x) = \lambda e^{-\lambda x} \quad \text{eqn 1}$$

where λ is the mean time taken to travel 1 distance unit.

I suggest that this discrepancy occurs because Johnson *et al.*'s data included not only position, but time. The radio-locations were taken throughout the day and night, when animals were both active and inactive. Thus distance travelled between locations was affected by the animals' inactivity – e.g. a short distance travelled per time may result from the caribou walking slowly, or walking in a tortuous pattern, or resting a lot. The analysis measures patterns in temporal scale as well as spatial scale, but my simulations only created patterns in spatial scale.

Johnson *et al.* (2002) have found potentially useful patterns in the plot of log(frequency) vs. movement rate, but it is currently not clear how to interpret them. Before this technique can be applied to animal movement data we need to understand how spatial and temporal scale, as well as sampling interval, affect the frequency histogram of animal movement rates.

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Taking the log of this function gives the expected null-model linear function of x . However, suppose now movements are measured over a time interval twice as long. An animal would travel a distance x in time $2t$ if it first travelled a distance x_1 in time t , and then distance $x - x_1$ in the second time t . An exponential distribution of time interval assumes independence between successive time intervals. Given this independence, the probability distribution function of the distance travelled x would be given by

$$f_2(x) = \int_0^x f(x_1)f(x - x_1)dx \quad \text{eqn 2}$$

which simplifies to

$$f_2(x) = \lambda^2 e^{-\lambda x} x \quad \text{eqn 3}$$

which is *not* an exponential distribution.

This can be illustrated by taking log of eqn 3, giving

$$\text{Log}(f_2(x)) = -\lambda x + 2\text{Log}(\lambda) + \text{Log}(x) \quad \text{eqn 4}$$

This is *not* a linear function of x . Thus the relationship between $\log(\text{frequency})$ vs. movement rate would not be linear – simply because of a different sampling time.

If the distance travelled is measured over n time intervals, it can be shown that the probability distribution of the distance travelled would be

$$f_n(x) = \frac{\lambda^{n+1} e^{-\lambda x} x^n}{n!} \quad \text{eqn 5}$$

This approaches the normal distribution for large n (the Mean Value Theorem).