



COMMENTARIES

Detecting oriented movement of animals

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(Received 30 January 2006; initial acceptance 23 February 2006;
final acceptance 7 April 2006; published online 26 September 2006; MS. number: AS-1307)

Animal movement affects biological processes at many organizational levels. Sometimes when animals travel they orient themselves towards a given goal, and whether or not they do so affects biological processes very differently. For example, on a small organizational level, when animals disperse to find new habitat patches, then very directed travel leads to a more heterogeneous distribution of animals in the landscape (Hein et al. 2004). On a higher organizational level, these differences in movement can affect population dynamics. For example, modelled brown treecreeper, *Climacteris picumnitis*, populations increase when individuals travel towards other individuals, but not when travelling randomly (Cooper et al. 2002). On a still higher organizational level, differences in movement mode affect biodiversity. While directed movement can lead to a spatial partitioning of species, random movement can maintain biodiversity through local coexistence (Armsworth & Roughgarden 2005). Thus, to understand how movement of specific animals affects biological processes, we need to know whether those animals travel in an oriented manner.

To test for movement oriented towards a given goal (hereafter 'oriented' movement), it helps to understand the biological distinctions between oriented movement and other types of movement. The key issue is the scale of the movement mechanism. Some animals orient towards certain locations (e.g. homing wood mice, *Apodemus sylvaticus*; Jamon & Benhamou 1989), some orient towards certain habitats (e.g. perceptual range of white-footed mice, *Peromyscus leucopus*; Zollner & Lima 1997), and some towards certain directions (e.g. cactus bugs, *Chelinidea vittiger* orient with wind; Schooley & Wiens 2003). All of these imply a long-distant orientation mechanism.

If animals do not orient themselves towards a given goal, then the behavioural mechanisms governing movement will act at a small spatial scale (hereafter 'unoriented' movement). Some of these mechanisms may involve

orientation, but they affect movement towards goals at a small scale. Some animals orient towards individual prey that they detect using their sense of smell (e.g. striped skunks, *Mephitis mephitis*; Nams 1991) or sound (e.g. coyotes, *Canis latrans*; Wells & Bekoff 1982). Alternatively, these mechanisms may just involve simple movement rules. Often the behavioural mechanism itself is ignored and the movement is modelled as a correlated random walk (CRW), where an animal makes discrete steps, and at each step, the turning angle is independent of the previous turning angle (Kareiva & Shigesada 1983; McCulloch & Cain 1989). The smaller the turning angle, the straighter the overall movement path. But there are many types of unoriented movements that cannot be modelled by CRWs. Some animals alternate turns, leading to straighter paths (e.g. cactus bugs; Schooley & Wiens 2003). Some animals tend to make successive turns in the same direction, leading to shorter paths (e.g. caribou, *Rangifer tarandus*; Bergman et al. 2000) or a looping pattern (e.g. Collembola; Bengtsson et al. 2004). Some animals also have autocorrelated step lengths (e.g. tundra swans, *Cygnus columbianus*; Nolet & Mooij 2002). All of these mechanisms act at a small spatial scale.

We can use these behavioural differences to test for oriented versus unoriented travel. There are two types of tests, and the choice of which test to use depends on the circumstances. For the first test, one must know a priori where the animal is supposed to be orienting. For example, in homing experiments, the animal is supposed to be orienting towards its home area. One then measures orientation based either on the success of the animal locating this home area, or on whether the path of the animal is in the direction of the home area (e.g. Mitamura et al. 2002). In measuring perceptual range, the animal is supposed to be orienting towards a certain habitat. One then measures the distance at which the animal changes movement path characteristics, or the success at finding the habitat (e.g. Zollner & Lima 1997; Gillis & Nams 1998). These types of tests are quite straightforward.

The second type of test is much more difficult because one does not know a priori where the animal is supposed to be orienting. Suppose one is tracking dispersing

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animals. How do you know whether the animal found the end-point habitat patch by random search, or by detecting it from afar? One could consider whether, at some closer distance, the shape of the movement path changed (Gillis & Nams 1998), but this would work only if the animal detected the end point during the tracking session. How would you know whether the animal began travelling with an oriented movement even before tracking began? What is needed is a test that uses the structural characteristics of the movement path to discern the mode of movement.

There have been various tests proposed to do this, but they assume specific models of animal movement. Kareiva & Shigesada (1983) developed a statistical test for a CRW. Marsh & Jones (1988) extended that test to differentiate between CRWs and a very specific model of directed walk. They also showed that the square of the net distance travelled increases quadratically or linearly with the number of steps depending on whether the movement is oriented or a CRW, and Benhamou (2004) developed a statistical test based on this idea.

All of these tests are useful, but they apply only to specific movement models. The idea of oriented versus unoriented movement is a general idea that does not have a specific mathematical description/model. What is needed is a generalized test to differentiate between these two movement types, irrespective of the specific model.

I propose such a test, based on the biological distinctions between oriented versus unoriented travel. The key difference is that the mechanisms driving unoriented movements act at a small scale, whereas the mechanisms driving the oriented walks act at a large scale. Thus, I propose that if we sample unoriented movements at larger scales, the small-scale differences between the various unoriented movements should disappear, and all unoriented movements should behave similarly. Thus, instead of myriad tests, each depending on a specific unoriented movement model, we only need one, but applied to paths sampled at large scales.

I propose to apply Kareiva's test for CRW to scaled movement paths (and, thus, I call this the 'scaling test' for oriented movement; a windows-based computer program to carry out the analysis is available). To do this, Kareiva's test needs some modifications because it does not give one statistic; instead, for any given number of steps, the test calculates the expected net distance² travelled. I propose a statistic called CRW_{Diff} , which measures how much further a movement path travels compared to a CRW, over a range of numbers of steps (Appendix 1). Thus CRW_{Diff} is zero if the movement path is a CRW, and positive if the movement path is longer than a CRW. I propose that, for oriented movement, CRW_{Diff} should be positive at all scales, but that for unoriented movement, CRW_{Diff} should go to zero at larger scales.

Methods

It is difficult to test a procedure like this for all types of movement paths, since the general idea of oriented versus unoriented movement paths is not based on specific

mathematical models. However, I tested the scaling test on a series of very different unoriented and oriented models of paths. I sampled each path at a series of scales from 1 to 20 step lengths, and estimated CRW_{Diff} at each scale. I then averaged the values for all 50 paths of each parameter combination. The units for all paths were in step lengths; thus, a scale of 2 was 2 step lengths. I sampled a path at a larger scale of size s , by walking along the path with dividers of lengths s , and generating new X , Y coordinates (Fig. 1). I then estimated CRW_{Diff} for the new X , Y coordinates.

Unoriented movement

I tested three types of unoriented movements. The first was a CRW (Appendix 2a). In a CRW, animals walk with discrete steps, and at each step, they turn in a random direction, with turning angles being independent of each other. I modelled a series of CRWs with fixed step lengths and a circular normal distribution of turning angles (Cain 1985). The parameter K describes the turning angle concentration, with larger K values representing straighter movement paths. I modelled 50 paths, each having a path length of 1000 steps, for each parameter value, using K values of 5, 10, 20 and 50. This range of values gives movement path tortuosities that encompass those seen in real data.

The second unoriented movement was an extension of a CRW, but with the correlation extending back for more than one step (Appendix 2b). This models an animal that has a tendency to walk in the same direction as it has been walking for the past several steps. I modelled this as a CRW, but with the direction of each step depending on the angle covered in the previous n steps, plus a random turning angle. When n is 1, then this is a CRW. I modelled 50 path lengths of 1000 steps for each parameter value, using K values of 5, 10, 20 and 50, and with the correlation depending on the previous three steps. I call this a 3-step CRW.

The third unoriented movement used autocorrelated turn directions (Appendix 2c). The constant k_2 determined how the turn direction was affected by the previous turn. When $k_2 = 0$, the movement path is a CRW. When $k_2 > 0$, the animal tends to alternate direction of turns, and when $k_2 < 0$ the animal tends to turn in the same direction as the previous turn. I modelled 50 path lengths of

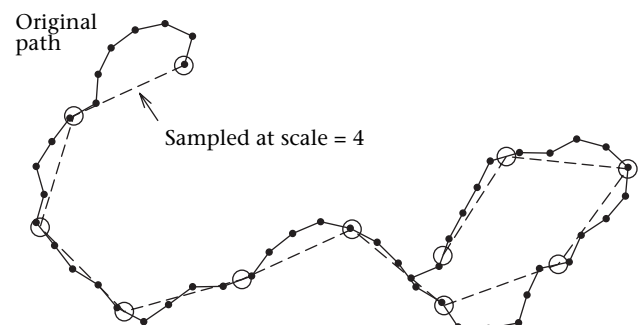


Figure 1. Example of sampling a movement path at a larger scale of 4 step lengths.

1000 steps for each parameter value, using K values of 5, 10 and 20, and k_2 values of -0.3 and 0.3 .

Oriented movement

I modelled three types of oriented movement. The first represented an animal orienting itself towards a specific location by changing direction (Appendix 2d). During each step, the animal tended to turn towards the desired direction, but each step also incorporated a random turning element. A constant K_{dir} determined how strongly the animal turned towards the desired direction, with K_{dir} ranging from 0 (a CRW) to 1 (each step the animal turned directly towards the desired direction). The random turning element was modelled in the same manner as for CRW. I modelled 50 path lengths of 1000 steps for each parameter value, using K values of 5, 10 and 20, and K_{dir} values of 0.05 and 0.3.

In the second oriented path, the animal altered path tortuosity rather than direction (Appendix 2e). For each step, the mean turning angle was smaller if the animal was pointed towards the desired location. I modelled 50 path lengths of 1000 steps for each parameter value, using all turning angle distributions with combinations of K_{min} values of 1 and 2, and K_{max} values of 20, 30 and 40.

The final oriented path was completely different. This was a fractal walk (Nams 2005; Appendix 2f). This model assumes that animals walk towards specific points, there are obstructions in the habitat, these obstructions are fractally distributed in space, and that 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. Path directedness was specified by the coefficient of deviation (C_{dev}), where C_{dev} of 0 means a completely straight path, and larger values are more tortuous paths. I modelled 50 paths of varying lengths of approximately 1000 steps for each parameter value, using C_{dev} values of 0.1, 0.2, 0.3, 0.4 and 0.5. This range of values gives movement path tortuosities that encompass those seen in real data.

Results

All unoriented paths travelled were shorter than or equivalent to the distances predicted by a CRW (i.e. $\text{CRW}_{\text{Diff}} \leq 0$) when sampled at larger spatial scales (Fig. 2). The simulated CRW was the only movement path that had a CRW_{Diff} value of zero at a scale of 1 (Fig. 2a); CRW_{Diff} then dropped to below zero at larger scales but increased back up to zero. The CRW with the angle depending on the last three steps had a positive initial CRW_{Diff} value (Fig. 2a), but also dropped below zero. The paths with alternating turn angles had positive CRW_{Diff} values at the start (Fig. 2b), whereas the paths

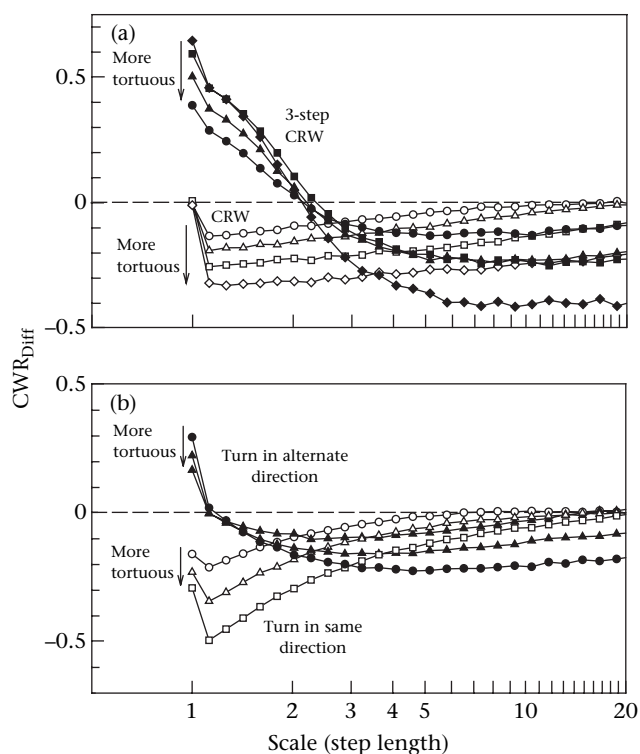


Figure 2. Scaling test applied to unoriented path simulations. (a) 3-Step CRW and CRW. (b) Autocorrelated turns. CWR_{Diff} measures how far the movement path travels compared to a CRW. Each point is the mean from 50 replicates. The nonpositive CWR_{Diff} values at large scales indicate random movement.

with same turn angles had negative CRW_{Diff} values at the start. For all unoriented paths, the more tortuous paths had more extreme CRW_{Diff} values (i.e. values were lower when negative and higher when positive).

All oriented paths showed CRW_{Diff} values that were positive at larger spatial scales (Fig. 3). Both of the oriented walks based on a CRW showed increasing CRW_{Diff} values, while the fractal walk seemed to show CRW_{Diff} values that levelled off. The paths with stronger directedness had higher CRW_{Diff} values.

Discussion

The scaling test successfully differentiated between oriented and unoriented movements for all six movement path models tested, at all 31 parameter combinations. All modelled oriented walks had positive CRW_{Diff} values at larger scales. The unoriented movements had various CRW_{Diff} values at small scales, but all had negative or zero CRW_{Diff} values at larger scales. The results are intuitively reasonable, since the premise of the test is based on the biology underlying the differences between the movement patterns. The biological mechanisms for unoriented paths act locally. Thus, if the path is sampled at scales larger than the scale at which these mechanisms act, then it is reasonable that the effects of the mechanisms would be hidden. Conversely, the biological mechanisms for oriented paths act at scales longer than the

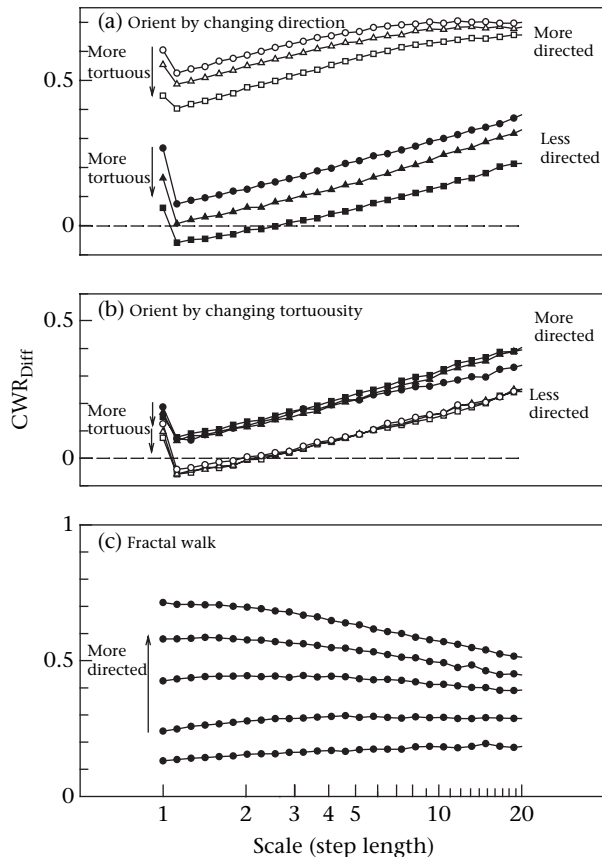


Figure 3. Scaling test applied to directed path simulations. CWR_{Diff} measures how far the movement path travels compared to a CRW. The positive CWR_{Diff} values at large scales indicate oriented movement.

length of the path (i.e. animals orient themselves towards a given goal). Sampling the path at any larger scale, which would still be shorter than the orientation distance, would not hide the effects of these mechanisms.

Simply applying Kareiva & Shigesada's (1983) CRW test to unscaled paths would not differentiate between oriented and unoriented movement, as shown by the CWR_{Diff} values at a scale of 1. Only the CRW paths have $CWR_{Diff} = 0$. All other paths failed Kareiva's test. All the oriented paths, as well as the unoriented paths with alternating turns and the 3-step CRW, travelled further than a CRW. The path with turns that were in the same direction as the previous step, travelled a shorter distance than a CRW. Kareiva & Shigesada's test tests specifically for CRW, not for unoriented movement in general.

One unexpected result is that most of the unoriented paths had negative, not zero, CWR_{Diff} values at larger scales, and even the CRW showed this. This means that if CRW are sampled at larger scales, they do not act like CRW; they travel shorter distances than expected. When CRW are sampled at smaller scales, they do not act like CRW; turns are autocorrelated (Turchin et al. 1991), and thus researchers have to ensure that they sample at a large enough scale. These effects at large scales are a new discovery.

There are some important consequences of this property. First, there is a native scale for CRWs. Finding the

correct scale might help to elucidate the biological mechanism for travelling, while choosing the incorrect sampling scale might lead us to incorrect conclusions about the movement mechanisms. Perhaps studies in the past that found that animals do not travel with a CRW may have simply used an incorrect sampling scale.

It is easy to find the native scale for CRW when animals have obvious discrete steps; however, many animals have continuous movement paths. If we want to apply a CRW model, which is based on discrete steps, we cannot simply use scales of convenience. More research is needed on the topic of modelling continuous movement with CRW.

Error estimates

Real-world applications require error estimates. These simulation results do not have error estimates because the extremely long movement paths minimize sampling variation; however, movement paths from real animals are typically much shorter. I suggest estimating confidence intervals for the CWR_{Diff} statistic at each spatial scale, and then considering whether the confidence intervals encompass zero. The statistical null hypothesis is thus that $CWR_{Diff} \leq 0$; that is, that the path is unoriented. The width of confidence interval would give information about the power of the test.

For example, Fig. 4 shows error estimates of CWR_{Diff} for male meadow vole, *Microtus pennsylvanicus*, and female red-backed vole, *Clethrionomys gapperi*, movement paths (from Nams 2005). The meadow vole path is 120 m long with 3066 data points, and the red-backed vole path is 50 m long with 4087 data points. The meadow vole path shows a significant orientation, with the confidence

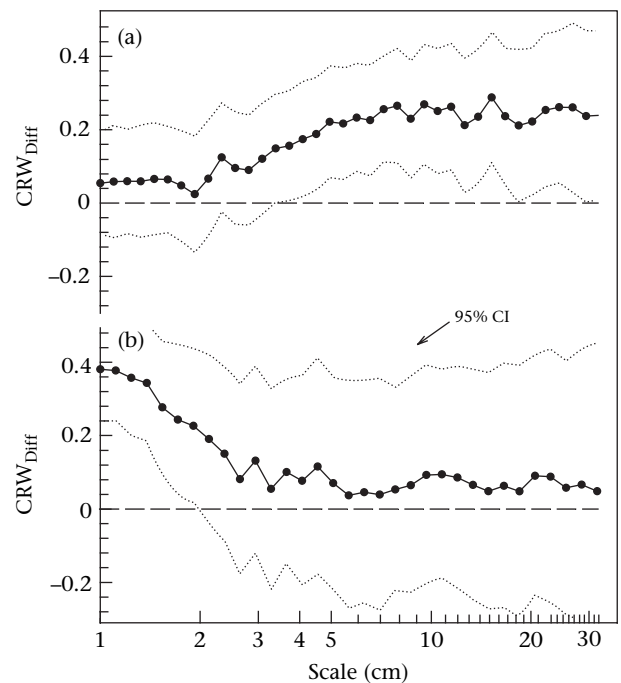


Figure 4. Scaling test analyses of movement paths from a (a) male meadow vole and (b) female red-backed vole. The significantly positive CWR_{Diff} values for the meadow vole (a) indicate oriented movement.

intervals not including zero CRW_{Diff} values at larger scales. However, while the red-backed vole path does not show significant orientation, with confidence intervals including zero CRW_{Diff} values, the confidence intervals are too broad to allow firm conclusions. The power of the test is too low.

The appropriate estimate of confidence intervals would depend on the type of data. For individual movement paths, one could use the variance estimates from Nams & Bourgeois (2004). While this is useful for assessing individual paths, it is not valid for comparing populations of movement paths. One should instead treat each path as an individual sample, with CRW_{Diff} values estimated for each path at each spatial scale, and then estimate the average over all paths, with standard errors of means calculated from variation among paths.

Applying the test

The scaling test would be affected by spatial and scalar heterogeneity. The test assumes spatially homogeneous movement (i.e. no change in movement parameters along the path). Such a problem would occur if the animal travels from one habitat to another, foraging differently in each habitat type. In this case, one could determine the scale of habitat patches, using the techniques of Nams (2005), and then test for oriented movement within each habitat type by analysing individual path segments. In addition, the test could be applied at larger scales to examine oriented movement on scales larger than those of habitat patch sizes.

Thus, the scaling test tests for orientation at large distances, not orientation in general. The movement mechanism of a unoriented moving animal may entail orientation but at a small scale. For example, wood mice travel in an oriented path towards individual bushes, but at a larger scale, they move from bush to bush randomly (Benhamou 1990). The path segments between bushes are the steps of the large-scale CRW. Thus, an analysis of the individual bush-to-bush path segments should show oriented travel, but an analysis of a path containing many such segments should show unoriented movement.

The relation between scale and orientation can be used to choose appropriate path lengths and scales for analysis. Paths should be short enough so that the animal orients past the end of the path, but not to several points within the path. For example, to find out whether bush-to-bush travel in wood mice is oriented, the paths should be divided into bush-to-bush segments.

The maximum scale range should be larger than the scale of movement mechanisms. For example, in Fig. 2, analysing only between scales of 1 and 1.5 would lead to the conclusion that some of those paths are oriented. The choice of the appropriate maximum scale range depends upon whether the movement mechanisms that might operate at small scales are known. For example, to test whether wood mice show oriented travel on a large scale, maximum scales larger than the mean distance between bushes should be used. If the movement mechanisms are unknown, then maximum scales as large as

possible should be used (i.e. until the confidence intervals get too large).

This issue suggests a potential further use of the scaling test. I presented this test as a tool for distinguishing between oriented and unoriented movement. However, since unoriented movement often involves orientation on a small scale, perhaps the scaling test can detect the scale of orientation, or the native scale of a CRW. For example, perhaps in the above example, the scaling test could detect the scale of movement between bushes without prior knowledge about the bushes. More research is needed to test this idea.

The key to applying the scaling test appropriately is to consider at which points the underlying movement mechanisms for the path segments change. For example, brown treecreepers make exploratory forays in search of breeding vacancies before finally dispersing (Doerr & Doerr 2005), so they would be expected to use different orientation mechanisms in the outward versus inward sections of the forays, and thus, those sections should be analysed separately.

The scaling test would be most useful for examining animals' movements in unfamiliar areas (e.g. with dispersers, or animals translocated to new areas) because then movement would not be affected by memories of past visits. It would be especially useful to answer the question of whether dispersing animals use forms of navigation. One could also address the question of the efficiency of search of animals for new habitats. Zollner & Lima (1999) showed that straighter paths are more efficient for discovering new habitat patches than more tortuous paths. However, only CRW were tested. Perhaps oriented paths are even more efficient.

I thank Iain Caldwell for discussions about his turtle tracks that initiated these ideas, and Maria del Mar Delgado for helpful comments on the manuscript. This research was funded by Canada's Natural Sciences and Engineering Research Council.

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Appendix 1: Testing for Correlated Random Walks

This is a derivation for a statistic to test for deviations from a CRW. If an animal path can be described by a CRW, then after n consecutive moves, the expected square of the net distance travelled is given by Kareiva & Shigesada (1983):

$$E(R_n^2) = nE(l^2) + 2E(l)^2 \frac{c}{1-c} \left(n - \frac{1-c^n}{1-c} \right), \quad (1)$$

where θ is the turning angle, c is $E(\cos \theta)$ and l is length of one move. $E(\cos \theta)$ is estimated by the mean $\cos(\theta)$, $E(l)$ is estimated by the mean move length and $E(l^2)$ is estimated by the mean (move length)².

Let \bar{R}_n^2 represent the observed mean (net distance)² for each number of n consecutive moves.

I propose the following statistic, CRW_{Diff} , as a measure of the overall deviation of the observed path from a CRW:

$$CRW_{Diff} = \frac{1}{k} \sum_{n=1}^k \frac{\bar{R}_n^2 - E(R_n^2)}{\text{Max } R_n^2 - E(R_n^2)}, \quad (2)$$

where $\text{Max } R_n^2$ is the maximum value of \bar{R}_n^2 at that n . Note that this equation is similar to the R_{Diff} statistic given by Nams & Bourgeois (2004), except for the added $\text{Max } R_n^2$ term in the denominator. R_{Diff} is quite dependent on n , and this formulation minimizes the dependence of CRW_{Diff} on n .

The maximum value of \bar{R}_n^2 occurs when the movement path is a straight line. Thus,

$$\text{Max } R_n^2 = (n\bar{l})^2, \quad (3)$$

where \bar{l} is the mean step length.

Combining equations (2) and (3) yields:

$$CRW_{Diff} = \frac{1}{k} \sum_{n=1}^k \frac{\bar{R}_n^2 - E(R_n^2)}{n^2 \bar{l}^2 - E(R_n^2)}. \quad (4)$$

Effectively, CRW_{Diff} is the scaled difference between the expected and observed net distance² travelled, averaged over a range of numbers of steps. CRW_{Diff} is normally distributed because the individual \bar{R}_n^2 are. Under the null hypothesis of a CRW, CRW_{Diff} will have a zero mean. CRW_{Diff} will be greater than zero for directed walks, with a maximum value at 1. If CRW_{Diff} is less than zero, then the movement path covers a shorter distance than a CRW.

Variance for this statistic is similar to the derivation in Nams & Bourgeois (2004).

Appendix 2: Animal Movement Models

Random movement

(a) *Correlated random walk*. The direction of each step depends on the direction of the previous step, as follows:

$$\theta_i = \theta_{i-1} + \varepsilon_i, \quad (5)$$

where θ_i is the direction of step i and ε_i is a random angle drawn from a circular normal distribution, with turning angle concentration of K (McCulloch & Cain 1989). Thus, turning angles are independent of previous turning angles.

(b) *3-Step CRW*. The direction of each step now depends on the direction of the previous three steps, as follows:

$$\theta_i = \theta_{i-1-3, i-1} + \varepsilon_i, \quad (6)$$

where $\theta_{i-1, i-1-3}$ is the direction of the vector sum of the previous three steps. Thus, the turning angles are now dependent on the previous turning angles.

(c) *Autocorrelated turn directions*. Some animals tend to alternate turns, so I modelled this by allowing the direction of turning angle, α_i , to depend on the previous turn direction.

$$\theta_i = \theta_{i-1-n, i-1} - k_2 \alpha_{i-1} + \varepsilon_i, \quad (7)$$

where k_2 is a constant, $k_2 \in [-1,1]$ and α_{i-1} is the turning angle of the previous step. When $k_2 = 0$, the movement path is a CRW. When $k_2 > 0$, the animal tends to alternate direction of turns, and when $k_2 < 0$, the animal tends to turn in the same direction as the previous turn.

Directed movement

(d) *Turning direction.* The animal orients towards a specific location by changing direction. Each step, the animal tends to turn towards the desired direction, but the direction also has a random turning element. The direction of step i is given by:

$$\theta_i = \theta_{i-1} + k_{3ei} + k_{3\tau i}, \quad (8)$$

where τ_i is the angle between the current direction and the desired location and k_3 is a constant, with $k_3 \in [0,1]$. When $k_3 = 0$, the movement path is a CRW, and when $k_3 = 1$, the animal walks in a straight line in the desired direction.

(e) *Turning tortuosity.* The animal orients towards a specific location by changing tortuosity. Each step, the tortuosity of the random turning angle depends on the desired direction. The direction of step i is given by:

$$\theta_i = \theta_{i-1} + \varepsilon_i, \quad (9)$$

where ε_i is a random angle drawn from a circular normal distribution, with turning angle concentration of K_{\min}^{ad} $K_{\max}^{1-\text{ad}}$, where ad is the absolute value angle between the current direction and the desired location, linearly scaled from 0 to 1. When turning tortuosity is constant (i.e. $K_{\min} = K_{\max}$), the path is a CRW.

(f) *Fractal walk (as in Nams & Bourgeois 2004).* I modelled this path by first choosing starting and ending points. Then, I modelled the effect of the largest obstructions 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 modelled the effect of the next largest obstructions by taking each of the two path segments and repeating the above procedure. I repeated this procedure down to a very small scale, and then saved the data at the scale of the animal's step size. The deviations were drawn from a normal distribution with a constant coefficient of tortuosity,

$$C_T = \frac{\sqrt{\text{var}}}{\text{segment length}}, \quad (10)$$

which is analogous to the coefficient of variation. A lower C_T gives a straighter path.