Effects of discretizing correlated random walks.

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Abstract

Animal movement models allow ecologists to study processes that operate over a wide range of scales - from local to landscape. Correlated random walk (CRW) models have been used both to model and to explore the biological mechanisms of movement. In a CRW an animal makes discrete steps, and at each step the turning angle is independent of the previous turning angle. Often the sampled path is gathered at a different scale than that of the animals' discrete steps; this is termed 'discretization'. This paper uses simulated CRWs and shows that discretizing CRWs causes smaller turning angles and creates correlations between successive turning angles. The only way to sample a movement path that is not discretized is by using natural end-points for the steps and by sampling them at the correct spatial scale, but without using natural end-points there is no known way to find the correct spatial scale. The discretization also biases statistical tests for CRWs and causes an overestimate in distances travelled; a correction is given for these biases. The discretization effect suggests that there is a natural scale to CRWs - that if CRWs are viewed at other spatial scales then they are no longer CRWs. On the other hand, while there is a natural scale to CRWs, distance-discretizated CRWs are in a sense, scale invariant. Authors need to be aware of the biases caused by discretizing correlated random walks, and deal with them appropriately.

Keywords: Correlated random walk; Discretization; Animal movement; Spatial scale.

1. Introduction

Animal movement is the glue that links individual behaviour to population dynamics. Spatially-explicit individual-based animal movement models allow ecologists to study processes that operate over a wide range of scales - from local to landscape. Although many behavioural mechanisms can explain animal movement, for the purposes of modelling, often the behavioural mechanism itself is ignored and the movement is modelled as some variation of a correlated random walk (Turchin, 1996). In a correlated random walk (CRW) an animal makes discrete steps, and at each step the turning angle is independent of the previous turning angle (Kareiva and Shigesada, 1983; McCulloch and Cain, 1989). This has been the basis of the movement models for a variety of animals, such as carabid beetles (*Pterostichus* sp.; Zar, 1999), wood mice (*Apodemus sylvaticus*, Benhamou, 1990) and caribou (*Rangifer tarandus*, Bergman et al., 2000). CRW models have been used to predict dispersal distances (Schtickzelle and Baguette, 2003), analyze foraging behaviour (Austin et al., 2004) , identify spatial scales of foraging areas (Bailey and Thompson, 2006), analyze the effects of corridors (Haddad, 2000) and predict population effects of water management (Richards et al., 2004).

CRWs have also been used to explore the biological mechanisms of movement. If animals' movement patterns do not follow a CRW, then this points to biological mechanisms that affect their movement. For example, after finding that movements did not conform to CRWs, Mårell et al. (2002) suggested that caribou follow linear terrain features, Morales and Ellner (2002) found that *Tribolium* beetles changed movement behaviours over time and Vernes and Haydon (2001) showed that northern bettongs (*Bettongia tropica)* use area-restricted search.

With a CRW model animals move with discrete steps, but often the sampled path is gathered at a different scale than that of the animals' discrete steps; this is termed 'discretization'. Discretization is done for several reasons. First, it may be too difficult or unprofitable to sample at such a small scale - for example, a mouse's discrete steps might be actual footsteps 1cm in length, but there is no practical way to follow their movements at such a small scale in the field. Second, it may be difficult to define what the natural step is. Although a terrestrial animal's legs might move with discrete steps, the animal's head and nose would move more continuously. Finally, movement paths may be analyzed at different scales than originally sampled in order to remove auto-correlation (Turchin, 1998). Thus many sampled movement paths are actually discretized paths.

Discretization may be done using equal distance or time intervals. Time-discretization is done when locating animals by telemetry (e.g. Reynolds and Laundre, 1990) or visually (e.g. Crist et al., 1992). Distance-discretization is done when following animals by threading (e.g. Boonstra and Craine, 1986) or fluorescent powder tracking (e.g. McShea and Gilles, 1992).

However discretization causes peculiar behaviour. I used discretization in a statistical test for animal orientation (Nams, in press); the test is based on ascertaining whether movement paths approximate CRWs when discretized at larger spatial scales. In developing this test I noticed that when discretized at larger scales, CRWs do not act like CRWs; they travel shorter distances than expected. It has been known that when CRWs are sampled at smaller scales then they do not act like CRWs (turns are autocorrelated; Turchin et al., 1991), but these effects at large scales are a new discovery and have implications for analyses of discretized path data.

This paper explores the effects of discretization on correlated random walk movement patterns.

2. Simulations

I modelled[1] a series of CRWs with 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 100 paths of length 10,000, 10,000, 20,000, 50,000, 70,000 and 100,000 steps for each K-value of 2, 5, 10, 20, 30, and 50. Step lengths were either fixed, or distributed with a uniform distribution with either 1 ±0.2 or 1 ±0.5 step lengths. Then each path was discretized using both distance and time-discretization.

With distance-discretization the paths were resampled at a series of scales ranging from 0.5 to 500 step lengths, and with time-discretization they were resampled at a series of scales ranging from 0.9 to 500 time units (1 time unit = time to travel 1 step). From each discretized path the following were estimated: mean cosine of turning angle, mean step length, mean (step length)^2, correlation between successive turning angles (Fisher and Lee, 1983), correlation between successive step lengths, and the correlation between step length and cos(turn angle). Then means of these were calculated over all 100 paths.

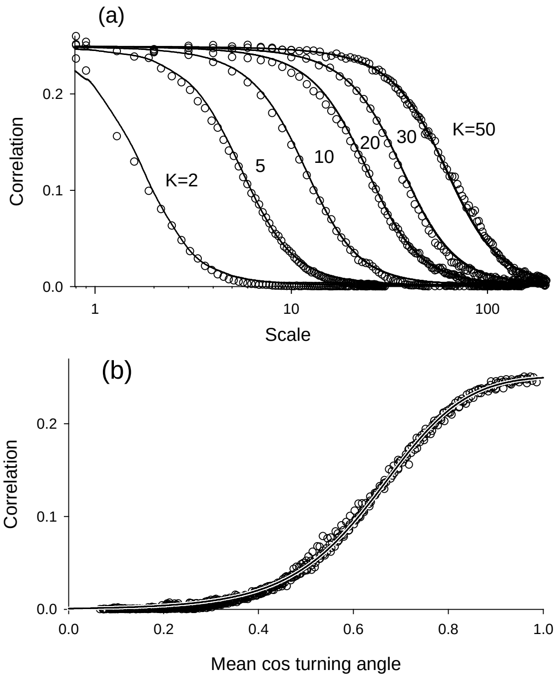

Fig. 1 Correlation between successive turn angles for 6 types of CRWs distance-discretized at various spatial scales: a) correlation vs spatial scale, b) correlation vs mean cosine of turn angle. The solid lines are fitted using: a) Eq. (1) and (2) and b) Eq. (1). Maximum correlation exists at small scales and high mean cosine of turn angles

Distance-discretization

I found that successive turning angles are positively correlated, and the correlation decreases with scale (Fig. 1a). Each discretized CRW has a different relationship between correlation vs scale, however, they all have the same relationship between correlation and mean cosine of turning angle (Fig. 1b). Thus, although correlations between adjacent turning angles decreases with scale of sampling, this is caused by the increase in path tortuousity alone, not by the scale of sampling.

The following curve was fitted (the solid line in Fig. 1b):

$$r = \frac{1}{4 + 4\exp\left(8.15(\arccos\left(c_d\right) - 0.863\right)}; \quad (1)$$

where:

θ = the turning angle, and
c_d = E(cosθ) of discretized path.

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[1] All simulations and analyses were carried out using Mathematica 5.1 ({Wolfram 2004 #2536}).

We can fit the scale vs correlation relationship by using the equations that Benhamou (2004) discovered relating scale to mean cosine of turning angle:

$$c_d = 1 - \frac{2}{\pi}\arctan\left(\frac{Y^2 \ scale}{2}\right); \qquad (2)$$

where:

$$Y = 2\left[l\left(\frac{1+c}{1-c} + cv^2\right)\right]^{-\frac{1}{2}}, \qquad (3)$$

c = E(cosθ),
l = expected step length, estimated by the mean step length, and
cv = coefficient of variation in step length.

Eq. (2) and Eq. (3) can be substituted into Eq. (1) to get the relationship between *scale* and r (the solid lines in Fig. 1a).

These equations show that not only do the sampled paths have correlations between turn angles, but they also have smaller turn angles. This can be seen by setting *scale* = 1, l = 1, and $cv^2 = 0$, in Eq. (2) and (3), and noting the increased mean cosine of turning angle.

Some other results are that there is no correlation between cos(turn angle) for lags of two or more, nor is there a correlation between adjacent step lengths. These simulations were carried out with constant step lengths and circular normal distributed turning angles. However the same relationships were also observed with variable step lengths and uniformly distributed turning angles (data for these analyses not shown).

Time-discretization

With time-discretization there are similar results, but with a slightly different equation fitting the correlation vs E(cosθ) relationship:

$$r = \frac{1}{4 + 4\exp(7.98(\arccos(c_d) - 0.941)}. \qquad (4)$$

In addition, there is a positive correlation between step length and cos(turn angle) - meaning that shorter steps tend to be followed by sharper turn angles. This relationship is only dependent on cos(turn angle), not sampling scale. The following curve was fitted (the solid line in Fig. 2(a) and (b):

$$r = -0.31 + \frac{2\,(0.31)}{1 + \exp(-6.0(\arccos(c_d)))}; \qquad (5)$$

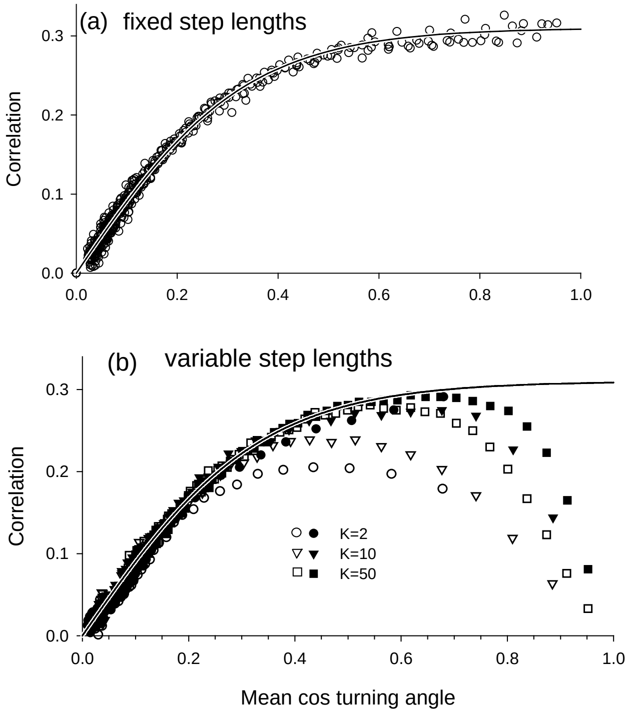


Fig. 2. Correlations between step length and cos(turn angle) vs mean cosine of turn angle, for CRWs time-discretized at various spatial scales: (a) fixed step lengths, and (b) variable step lengths. The solid lines are fitted using Eq. (5). The K's in (b) represent turning angle concentrations for the CRW simulations. The solid symbols represent a step length variation of ±0.2 and the open symbols ±0.5.

When step lengths were varied then the same relationship was observed for correlation vs E(cosθ) (data not shown), but the correlation between step length and cos(turn angle) now is also affected by sampling scale (Fig. 2b)

Some other results are that there is no autocorrelation in turn angles at a lag of two or more, nor is there a correlation between adjacent step lengths. Although Benhamou's (2004) equation relating turn angle correlation to mean cos turning angle (Eq. (2) and Eq. (3)) was originally developed for distance-discretized paths, my simulations show that it also fits time-discretized paths, with both fixed and varying step lengths (data for these analyses not shown).

3. Causes of discretization effects

I have shown that discretizing a CRW, whether using distance- or time-discretization, creates a path that is not a CRW. Discretizing creates correlated adjacent turn angles and straighter turn angles. Time-discretizing also creates correlations between step lengths and turn angles.

These effects are not just caused by sampling the path at a larger scale than the native scale - they are caused by the act of discretization. This is demonstrated by the fact that the largest correlations occur at a scale of the original step length (Fig. 1a), and that the path tortuousity completely explains the correlations (for distance-discretization; Fig. 1b).

In order to explore the reason for these discretization effects, I carried out the following simulations to represent the likelihood for the underlying movement path given a certain discretized step.

To explore the correlations between turns, a CRW was simulated with 200,000 steps, K = 20, and fixed step lengths. It was then distance-discretized to a scale of 10 step lengths. All discretized turns with turn angles between 1.24 - 1.30 radians were selected, along with the respective underlying path segments, and then they were plotted on one graph (Fig. 3).

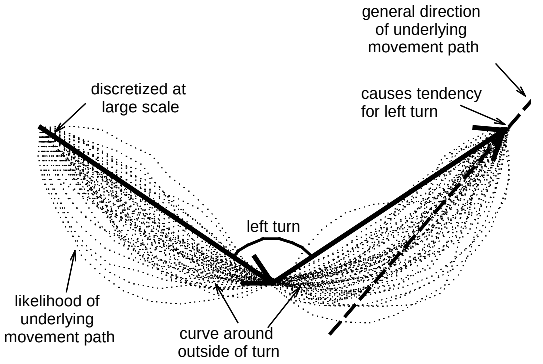
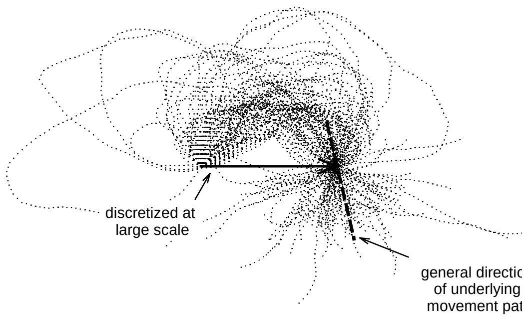


Fig. 3. Simulation for explanation of the discretization effect for turn angles. Dotted lines are segments of the original movement path, which was then distance-discretized at a scale of 10 (solid line). The dotted lines represent the likelihood for the underlying movement path given a discretized step.

Fig. 3 suggests the following explanation for the discretization effect on turn angle correlations. Because directions are correlated in a CRW, the likelihood for the movement path tends to curve around the outside of the turns of the large-scale steps. This curving causes the movement path to reach the end of the second step pointed slightly in the direction of the previous turn - creating a new, large-scale turn, slightly in the same direction as the previous one. This causes a positive correlation between successive turn angles.

To explore the correlations between step lengths and turn angles, a CRW was simulated with 100,000 steps, K = 20, and fixed step lengths. It was then time-discretized to a scale of 49.9 time units (1 unit = time to travel 1 step). Two sets of discretized turns were selected (the short steps were a length of 10-30, and the long a 46-48), along with the respective underlying path segments, and then they were plotted on one graph (Fig. 4).

(a) Short discretized step



(b) Long discretized step

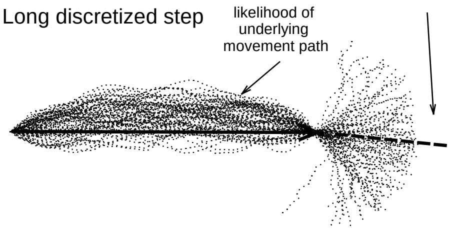


Fig. 4. Simulation for explanation of discretization effect for step lengths and turn angles. Dotted lines are segments of the original movement path, which was then time-discretized at a scale of 49.9 (solid line). For clarity, only half of the segments were plotted - those that curved above the discretized line. The dotted lines represent the likelihood for the underlying movement path given a discretized step..

Fig. 4 suggests the following explanation for the discretization effect on path length and turn correlations. Shorter discretized steps are caused by more tortuous segments of the underlying movement path. Because directions are correlated in a CRW, the likelihood for the movement path for more tortuous segments (Fig. 4a) reaches the end of the discretized step at a greater angle than for less tortuous segments (Fig. 4b). Thus shorter discretized step lengths are usually followed by greater turn angles. This causes a positive correlation between step lengths and turn angles.

The discretization effect also explains the unexpected results in the animal orientation study (Nams, in press). I had found that when CRW paths were sampled at larger scales, they travel shorter distances than expected. This is caused by the sampled movement pattern having correlated turning angles (Fig. 1).

4. Sampling implications

Many sampled movement paths will show this discretization effect, because most sampled paths are discretized. The only way to sample a movement path that is not discretized is by using natural end-points for the steps and by sampling them at the correct spatial scale. If you use natural end-points then you could find the correct spatial scale by choosing the scale at which turn angle correlations are zero; however if you do not use natural end-points then there is no known way to find the correct spatial scale.

Note that Fig. 1a suggests that the discretization effect does not occur when the sampled path is very tortuous (i.e. zero correlation at larger scales), suggesting that one should sample at large spatial scales. However sampling paths at very large scales gives little useful information because the path is now a completely random walk (Johnson et al., 1992).

The discretization effect biases choices of appropriate sampling scales. Two ways that researchers choose sampling scales are first, by increasing the scale until the correlation in turn angles is zero (Turchin, 1998), and second, by increasing the step lag between turns until the correlation is zero (Vernes and Haydon, 2001). The first method will result in choosing a very large scale because the correlation caused by discretization is zero only at very large scales (Fig. 1a). The second will result in choosing a scale twice the original scale, because correlations between turn angles at lags more than one are not correlated.

5. Statistically testing for CRWs

The discretization effect also biases statistical tests for CRWs. However the problem can be corrected, as follows. The most common statistical test for CRWs is based on comparing observed to predicted net distance^2 travelled. After n consecutive moves, the expected net distance^2 travelled for a CRW is given by (Kareiva and Shigesada, 1983):

$$R_n^2 = nl^2 + 2l_2 \frac{c}{1-c}\left(n - \frac{1-c^n}{1-c}\right); \quad (6)$$

where:

R^2_n = expected net distance^2 travelled, estimated by mean (net distance^2),

c = E(cosθ), estimated by mean (cos turn angle), and

l_2 = expected (step length)^2, estimated by mean (step length)^2.

However this equation does not apply to discretized CRWs because turning angles are both smaller and positively correlated. Furthermore, we do not know the specific underlying CRW that generated the discretized path; a series of such CRWs are possible, each with a different step length.

The test can be adapted for discretized CRWs (I will call this the 'discretized CRW test') by choosing a CRW that would generate the observed discretized path, and that has the same step length as the discretized path. We do this by combining Eq. (2) and (3), setting *cv* = 0, *scale* = *l*, and solving for *c*, getting:

$$c = 1 - \frac{2}{1 + 2\ \tan\left(\frac{c_d\ \pi}{2}\right)}. \qquad (7)$$

This estimate for E(cosθ) for the underlying CRW is what we would use in Eq. (6) to test for CRWs in discretized movement paths.

The following simulation gives an example of the discretized CRW test[2], Thirty CRWs were simulated, each with 1000 steps of constant length, and K = 50. The 95% confidence intervals for net distance^2 were based on among-path variation. Using the original paths, the observed net distance^2 fit the original expected CRW values from Eq. (5) (Fig. 5a). However, if the paths are discretized at a scale of 1.1 (Fig. 5b), or 5 (Fig. 5c) then the observed values no longer fit the expected CRW values, but they do fit the values for the discretized CRW test (Eq. (5) and (6)).

The discretized CRW test also applies to time-discretized paths. Although the key relationship it depends on (Eq. (2)) was developed for distance-discretized paths (Benhamou, 2004), my simulations show that it also fits for time-discretized paths.

6. Modelling implications

There are several modelling implications to the discretization effect. First, one may incorrectly reject a CRW model for an animal's movement pattern. CRW models are often used as null movement

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[2] A Windows-based computer program to carry out this adapted test is available for download by contacting the author

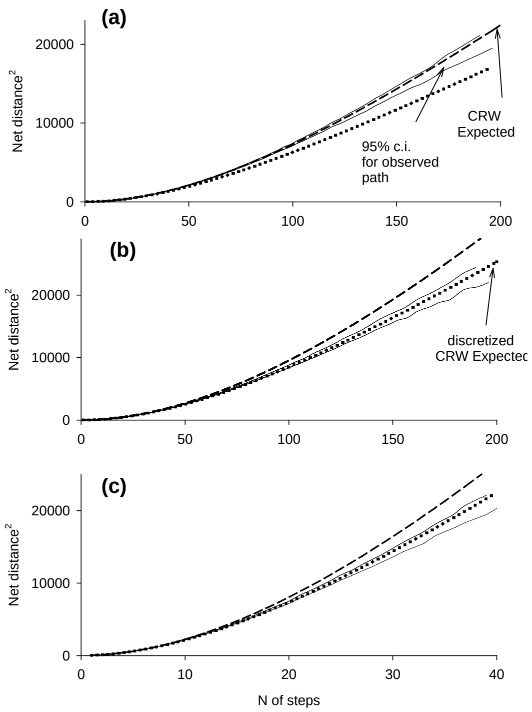

Fig. 5. Mean net distance^2 for a simulated CRW, and expected values based on the original and the discretized tests: (a) original path (b) path distance-discretized at a scale of 1.1, and (c) at a scale of 5. The expected CRW values lie within the 95% bounds of the original path (a), and the expected discretized CRW values lies within the bounds of the discretized paths (b and c).

models (Turchin, 1996; Hutchinson, 2000), the rejection of which lead to hypotheses about biological mechanisms of movement, and the devising of more complicated models.

Second, created models may overestimate distances travelled. The purpose of many movement models is to predict dispersal distances (e.g. Haddad, 1999; Schtickzelle and Baguette, 2003). The overestimate in predicted distance travelled can be estimated by the following ratio:

$$bias = \frac{R_n^2}{R_n^2 \,(\text{using adjusted c})} . \qquad (8)$$

We can calculate the bias for large numbers of steps by substituting Eq. (6) and (7) into (8), and taking the limit as $n \longrightarrow \infty$ (for simplicity, consider constant step lengths, i.e. $l_2 = l^2$):

$$\lim_{n\to\infty} bias = \frac{1+c}{2(1-c)\tan\left(\frac{c\pi}{2}\right)} . \qquad (9)$$

This is the ratio of expected net distances^2. In order to estimate the bias for the net distance travelled we note that the expected net distance can be estimated by:

$$R_n = \mathrm{k}\sqrt{R_n^2} \; , \qquad (10)$$

for some constant k (Byers, 2001). Thus in Eq. (8) k cancels out, and to estimate the overestimate in net distance travelled we only need to take the square root of Eq. (9).

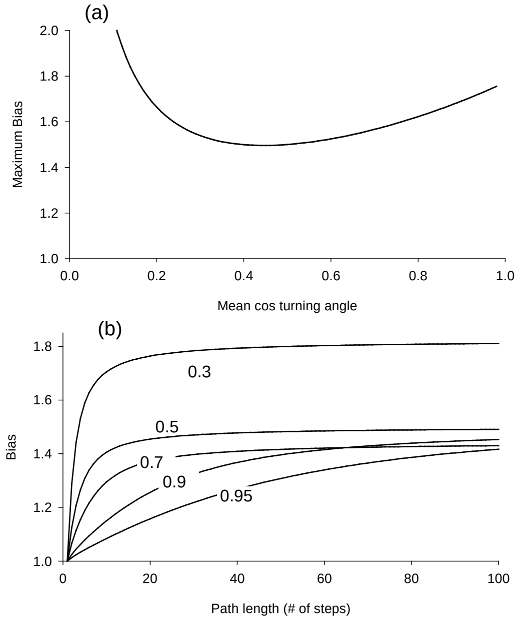

Fig. 6. Bias in estimated net distance travelled for a CRW model when estimates of parameters are based on discretized movement paths: (a) bias for large movement paths (b) bias vs path length for various values of E(cosθ). Bias is the amount overestimated, as a proportion.

This overestimate depends only on the mean turn angle of the discretized path (Eq. (9)), and is very large. For long movement paths discretization overestimates net distance travelled by a factor of at least 1.5 (Fig. 6a), and for shorter movement paths the maximum overestimate is already reached by ~50 steps (Fig. 6b).

Note that the discretization effect also affects other movement models besides CRWs. The key issue is biased estimates for mean turning angles and correlations between successive turning angles. Any models that require turning angle estimates from sampled paths should use the adjustment given in Eq. (7).

7. Theoretical implications

The discretization effect suggests that there is a natural scale to CRWs - that if CRWs are viewed at other spatial scales then they are no longer CRWs. Turchin (1998) has pointed out that there is a minimum natural scale, but this is the first study to find that there is a maximum natural scale. But, it is not known how to discover what that natural scale is.

On the other hand, while there is a natural scale to CRWs, distance-discretizated CRWs are in a sense, scale invariant. Since Eq. (1) is only dependent on E(cosθ), one cannot tell if a distance-discretizated path came from a straight CRW with short step lengths, or a tortuous CRW with long step lengths. Benhamou (2004) alluded to this when he showed that one can predict the E(cosθ) of a discretized path solely from the sinuosity and sampling scale of the underlying CRW (Eq. (2)). Thus there is only one type of distance-discretizated CRW, no matter what the underlying CRW they come from. This is an interesting theoretical result which should be explored further.

8. Field studies

Some field studies have corroborated the discretization effects. For example, grey seal (time-discretization; Austin et al., 2004) and northern bettong (distance-discretization; Vernes and Haydon, 2001) movements showed autocorrelations in turn angles at a lag of 1 but not past that. In addition, the northern bettong movements showed correlations between turn angles and step lengths. Finally, caribou movements (time-discretization; 2000) showed autocorrelations in turn angles and also shorter net distances travelled than predicted by Kareiva and Shigesada's (1983) test.

On the other hand, other field studies have not found significant correlations between turn angles (e.g. Nolet and Mooij, 2002; Fortin et al., 2005) nor that movement paths fail Kareiva and Shigesada's (1983) test (e.g. Austin et al., 2004). But it is difficult to evaluate these because typically authors do not report the correlation values nor errors of them when they find no significant autocorrelations, and thus it is not known how powerful their tests are. Correlation estimates have a high variance and thus long path lengths are required in order to detect non-zero correlations.

However technological advances will increase sampled path lengths. In the last decade animal-mounted GPS tracking devices have been developed to automate the collection of movement data (Edenius, 1997; Johnson et al., 2002). As with all computer-based technology, smaller devices are being developed, allowing them to be used on smaller animals. Furthermore, the accuracy of locations has increased since Selective Availability was removed from the GPS system in year 2000. Now one can automatically track larger mammals, recording 10,000 positions per movement path to an accuracy of ±10m.

These increased path lengths will increase statistical power and thus accentuate the discretization effect. Authors need to be aware of the biases caused by discretizing correlated random walks, and deal with them appropriately.

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