Characteristic Spatial and Temporal Scales Unify Models of Animal Movement

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Abstract: Animal movements have been modeled with diffusion at large scales and with more detailed movement models at smaller scales. We argue that the biologically relevant behavior of a wide class of movement models can be efficiently summarized with two parameters: the characteristic temporal and spatial scales of movement. We define these scales so that they describe movement behavior both at short scales (through the velocity autocorrelation function) and at long scales (through the diffusion coefficient). We derive these scales for two types of commonly used movement models: the discrete-step correlated random walk, with either constant or random step intervals, and the continuous-time correlated velocity model. For a given set of characteristic scales, the models produce very similar trajectories and encounter rates between moving searchers and stationary targets. Thus, we argue that characteristic scales provide a unifying currency that can be used to parameterize a wide range of ecological phenomena related to movement.

Keywords: autocorrelation, correlated random walk, diffusion, encounter rates, correlated velocity movement model.

Introduction

Animal movement is fundamental to many ecological phenomena occurring on a wide range of temporal and spatial scales. At the smallest scales, movements reflect immediate tactical responses to stimuli. At the largest scales, movements are related to dispersal, migration, and colonization. Processes related to foraging, predator avoidance, or mate encounter often occur at intermediate scales. At all scales, movements are constrained by bioenergetic limitations, physical constraints, and behavioral imperatives.

Because animal movements are the result of complex behavioral responses to internal states, environmental cues, and biophysical constraints, it is generally impossible to measure or model all of these interactions explicitly (Codling et al. 2008; Nathan et al. 2008). Consequently, movements are often modeled as a stochastic process with intrinsically random velocities and orientations summarized by probability densities. The earliest models of random movement were based on simple random-walk assumptions of Brownian motion, leading to diffusion (Skellam 1951; Okubo 1980; Turchin 1998). Diffusion models, which are well understood mathematically (Ovaskainen and Cornell 2003; Ovaskainen 2008), have proven useful for modeling a variety of complex systems, including identifying and predicting patterns of dispersal in heterogeneous habitats (Turchin 1998; Ovaskainen et al. 2008b) and explaining variability in heterogeneous populations of migrating and dispersing organisms (Gurarie et al. 2009b). Brownian motion can be a useful model of movement at temporal scales substantially greater than the scale of autocorrelation (Bartumeus et al. 2005; Visser and Kiorboe 2006) and have consequently been most fruitfully applied to explain relatively coarse-resolution data such as mark-recapture data (Ovaskainen et al. 2008a).

A natural extension of the simple random-walk model is the correlated random-walk (CRW) model, which includes directional persistence. While an extensive mathematical analysis of CRWs dates over half a century (Patlak 1953a, 1953b), CRWs gained prominence only after a seminal study of butterfly movements by Kareiva and Shigesada (1983). Since then, parameters of the CRW have been estimated for a variety of actual animal movement data sets (e.g., Byers 2001; Morales et al. 2004; Fortin et al. 2005; Coltelli et al. 2008; Patterson et al. 2008). In parallel, the statistical properties of the CRW have been extensively explored (see Bovet and Benhamou 1988; Viswanathan et al. 2005; Bartumeus et al. 2008).

While the CRW is most directly applicable to discretely sampled movements with independent steps, an alternative approach is to model movement as the integral of a stochastic velocity process. A straightforward example is the Ornstein-Uhlenbeck (OU) mean-reversion process (Uhlenbeck and Ornstein 1930), which was developed as a velocity model to describe the movements of video-tracked...
microscopic organisms (Dunn and Brown 1987; Alt 1988, 1990). Alternative formulations of this model have been studied and applied to a variety of organisms, ranging from motile algae to marine mammals (Blackwell 1997; Johnson et al. 2008; Gurarie et al. 2009, 2011). These correlated velocity models are most relevant to very high-resolution data with non-independent steps or irregularly sampled data where a continuous description of movement is a natural starting point (Johnson et al. 2008; Gurarie et al. 2009; Nouvellet et al. 2009).

The approaches outlined above differ with respect to their structural assumptions and the scales at which they operate. On the one hand, correlation in movement is necessarily observed at high sampling rates; on the other, diffusion models are valid at scales that are longer than the length and time scales of autocorrelation in the movement. Several studies have approached the question of identifying the scales that characterize the transition between ballistic and diffusive limits, leading to alternative definitions of characteristic scales derived for various CRW (Jeanson et al. 2003; Viswanathan et al. 2005; Visser and Kiorboe 2006) and continuous—movement (Nouvellet et al. 2009; Gurarie et al. 2011) models. All of these results share the same intuitive interpretation in terms of quantifying the time scale at which correlated movements become uncorrelated.

In this study, we propose a definition for the temporal and spatial scales of stochastic movements that can be applied to general discrete- and continuous—movement models. These scales rigorously quantify the transition between the ballistic and diffusive limits, provide a common currency by which to compare diverse types of movement models, and thus generalize and unify the special cases presented in the earlier literature. We illustrate via simulation the utility of the characteristic scales by showing that they are sufficient for predicting mesoscale phenomena such as encounter rates between searchers and targets. We thus argue that the characteristic scales of movement are sufficient for parameterizing a wide range of ecological phenomena.

Methods

Movement Models

Though actual movements contain many different behavioral modes and may be influenced by a variety of external stimuli, the discussion here is constrained to a single behavioral unit of movement that is homogeneous and stationary, that is, described by the same set of parameters independent of absolute spatial location and time and with no external biases. Homogeneous and stationary movements will tend toward diffusion behavior at long time scales while having a varying degree of autocorrelation at the short scale. We consider here for simplicity only two-dimensional movement processes and denote the position of the individual at time $t$ by $z(t) \in \mathbb{R}^2$, and we analyze models in which finite steps are taken at regular or random intervals and models in which the organism moves continuously in time.

**Correlated Random Walks.** Correlated random walks (CRWs) are movement models in which the individual takes discrete steps at finite time intervals. Step lengths $L > 0$ and time intervals $T > 0$ can be drawn from arbitrary joint or independent distributions. An important summary statistic is the velocity variability parameter,

$$\lambda = \frac{\langle |v|^2 \rangle}{\langle |v| \rangle^2},$$

where the speed $|v| = L/T$, (all symbols used to describe the movement models and encounter rate simulations are summarized in table 1). Note that $\lambda = 1$ if the organism moves with constant speed, while $\lambda > 1$ for any random distribution of $|v|$. We restrict the discussion here to two special cases. If the locations of the organism are measured at regular intervals, it is natural to use the fixed-interval CRW with a constant interval $T$. In the exponential-interval CRW, the intervals are drawn from an exponential distribution with mean $\langle T \rangle$. The fixed-interval CRW is a Markov chain in discrete time, while the exponential-interval CRW is a Markov process in continuous time (Grimmett and Stirzaker 2001).

The turning angles $\theta$ between steps are derived from a distribution in $[-\pi, \pi]$, typically assumed to be unimodal and symmetric around 0. The degree of correlation can be measured by the mean cosine of the turning angles, $\kappa = \langle \cos(\theta) \rangle$: $\kappa = 0$ corresponds to an uncorrelated random walk, and $\kappa = 1$ corresponds to perfectly linear movement.

**Correlated Velocity Models.** The second family of movement models is based on formulating a stochastic model for velocity $v(t)$ and obtaining the position by integrating the velocity of the organism over time via

$$z(t) = z(0) + \int_0^t v(t') dt'.$$

As one example, a two-dimensional version of the OU process (Uhlenbeck and Ornstein 1930; Gillespie 1996), formulated as the stochastic differential equation
Characteristic Scales of Movement

The fundamental descriptions of the CVM and CRW models suggest that they cannot be mapped to each other one-to-one. For example, the CVM is defined regardless of the frequency at which it is sampled, whereas the assumption of independent move lengths and turning angles between consecutive steps makes the properties of the CRW depend profoundly on the sampling intervals. In order to introduce a common currency for both kinds of movement models, we interpret the CRW as a continuous-time process. Thus, rather than considering the intervals $T_i$, we consider movement between positions $z_i$ and $z_{i+1}$ as occurring at constant speed $L_i/T_i$.

The short-term behavior of a movement process can be characterized by the velocity autocorrelation function (VAF; Alt 1990; Takagi et al. 2008),

$$\langle v(t - \Delta t) \cdot v(t) \rangle / \langle |v(t)|^2 \rangle, \quad (2)$$

where the expectation is taken over initial times $t$. For a homogeneous movement process in continuous time with no bias or persistent rotation, such as the CVM, the VAF has the simple exponential form (Alt 1988)

$$C_v(\Delta t) = e^{-\Delta t/\tau}. \quad (3)$$

The autocorrelation function of the CRW is not exactly exponential, so the CVM and the CRW cannot be matched exactly for their detailed short-scale behavior. However, we can define a characteristic time scale by determining exactly for their detailed short-scale behavior. However, we can define a characteristic time scale by determining a specific target value for the VAF. Because it is natural to consider $\tau$ as the characteristic time scale of the CVM, we define the characteristic time scale $\tau$ for any movement process as the time lag at which the velocity autocorrelation function attains the value of $C_v(\tau) = 1/e$.

At long times, most unbiased and unconstrained stochastic movements are asymptotically diffusive; that is, the expected squared displacement increases linearly with time as

$$\langle |z(t) - z(0)|^2 \rangle = 2Ddt + o(t), \quad (4)$$

where the constant $D$ is commonly referred to as the diffusion coefficient; $d$ is the dimensionality of the process, restricted to $d = 2$ in our discussion; and $o(t)$ is a term that becomes negligible at large $t$ (Codling et al. 2008). The diffusion constant is sufficient to describe the asymptotic behavior of a movement process. However, $D$ has a nonintuitive unit of distance squared over time, so we replace it with the spatial distance scale, which (in two dimensions) can be expressed as

$$\sigma = 2\sqrt{Dr}, \quad (5)$$

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Quantity</th>
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<tbody>
<tr>
<td>$\kappa$</td>
<td>Angle clustering coefficient: $\langle \cos(\theta) \rangle$</td>
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<tr>
<td>$\lambda$</td>
<td>Velocity variability index: $\langle</td>
</tr>
<tr>
<td>$\langle L \rangle, \langle L^2 \rangle$</td>
<td>Moments of step length distribution</td>
</tr>
<tr>
<td>$\langle T \rangle, \langle T^2 \rangle$</td>
<td>Moments of time interval distribution</td>
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Correlated velocity movement:

- $\tau$: Time scale of autocorrelation
- $\beta$: Standard deviation of Wiener stochasticity

All movements:

- $\tau$: Characteristic time scale of autocorrelation
- $\sigma$: Characteristic length scale of autocorrelation

Encounter rates:

- $\alpha$: Encounter radius
- $\rho$: Mean density of targets
- $\eta$: Mean number of targets per cluster
- $\gamma$: Mean distance of targets from center of respective cluster

Table 1: Key parameters and quantities
such that the coefficient of proportionality of the expected squared displacement at large time is just $\sigma^2/\tau$.

The characteristic length and time scales of movement ($\sigma, \tau$) can be computed for any movement model following the definitions above. While these two parameters do not capture all details of a movement process, we hypothesize that many ecologically relevant key features of the movement process at all scales (short, long, and intermediate) are summarized by these parameters.

Can Characteristic Scales Predict Encounter Rates?

To test the extent to which the characteristic scales ($\sigma, \tau$) provide a common currency to compare different model types, we first derive them for the three movement models introduced above, reparameterize the movement models in terms of the scales, and examine the properties of the ensuing trajectories. We explore whether the characteristic scales are sufficient to predict a nontrivial ecological process, using encounter rates as a test statistic. Encounter rates are fundamental to many ecological processes, such as foraging, predator avoidance, and mate encounter, and they depend nontrivially on short- and long-term characteristics of movements (Hutchinson and Waser 2007). While there are many ways to define encounter rates, we consider here the mean first hitting time, that is, the expectation of the time that a searcher released in a random location in a space populated with point targets first comes within a certain distance of any target. We denote the location in a space populated with point targets first comes within a radius $r$ of any target by $\z(t)$ and the expected squared displacement after $n$ steps for a two-dimensional CRW was derived by Kareiva and Shigesada (1983). With some reorganization, their result can be expressed (for both the fixed-interval CRW and the random-interval CRW) as $\langle (\z(t) - \z(0))^2 \rangle = \sigma^2 r t + o(t)$, where

$$\frac{\sigma^2}{\tau} = \frac{\langle L^2 \rangle + \langle L \rangle^2 [2\kappa/(1 - \kappa)]}{\langle T \rangle},$$

and $o(t)$ represents a term that grows slower than linearly with time. In general (see app. A), the VAF of a CRW is given by

$$C_s(\Delta t) = p_s(\Delta t) + \frac{1}{\lambda} \sum_{i=1}^{\infty} p_i(\Delta t) i,$$

where $p_s(\Delta t)$ is the probability that $i$ steps have been taken in time interval $\Delta t$, starting from any random time.

Fixed-Interval CRW. Because of our continuous-time interpretation of CRW, $p_s(\Delta t)$ decreases linearly from 1 to 0 in the interval $0 \leq \Delta t \leq T$ while $p_i(\Delta t)$ increases linearly from 0 to 1 over the same interval. A general formula for $p_i(\Delta t)$ is derived in appendix A. Substituting these results into equation (7) yields

$$C_s(\Delta t) = \begin{cases} 
1 - \frac{\Delta t}{T} & \text{for } \Delta t \leq T \\
\frac{1}{\lambda} \kappa^{\Delta t T} & \text{for } \Delta t > T.
\end{cases}$$

The second case in equation (8) is, in fact, exact only for integer multiples of $T$, that is, $\Delta t = n T$. At fractional multiples, the exact solution is a linear interpolation between the integer multiple values (fig. 1A). From the definition of $\tau$, we obtain

$$\tau = \begin{cases} 
\left(1 - \frac{\lambda}{\kappa} \frac{\lambda}{e} \right) T & \text{for } \kappa \leq \frac{\lambda}{e} \\
\log(\lambda) - 1 & \text{for } \kappa > \frac{\lambda}{e}.
\end{cases}$$

Note that for the simple fixed-interval random walk, $\kappa = 0$ and $\tau = (1 - 1/e)T$; that is, the characteristic time scale is, somewhat counterintuitively, shorter than the interval between steps. As expected, $\tau$ increases with $\kappa$; that is, the characteristic time scale is long if the random walk has a high level of persistence. Corresponding formulae for $\sigma$ can be obtained directly from equation (6).

Exponential-Interval CRW. In this model, the number of steps taken within time $\Delta t$ is Poisson distributed with parameter $\Delta t \langle T \rangle$, yielding

$$C_s(\Delta t) = \exp\left(-\frac{\Delta t}{T}\right)\left[1 + \frac{1}{\lambda} \left[-1 + \exp\left(\frac{\kappa \Delta t}{T}\right)\right]\right],$$

from which $\tau$ can be solved by requiring that $C_s(\tau) =$
Figure 1: Simulations of movement models (left panels) and empirical and theoretical velocity autocorrelation functions (VAFs; right panels). A, Correlated random walk (CRW) with a fixed-interval time step $T = 1/2$; B, exponential-interval CRW with $\langle T \rangle = 1/2$. Velocities have a Weibull distribution, with shape parameter 2, such that $\lambda = 4/\pi$, and values of $\kappa$ have been selected so that the characteristic time scale $\tau$ is 1, 2, or 4, matching the values of $\tau$ in the correlated velocity movement (CVM) trajectories (C). For all models, values of $\sigma$ are set equal to $\tau$ by selecting appropriate mean step lengths $\langle L \rangle$ for the CRW and the $\beta$ parameter for the CVM. The right panels illustrate corresponding empirical VAFs (circles) obtained by averaging over 100 trajectories and theoretical VAFs (lines) from equations (3), (8), and (10). The dotted horizontal lines show $1/e$, illustrating the definition of the characteristic time scale.
1/e and $\sigma$ can be obtained using equation (5). The dependency of $\tau$ on model parameters is illustrated in figure 2. While the general solution can be obtained only numerically, two limiting cases are worth noting. First, for constant speed ($\lambda = 1$), $\tau = (T)/(1 - \kappa)$ and $\sigma = \langle L \rangle[(1 + \kappa)/(1 - \kappa)^2]^{1/2}$. Second, for uncorrelated random walk ($\kappa = 0$), $\tau = \langle T \rangle$ and $\sigma = \langle L \rangle/(1/\lambda)^{1/2}$.

**Characteristic Scales of CVM**

The CVM model is parameterized in terms of its characteristic scales in a more natural way than the CRW model. In particular, the VAF of the CVM is given exactly by equation (2), and thus, its characteristic time scale is directly the parameter $\tau$ (fig. 1C). Furthermore, it can be shown (app. B) that

$$\langle |z(t) - z(0)|^2 \rangle = 2\beta^2\tau^2\frac{\kappa}{\tau} + e^{-\kappa\tau} - 1.$$  \hspace{1cm} (11)

At time scales greater than $\tau$, the second and third terms in parentheses are negligible, giving $\sigma = (2\tau)^{1/2}\beta$. We note additionally that the expected stationary speed of movement of a CVM, defined as $\nu = \lim_{t \to \infty} \langle |v(t)| \rangle$, can be expressed in terms of the characteristic scales (app. B)

$$\nu = \frac{\sqrt{\pi}}{2\sqrt{3}r} \approx 0.627 \frac{\sigma}{\tau}.$$  \hspace{1cm} (12)

For a comprehensive treatment of the statistical properties of the OU process, from which all the properties of the CVM are derived, the reader is encouraged to consult Gillespie (1996).

**Simulation Results**

Simulated trajectories of the fixed-interval CRW, the exponential-interval CRW, and the CVM models look visually very similar when their characteristic scales ($\sigma, \tau$) are equal (fig. 1). Higher values of $\kappa$ for the CRW models lead to less tortuous movements than do lower values of $\kappa$, as do higher values of $\tau$ for the CVM (figs. 1, 2). Figure 1 further confirms that the velocity autocorrelation functions derived above correspond to simulation results. In

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**Figure 2:** Plots of the characteristic scale $\tau$ as a function of the velocity variability index $\lambda$ (right) and the clustering coefficient $\kappa$ (left) for fixed-interval (top) and exponential-interval (bottom) correlated random walks. The fixed-interval results are based on equation (9) and the exponential-interval results on equation (10). The fixed and mean step durations $T$ and $\langle T \rangle$ are set to 1 in both cases.
the CVM, the velocity autocorrelation function decays exponentially, while for the CRWs, the decay is only approximately exponential.

Simulation results of the hitting-time experiment are presented in figure 3. Differences in hitting times spanned many orders of magnitude, depending on the density and distribution of targets and on the parameters of the movement model. As expected, hitting times decrease with increasing target density, and more directed movement (high values of \( \sigma = \tau \)) leads to shorter hitting times than does tortuous movement. The regular lattice had lower mean hitting times than the Poisson target geometry, which had lower hitting times than the clustered target geometry. In line with our hypothesis, all movement models led to almost identical hitting times when their characteristic scales were matched. This is a nontrivial result, given the wide overall variation in hitting times and the fact that qualitatively different models were matched using the two parameters only.

**Comparisons with Earlier Results**

The concept of characteristic scales has been addressed several times in the literature on movement analysis. We briefly review these studies here, with the aim of illustrating the equivalence to our more general results. In all cases,

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**Figure 3:** Hitting-time simulations. Upper panels are schematics of three different target geometries: hexagonal lattice (A), Poisson point process (B), and clustered landscape (C; \( \gamma = 10, \gamma = 5 \)). The lower panels are corresponding simulation results. The points and the error bars show the means ± 2 SEs based on 200 replications of the first hitting-time process. The symbols refer to the three movement models: fixed-interval correlated random walk (CRW; circles), exponential-interval CRW (triangles), and correlated velocity movement (CVM; squares). Simulations were performed for a range of density (\( \rho \)) values between 0.001 and 0.008, coded by color, and for a range of characteristic scale values \( \sigma = \tau \) from 0.5 to 8. Other parameter values are as in figure 1.
we restate the earlier results in terms of the notation introduced here.

Viswanathan et al. (2005) analyzed a CRW with constant step length, citing the exponential decay typical of Markov processes to identify a dimensionless correlation function equivalent to a discrete version of the VAF (eq. [2]). The approximate exponential decay term is then expressed as \( \tau = -T \log(\kappa) \). This corresponds to a special case of equation (9) for constant step lengths (\( \lambda = 1 \)) and constrained to \( \kappa > e^{-1} \approx 0.368 \). It bears noting that this study was later revisited in some detail by Bartumeus et al. (2008) in the context of extensive simulations of encounter rates.

In a study exploring the transition between ballistic and diffusive movement and encounter rates, Visser and Kiorboe (2006) consider the characteristic temporal and spatial scales of "run-tumble" movements, which are similar to the random-interval CRWs discussed here. Citing a general result applicable to one-dimensional autocorrelated movements (Berg 1993), they report a characteristic time scale \( \tau = \langle T \rangle / (1 - \kappa) \). This is equal to the characteristic time scale of the exponential-interval CRW obtained here (eq. [10] and accompanying text) in the special case of constant speed (\( \lambda = 1 \)). Our results thus generalize the cited results by showing how variability in step length and speed alters the characteristic spatial and temporal scales (fig. 2).

More recently, Nouvellet et al. (2009) presented a general model of continuous stochastic movements, also defining position as an integral of velocity. Rather than define an explicit model for velocity, the authors simply assumed that velocity follows some autocorrelation function \( C_v(\Delta t) \). They considered (among other options) the exponential form \( C_v(\Delta t) = \exp(-t/\tau) \), corresponding to the CVM presented here, noting that \( \tau \) "concisely characterizes the decay of correlations," matching our concept of the characteristic time scale (Nouvellet et al. 2009, p. 509). The authors propose that an estimate for \( \tau \) can be obtained from the behavior of the mean square displacement \( \langle (z(t) - z(0))^2 \rangle \), which can be estimated from data directly without assuming any specific movement model. They proposed (though did not formally prove) that \( \tau \) corresponds to the lag time that leads to \( \langle (z(2r) - z(0))^2 \rangle / \langle (z(r) - z(0))^2 \rangle = 3 \). From equation (11), we obtain

\[
\frac{\langle |z(2r) - z(0)|^2 \rangle}{\langle |z(r) - z(0)|^2 \rangle} = \frac{1}{e} + e = 3.086161 \ldots 
\]

thereby showing that the authors’ assertion is indeed a very good approximation, at least in the case of the CVM.

**Discussion**

The idea of scales of movement that characterize the transition between short-term correlated movements and long-term diffusive behavior has cropped up with increasing frequency in the literature on movement modeling (e.g., Taylor 1921; Berg 1993; Jeanson et al. 2003; Viswanathan et al. 2005; Visser and Kiorboe 2006; Nouvellet et al. 2009). Most often, the question of characteristic scales has been addressed out of necessity when dealing with intricacies of characterizing movements, complex simulations of ecological processes, or interpretation of detailed movement data. In this work, our aim has been to define the characteristic scales in such a way that they apply to any kind of homogeneous stochastic movement model and thus to unify the earlier results.

Because the characteristic scales are an intrinsic property of any unbiased homogeneous stochastic movement, they also allow for a unification of diverse types of movement models. One immediate application is the unification of the very movement models considered here. The CVM is, perhaps, a theoretically more appealing model than the CRW because many of its asymptotic and short-scale properties are analytically tractable and it describes a continuous process independent of the sampling interval. On the other hand, the CRW parameters have the advantage of being very straightforward to estimate from empirical data. The characteristic scales lead to an immediate parameterization of the CVM with respect to the measured CRW parameters.

Our primary conclusion is that these two parameters provide a compact summary of a movement process. Short-term behavior, specifically the nature of the autocorrelation function and the tangential velocity of movement, are governed by the ratio of the length scale and the time scale. Long-term behavior is related via the diffusion coefficient to the ratio of the square of the length scale and the time scale. The strength and the limitation of our approach are the use of only two parameters. Obviously, more degrees of freedom are needed to capture the full behavior of the movement model. For example, Nouvellet et al. (2009) proposed characterizing movements through the behavior of mean-squared displacement over time, that is, a function rather than a scalar. Because our characteristic temporal scale is defined through the velocity autocorrelation function, it depends both on the geometry of the track and on variation in movement speed and thus cannot disentangle these two aspects of movement. Nonetheless, our simulations included a range of movements from much smaller to much greater scales than the typical distances between targets, yet the encounter rates were well predicted by the scales. The agreements between the simulation results suggest that the characteristic scales also captured essential processes occurring at intermediate scales, regardless of the specific movement model.

Another important limitation of our approach is that
we have considered only homogeneous and unbiased processes, both generally unrealistic assumptions. Often, the long-term behavior of a movement process cannot simply be extrapolated from the short-term behavior, as it may be significantly influenced by behavioral switching, rare long-distance dispersal events, or environmental constraints. For example, many empirical data on organisms ranging from unicellular algae to whales indicate shifts between foraging movements and more linear displacement movements (e.g., Laidre et al. 2004; Polin et al. 2009) or behavioral transitions (Gurarie et al. 2009a), often without a significant change in actual movement speeds. Each movement mode, however, fulfills a different ecological purpose and is associated with its own characteristic scales. Thus, identifying the scales of each movement mode may aid in compactly summarizing the heterogeneous process and may shed light on the ecological role of that movement.

It has been noted before that tortuous movements (i.e., with small magnitudes of the characteristic scales) are inefficient for encountering targets, regardless of the absolute velocity of the movement (Visser and Kiørboe 2006; Bartumeus et al. 2008), a prediction that is supported by the results of the encounter rate simulations presented here. This observation has led to the hypothesis that movement scales should be greater than the encounter scales of targeted prey yet smaller than the encounter scales of respective predators (Visser and Kiørboe 2006). We hope that the identification of the characteristic scales as a fundamental, tractable property of movement will facilitate the eventual development of a consistent theory of encounter rates, in which encounter rates can be predicted as analytic functions of the movement scales, densities, encounter radii, and target geometry. We hope further that the identification of these scales will serve as a first step for developing a theory for animal movement that is flexible enough to capture ecologically relevant characteristics and facilitate comparisons between study systems while avoiding the level of detail often present in individual-based simulation models. A theory of this type is needed to understand the interactions between inherent properties of animal movement, inter- and intraspecific interactions, and environmental variability, as all of these interactions depend on their spatial and temporal scales.

Acknowledgments

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APPENDIX A

Velocity Autocorrelation Function of Correlated Random-Walk Model

We first consider any type of a correlated random walk (CRW; fixed or exponential time intervals) with \( \langle \cos(\theta) \rangle = \kappa \). Letting \( \mathbf{v}_i \) denote the velocity for step \( i \) and \( \theta_i \) the turning angle after the \( i \)th step, it holds that

\[
\mathbf{v}_i \cdot \mathbf{v}_{i+k} = \left| \mathbf{v}_i \right| \left| \mathbf{v}_{i+k} \right| \cos(\theta_i + \theta_{i+1} + \ldots + \theta_{i+k-1}).
\]

Because the step lengths and turning angles are assumed to be independent, we obtain

\[
\langle \mathbf{v}_i \cdot \mathbf{v}_j \rangle = \left\langle \frac{I}{T} \right\rangle^2,
\]

\[
\langle \mathbf{v}_i \cdot \mathbf{v}_{i+k} \rangle = \kappa \left\langle \frac{I}{T} \right\rangle^2.
\]

To proceed to higher-order steps, we note that

\[
\cos(\alpha + \beta) = \cos(\alpha) \cos(\beta) - \sin(\alpha) \sin(\beta)
\]

and that consecutive turning angles are assumed to be independent. Assuming that the turning-angle distribution is symmetric around 0, \( \langle \sin(\theta) \rangle = 0 \), \( \langle \cos(\theta_i + \theta_{i+1}) \rangle = \kappa^2 \), and, more generally, \( \langle \cos(\theta_i + \theta_{i+1} + \ldots + \theta_{i+k-1}) \rangle = \kappa^k \) (see also Benhamou 2006). This yields

\[
C_v(\Delta t) = p_0(\Delta t) + \frac{1}{\lambda} \sum_{i=1}^{\infty} p_i(\Delta t) \kappa^i,
\]

where \( p_i \) is the probability that, starting from a random time, \( I \) steps are taken before time \( \Delta t \).

In the case of fixed-time CRW, if \( \Delta t \leq T \), \( p_0 = 1 - \Delta t/T \), \( p_1 = \Delta t/T \), and \( p_{i>1} = 0 \). In this case, equation (A1) reduces to

\[
C_v(\Delta t) = \left(1 - \frac{\Delta t}{T}\right) + \frac{\kappa \Delta t}{\lambda}.
\]

For \( \Delta t > T \), we note that at the discrete times \( \Delta t = jT \), where \( j = (1, 2, 3, \ldots) \), \( p_{j>1} = 1 \) and \( p_{j>1} = 0 \). Thus, \( C_v(T) = \kappa/\lambda \), \( C_v(2T) = \kappa^2/\lambda \), \( C_v(3T) = \kappa^3/\lambda \), and so on, and equation (A2) is approximately
\[ C_r(\Delta t) \approx \frac{1}{N} e^{-\Delta t}. \] (A3)

This approximation is exact for integer multiples of \( T \), while fractional values are linear interpolations between the integer multiples. Using the expressions in equations (A2) and (A3) and setting \( C_r(\tau) = 1/e \) leads to the CRW characteristic time scale in equation (9).

APPENDIX B

Properties of the Correlated Velocity Movement Model

We aim first to derive the expected stationary velocity of the correlated velocity movement (CVM) model, defined as

\[ r = \lim_{t \to \infty} \langle |v(t)| \rangle, \]

assuming a CVM with parameter values \( \beta \) and \( \tau \), initial position \( Z(0) = 0 \), and arbitrary initial velocity \( (v_x, v_y) \). Each of the individual components of velocity are one-dimensional Ornstein-Uhlenbeck (OU) processes (Uhlenbeck and Ornstein 1930) and have a Gaussian distribution (Gillespie 1996), with

\[ \langle V_x(t) \rangle = v_x e^{-\tau t}, \]
\[ \langle V_y(t) \rangle = v_y e^{-\tau t}, \]
\[ \text{Var}(V(t)) = \frac{\beta^2 \tau}{2} (1 - e^{-2\tau t}), \] (B1)

where \( k \in x, y \) is the index of dimension. In the long term, the exponential terms in the mean and variance die out, leading to stationary-velocity variables with mean 0 and variance \( \beta^2 \tau/2 \). Thus, we obtain

\[ v_k = \lim_{t \to \infty} \langle v_k(t) \rangle = \beta \sqrt{\tau}, \]
\[ \langle X(t) \rangle = \beta \sqrt{\tau} (X^0). \] (B2)

where \( X_k \) and \( X_0 \) represent independent standard normal variables (mean 0, variance 1). The root-squared sum of two standard independent normal variables is a \( \chi \) distribution, with 2 df, the mean of which is \( \sqrt{\pi}/2 \), giving

\[ \langle \chi(t) \rangle = \frac{\sqrt{\pi} \beta \sqrt{\tau}}{2} = \frac{\sqrt{\pi} \sigma}{2 \sqrt{\tau}}. \] (B3)

To obtain the expected squared displacement of a CVM with initial position \( Z(0) = 0 \), we note that

\[ \langle \dot{Z}^2(t) \rangle = \langle Z_x^2(t) \rangle + \langle Z_y^2(t) \rangle. \] (B4)

Recalling that \( Z_i(t) \) is a Gaussian variable (Gillespie 1996), we can rewrite \( Z_i(t) \) in terms of the standard normal variable \( X \) via \( Z_i(t) = s(t)X + m(t) \), where the mean \( m(t) \) and variance \( \dot{s}^2(t) \) are given by (Gillespie 1996)

\[ m(t) = \langle Z_i(t) \rangle = v_x \tau (1 - e^{-\tau t}), \] (B5)
\[ \dot{s}^2(t) = \text{Var}(Z_i(t)) \]
\[ = \beta^2 \tau \left(t - 2(1 - e^{-\tau t}) + \frac{1 - e^{-2\tau t}}{2}\right). \] (B6)

The mean of the expanded squared displacement is

\[ \langle \dot{Z}^2(t) \rangle = \langle (s(t)X + m(t))^2 \rangle \]
\[ = \dot{s}^2 \langle X^2 \rangle + m^2(t) + 2s(t)m(t)\langle X \rangle \] (B7)
\[ = \dot{s}^2(t) + m^2(t). \]

Equations (B5)–(B7) give the expected squared displacement for a one-dimensional OU process (Uhlenbeck and Ornstein 1930) with arbitrary initial velocity \( V_i \). To obtain an overall expectation, we integrate \( V_i \) over the stationary velocity \( \lim_{t \to \infty} \langle V_i(t) \rangle \). By equation (B1), \( \lim_{t \to \infty} \langle V_i(t) \rangle = \beta^2 \tau/2 \), leading to \( m^2(t) = \beta^2 \tau^2 [1 - \exp(-t/\tau)]/2 \). Substituting these results into equation (B7) and summing the two components in equation (B4) gives the final expression

\[ \langle \dot{Z}^2(t) \rangle = 2\beta^2 \tau^2 (\tau + e^{-\tau t} - 1). \]

Literature Cited


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