Incorporating random movements and population level heterogeneity into encounter rate models

A very very rough draft...

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Contents

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1 Introduction

Encounters between organisms are universal prerequisites for many fundamental ecological processes. Feeding depends on an organisms ability to encounter food items or prey, survival can be strongly dependent on avoiding encounters with predators, and successful reproduction depends on mates encountering each other. The most widely applied null-model of encounter rates is essentially a variation of one developed by Clausius (1859) and Maxwell (1860) to describe the statistical-mechanical behavior of gases. Their result relates collision rates of "ideal free gases", i.e. perfectly elastic, deterministically moving spheres of fixed radius, via a straightforward function of mean velocities, interaction area and density. A fundamental assumption behind the derivation is that each particle moves linearly with a constant velocity. Clausius assumed all particules move with a single homogenous velocity while Maxwell solved the collision rate problem for particles whose velocities are distributed according to the Maxwell-Boltzmann distribution - i.e. where the x, y and z components of velocity were each normally distributed. These equations were generalized to a predator-prey type scenario in a widely cited and influential model of Gerritsen and Strickler (1977), hereafter referred to as GS, which predicted encounter rates between prey (in their case, zooplankton) moving at velocity u and predators moving at velocity v. The GS model in integral form accounts for any population-wide distribution of velocities $g(u)$ and $f(v)$ for the prey and predators respectively, but the fundamental movement of the individuals remains linear and deterministic as in the classic ideal gas case.

While encounter rate modelling is dominated by heterogeneous populations of individuals moving in a deterministic way, most historical models of population dispersal are governed by the inverse case, namely a homogenous population of randomly moving individuals. Among many studies along these lines, one might cite Skellam (1951), Turchin (1998), Okubo and Levin (2001). In another example of biology taking it's cues from results in physics, these movements are described as approximately Brownian, i.e. consisting of infinitesemal length, infinitesemally short time steps in random directions. While clearly not realistic, this model has the advantage of being mathematically related to processes of diffusion and an extensive family of differential equation-based approaches to modelling dispersal (Okubo and Gruenbaum 2001). Rates of 'diffusion' have been related to individual parameter of movement and thereby to actual measurements of animal movements via random

walk (RW) and correlated random walk models (CRW), notably in an several early mathematical studies by Patlak (1953a;b) and a highly influential model by Kareiva and Shigesada (1983). Much of the theoretical work in diffusive dispersion has considered homogenous populations of randomly moving individuals, though several recent studies have explicitly modelled heterogeneity in the populations (Skalski and Gilliam 2000, Yamamura 2002, Skalski and Gilliam 2003, Gurarie et al. 2008).

Lotka (1924), who used an ideal gas model to justify the density-dependence of his famous predation model, remained fully aware that his models were great simplifications of reality, warning that: "the type of motion presented by living organisms ... can be regarded as containing both a systematically directed and also a random element ... mathematical treatment ... may appear to threaten formidable difficulties. It is to be hoped that this will not altogether prevent its attack." (Lotka 1924). Several studies have since addressed the issue of random movement in ideal gas models. In particular, Hutchinson and Waser (2007), in their excellent review of ideal gas models, performed simulations of encounter rates between organims moving as correlated random walks, stating that "turning angle distributions, detection distance, step length and step number all have interacting non-linear effects, so quantitative predictions are only possible using simulation". Nonetheless, Anderson et al. (2005) present an analytical model of encounter rates between prey migrating through a field of predators which aggregates the effect of a directed velocity v and "net random velocity" ω, concluding that the strength of dependence of survival on travel distance versus travel time is controlled by the relative net randomness of the movement. Specifically, linearly travelling advective prey survival is independent of the speed of travel since the same gauntlet of predators is encountered, whereas more random movements increase encounter rates due to the possibility of backtracking. An weakness of the XT-model is that randomness of movement is poorly defined, with no suggestion as to how to estimate ω from individual movements, or what it's relationship to a rate of dispersion or diffusion might be.

This paper presents a mathematical model of encounter rates which incorporates a mixture of random and directed movements for heterogeneous populations. The resulting expression is relatively simple and tractable without the benefit of simulation. While broadly corroborating previous results, especially the correction to the GS model proposed by Evans (1989) and the migration survival model of Anderson et al. (2005), it is more rigorously parametrized in terms of individual movements.

In developing the argument, I present a very general parametrization of random movement. Next, I derive a one-dimensional encounter rate for unbiased and biased walkers moving through a field of moving and stationary predators and discuss applications to survival probabilities of migrating fish. Finally, I extend the encounter rate model to 2 dimensions.

2   The MST-walk

Actual animal movements are the result of a complicated behavioral and biophysical responses to internal states, environmental cues, and constraints. Because it is impossible to model all of these interactions, especially for mass movements, movements of organisms are often modelled statistically as stochastic processes. A generalized homogenous stochastic movement is defined as a continuous time process, $\boldsymbol{W}(t)$, that can be discretized such that at at some interval $t - s = \tau$

$$\boldsymbol{W}(t+\tau) = \boldsymbol{W}(t) + \boldsymbol{X} \tag{1}$$

where $\boldsymbol{X}$ is the *step distribution*, a random variable with some constant mean vector $\boldsymbol{\mu}$ and variance-covariance matrix $\boldsymbol{\Sigma}^2$ (bold-facing here indicates vector quantities). The time interval τ, defined as the characteristic time-scale of auto-independence, is the minium time interval at which independence between subsequent Φ's occur.

In two dimensions, for example, the process defined as $\{W_x(t), W_y(t)\}$ would be fully characterized by six parameters of step : μ_x, μ_y, σ_x^2, σ_y^2, σ_{xy} and the temporal independence scaling parameter τ. The case where $\mu_x = \mu_y = 0$ can capture the statistical behavior of any correlated random walk, since there is no absolute orientational trend to CRW movements. In that case, τ is the subsampling interval at which turning angles become uniformly distributed. If either mean parameter is different then zero, then the movement has an advective trend, the velocity of which is μ/τ.

The movement defined in equation 1 will be referred to as an MST-walk, since it is fully defined by the parameters μ, σ and τ. If track data exists, these parameters can be obtained by an appropriate decomposition of the movement data (see section 4.1).

3 One-dimensional encounter rate models

3.1 Unbiased walker

Assume that an individual is moving one-dimensionally as an unbiased MST-walk, i.e. $\mu = 0$, $\sigma > 0$ and $\tau > 0$ through a field of immobile targets (either food items or ambushing predators) with fixed density ρ such that in general the distance between predators is much lower than the size of a prey's step $1/\rho \gg \sigma$. The walk itself is defined as

$$W(t) = \sum_{i=0}^{t/\tau} X_i \tag{2}$$

where X_i is the step random variable: X_i are iid random variables with mean $\mu = 0$ and variance σ^2.

3.1.1 Non-destructive encounters

If the encounters are not "destructive" - i.e. the mover can reencounter any given target an unlimited amount of times - then we expect in an isotropic system for encounters to occur randomly with an asymptotically constant rate.

The expected number of encounters as a function of time is approximated as

$$E_p(t) = N_p(t)R_p \tag{3}$$

where N_p is the total number of *unique* predators encountered and R_p is the mean number of times each predator is encountered. The total number of unique predators encountered is just the density ρ of predators times the total range of a given random walk, denoted $W_{max} - W_{min}$. The mean number of revisits per predator is the total expected length of the trajectory, denoted L_W, divided by the total range. It should be clear that total length is the sum of the absolute lengths of each time step, i.e. $L_W = \sum_{i=1}^{t} |X_i|$, and is distinct from the total displacement. Thus, we can rewrite 3 as

$$E_p(t) = \rho\,(W_{max} - W_{min})\frac{L_X(t)}{(W_{max} - W_{min})} = \rho\,L_X(t) \tag{4}$$

Recalling that time is discretized in units of τ, the total length of the walk is:

$$L_X(t) = \sum_{i=1}^{\frac{t}{\tau}} |X_i| \tag{5}$$

and the expected encounter rate is

$$E_p(t) = \rho \langle L_X(t) \rangle = \frac{\rho t}{\tau} \langle |X| \rangle \tag{6}$$

Since the encounter rate is just the number of encounters per unit time,

$$E_r = \frac{\rho \langle |X| \rangle}{\tau} \tag{7}$$

The value of the expected absolute step length, and consequently the encounter rate, *depends on the nature of the step distribution*. This is a somewhat surprising result, since most aggregate statistical properties of random walks and diffusion processes, including dispersal rates and arrival times, are identical as long as the first two moments are equivalent. Indeed, this principle has been formalized and is referred to as *Wald's identity* (Wald 1947).

We now consider three different random walk models, each with step mean equal to zero and variance σ^2:

Case I: A discrete unbiased random walk with variance σ^2 has fixed step length σ. The encounter rate then becomes:

$$E_r = \frac{\rho \sigma}{\tau} \tag{8}$$

Case II: A Gaussian random walk, or discrete Gaussian jump process, has a normal step distribution: $X \sim \text{Normal}\{0, \sigma^2\}$. The expected absolute step length $\langle |X| \rangle = \sqrt{2/\pi}\sigma$, and the encounter rate is

$$E_r = \sqrt{\frac{2}{\pi}} \frac{\rho \sigma}{\tau} \tag{9}$$

Case III: Another reasonable model for step length distributions is a double ex-

ponential model where the step length distribution is

$$X \sim f(x) = \frac{\sqrt{2}}{\sigma} e^{-\frac{\sqrt{2}}{\sigma}|x|} \tag{10}$$

The expected absolute value of a step is $\langle |X| \rangle = \sigma/\sqrt{2}$ such that the encounter rate becomes

$$E_r = \frac{1}{\sqrt{2}} \frac{\rho\sigma}{\tau} \tag{11}$$

In general, the encounter rate for this process is:

$$E_r = \kappa \frac{\rho\sigma}{\tau} \tag{12}$$

where κ is a constant less than or equal to 1. The case where $\kappa = 1$, the discrete unbiased random walk, is in some ways an extreme case, as the distribution is a split Delta dirac function. For "reasonable" step distributions, κ is inversely related to the kurtosis of X. The kurtoses of the discrete, Gaussian and double-exponential cases are {-2, 0 and 3} respectively, corresponding to values for κ of {1, 0.798 and 0.707}. Since the double-exponential case is itself particularly fat-tailed, it is safe to assume that for any real movements the coefficient κ will range between 0.5 and 1.

Simulations of the movement process confirm these results with great precision (figure 1).

3.1.2 Destructive encounters

A destructive encounter is one in which the target is annihilated upon encounter. In this case, there is no constant encounter rate, as the density of targets is consistently depleted. Nonetheless, the expected number of encounters as a function of time is simply the range of the walk times the density. Thus

$$E_p(t) = \rho \left(W_{max}(t) - W_{min}(t) \right) \tag{13}$$

The range of a random walk is given by $\langle W_{max} - W_{min} \rangle = \frac{2}{\pi}\sigma\sqrt{t}$ (see Weiss (1994) for a derivation). The encounter rate of a destructive, unbiased one-dimensional walk consequently decreases as the square root of time as

$$E_r = \frac{2}{\pi} \frac{\sigma\rho}{\sqrt{t}} \tag{14}$$

We note that this result holds regardless of the nature of the step length distribution.

3.2   Advective random walkers

If an MST-walker moves deterministically through a field of targets with velocity μ/τ and step variance $\sigma^2 = 0$, the expected number of targets encountered at time t is just $E_p(t) = \rho\mu\frac{t}{\tau}$. The addition of a random component in the movement will have an impact on encounter rates only if there is some probability that the walker returns to a previously visited site. Clearly, this probability will be positive only if the random component has some probability of exceeding the magnitude of advective step μ. Thus, in the advective case, the nature of the step-process has particular bearing on the encounter rate. Since it is straightforward to scale any of these processes in time, we will assume $\tau = 1$ for the subsequent dicussion.

3.2.1   The biased discrete random walk

A form of random movement for which an analytic solution of advective encounter rates can be obtained is the biased discrete random walk, where the probability a random walker takes a step of length b to the right with probability p or to the left with probability $q = 1 - p$ such that

$$W(t) = b \sum_{i=0}^{t} (2B_i - 1) \tag{15}$$

where B are independent Bernoulli trials with probability p. The mean and variance of this walk are

$$\langle W(t) \rangle = b(p - q)t \tag{16}$$
$$\text{Var}\left[W(t)\right] = 4b^2 pqt. \tag{17}$$

The analogous statistical properties of the MST walk are

$$\langle W(t) \rangle = \mu t \tag{18}$$
$$\text{Var}\left[W(t)\right] = \sigma^2 t. \tag{19}$$

Equating the expressions for the means (16,18) and the variances (17,19), we obtain the following equivalences:

$$b = \sqrt{\sigma^2 + \mu^2} \tag{20}$$

$$p = \frac{1}{2}\left(1 + \frac{\mu}{\sqrt{\sigma^2 + \mu^2}}\right) \tag{21}$$

$$q = \frac{1}{2}\left(1 - \frac{\mu}{\sqrt{\sigma^2 + \mu^2}}\right). \tag{22}$$

Note that if $\sigma = 0$, then $p = 1$ and $b = \mu$, i.e. the motion is deterministic with fixed step-length μ. If $\mu = 0$, the motion is asymptotically equivalent to an unbiased random walk with $p = q = 1/2$ and step-length $b = \sigma$.

While every target must eventually be encountered by a discrete biased random walker, some targets will be encountered multiple times as there always exists some finite probability of returning to a previously visited site. The expected number of times a target is encountered is denoted R_p. In order to derive this quantity, we first consider the probability of recurrence p_{00} for a discrete biased random walk:

$$p_{00} = 1 - \sqrt{1 - 4pq}. \tag{23}$$

[see Hughes (1995) for a derivation of this result]. The expected number of returns is given by

$$R_p = \sum_{i=1}^{\infty} i P_i \tag{24}$$

Where P_i is the probability distribution of i returns. The probability of arriving a first time is unity. The probability of returning at least once after that is p_{00}, and the probability of returning at least twice is p_{00}^2. Thus, the probability of returning *exactly* twice is $P_2 = p_{00} - p_{00}^2$. In general,

$$P_i = p_{00}^{i-1} - p_{00}^i \tag{25}$$

The sum (24) can be solved:

$$R_p = \frac{1}{1 - p_{00}} \tag{26}$$

Plugging in our expression for p_{00} from equation (23) and converting to the MST parameters via equations 21 and 22 we obtain the following expression for the number of encounters per target:

$$R_p = \sqrt{\left(\frac{\sigma}{\mu}\right)^2 + 1} \tag{27}$$

We note that when $\sigma = 0$, there is exactly one encounter per target over the entire trajectory, whereas as if $\mu = 0$ there is an infinite expected number of encounters, a restatement of the recurrence property of unbiased random walks.

As time goes to infinity, the expected number of unique targets encountered is the expected distance travelled times the density:

$$N_p(t) = \langle W(t) \rangle = \rho\,\mu\,t \tag{28}$$

The product of the number of individual targets encountered per unit time and the number of encounters per target yields the encounter rate

$$E_r = N_p R_r = \rho\sqrt{\sigma^2 + \mu^2} \tag{29}$$

Scaling to discrete units of τ gives

$$E_r = \frac{\rho}{\tau}\sqrt{\sigma^2 + \mu^2} \tag{30}$$

Equating equation (30) to the non-advective encounter rate (12), we can generalize the advective encounter rate to accomodate different distribution shapes as

$$E_r = \frac{\rho}{\tau}\sqrt{(\kappa\sigma)^2 + \mu^2} \tag{31}$$

where κ is generally defined by $\langle |X| \rangle = \kappa\sigma$, with the very important constraint that if $\max(|X|) < \mu$, then revisits are impossible, $\kappa = 0$, and the expected encounter rate will always be equal to $E_p = \rho\mu$. Simulations of the process indicate that this model does an excellent job of predicting encounter rates for the biased discrete random walk (figure 4A). For the advective Gaussian walk (figure 4B), the model has the appropriate limiting behavior at ($E_p = \rho\kappa\sigma$ where $\mu \ll \sigma$ and $E_p = \rho\kappa\mu$ for $\mu \gg \sigma$), but slightly overestimates actual encounter rates for intermediate values

(figure 4B). While a mathematical explanation for this divergence is elusive, for all practical purposes it can be considered negligible.

3.2.2 Randomly moving targets

Within the framework of this derivation, it is relatively straightforward to predict the effect of randomly moving targets. We consider an advective random walker performing movement $W_a(t)$ with parameters $\mu_a > 0$, $\sigma_a > 0$ and $\tau > 0$ through a field of unbiased randomly moving targets $W_b(t)$ with step distribution X_b having $\mu_b > 0$ and some $\sigma_b > 0$ at a similar time-scale τ. The distance $\Delta W(t) = W_a(t) - W_b(t)$ between the walkers and any moving target is simply

$$
\begin{aligned}
\Delta W(t) &= W_a(t) - W_b(t) \\
&= \sum_{i=1}^{t/\tau} X_{ai} - \sum_{i=1}^{t/\tau} X_{bi} \\
&= \sum_{i=1}^{t} \Delta X_i
\end{aligned}
\tag{32}
$$

where $\Delta X = X_a - X_b$. For independent processes with well-behaved distributions, ΔX will have mean $\mu_a - \mu_b$ and variance $\sigma_a^2 + \sigma_b^2$. Thus, from the reference point of any given target, the process is identical as if the target were stationary and the random walker were moving with transformed MST parameters $\mu' = \mu_a + \mu_b$ and $\sigma' = \sqrt{\sigma_a^2 + \sigma_b^2}$. We can substitute these results directly into (31) and obtain the following expression for the encounter rate

$$
E_p = \frac{\rho}{\tau} \sqrt{\kappa^2(\sigma_a^2 + \sigma_b^2) + (\mu_a - \mu_b)^2}
\tag{33}
$$

Simulations (figure 3) confirm that this model gives accurate predictions of encounters.

3.3 Discussion of 1-D model

Here I discuss applications of the 1-D model to migrating fish survival, time-space dependence, possibilies of estimating predator densities from survival data etc. Also, possibly some discussion of heterogeneity in migrations and estimating parameters from hydroacoustic data.

4   Extension to two dimensions

Consider a walker moving through a two-dimensional field of stationary targets of density ρ at constant velocity v with an encounter radius a. An encounter occurs whenever the detection area of the walker includes a target. The number of encounters is given by $N(t) = \rho A(t)$ where $A(t)$ is the area swept out by the movement: $A = 2avt$. Thus the encounter rate is

$$E_r = 2\rho av \qquad (34)$$

Adapting this solution to a random walker is complicated by the definition of random movements. Intuitively, the less sinuous a path, the closer an encounter rate estimate will be to the determinstic model above, whereas a windier path, with slower dispersal and higher probability of reencounters, will have some impact on encounter rates (see schematic in figure 5). The only attempts I am aware of to consider the impact of random movements on encounter rates are simulation studies performed by Bartumeus et al. (2002) comparing the encounter rate efficiency of "Brownian walks" to "Lévy walks" and by Hutchinson and Waser (2007) where the effect of a correlated random walk on expected ideal-free gas type encounter rates was numerically assessed. The authors conclude that: "It is apparent that turning angle distribution, detection distance, step length and step number all have interacting non-linear effects, so quantitative predictions are possible only using siimulation."

Indeed, mathematically predictions of encounter rates depend to some extent on the way in which random movement is modelled. There exists much discussion in the literature as to what consistitutes a true random walk (RW) or a correlated random walk (CRW), how to characterize the "sinuosity" or "tortuosity" of a walk, and what impact different models have on expected dispersal distances (Skellam 1951, Patlak 1953a, Shigesada 1980, Kareiva and Shigesada 1982, Byers 2001, Benhamou 2004a;b). However, much of this debate seems somewhat spurious, since almost all movements are necessarily correlated at a small enough time scale and uncorrelated at a large enough time-scale. Exceptions to this rule are processes that are inherently, such as the movement of moths between flowers (Skellam 1951) or of elk between snow craters (Fortin et al. 2005). It is generally not meaningful to discuss whether movement itself is "correlated"; rather, *movement data* acquired on an organismis may or may not be correlated depending on the temporal resolution of data acquisition

compared to the time scale of independence (τ^*). In fact, an assertion can be made that the identification of the time and length scales of independence largely determine encounter rates, regardless of the specific nature of the correlated walk. This assertion is explored in the following section.

4.1 Decomposing movement

There are presumably as many ways to identify the length scale (σ^*) and time scale (τ^*) of independence as there are ways to model correlated random walks. However, any such method must be based on an incremental decomposition of a correlated track. Consider a smooth walk generated by obtaining a series of N step-lengths r and turning angles θ which are tightly and symmetrically clustered around zero degrees. A widely used example of a circular distribution for turning angles is the wrapped Cauchy distribution

$$f(\theta) = \frac{1}{2\pi} \frac{1 - \nu^2}{1 + \nu^2 - 2\nu \cos(\theta)} \tag{35}$$

where $\nu \in \{0, 1\}$ is a clustering parameter such that when $\nu = 0$, the angles are distributed uniformly between $-\pi$ and π and when $\nu = 1$, the distribution is a delta function at $\theta = 0$. While any circular distribution that accounts for clustering would work as well [see Fisher (1993) for a thorough discussion of this and other circular distributions], a convenient feature of the wrapped Cauchy distribution is that $\langle \cos(\theta) \rangle = \nu$. This dovetails nicely with a result by Kareiva and Shigesada (1983), who provide an analytical expression for the expected square of the displacement after n steps in terms of ν

$$\left\langle R^2(n) \right\rangle = n \left\langle r^2 \right\rangle + 2 \left\langle r \right\rangle^2 \frac{\nu}{1 - \nu} \left(n - \frac{1 - \nu^n}{1 - \nu} \right) \tag{36}$$

While an exact expression for expected displacement is difficult to obtain, Bovet and Benhamou (1988) suggest that for a reasonable amount of steps ($N > 10$) a good estimate of the actual expected distance is

$$\langle R(n) \rangle \sim \sqrt{\frac{\pi}{4} \left\langle R^2(n) \right\rangle} \tag{37}$$

Subsampling this walk at various intervals τ yields sets of step lengths $\mathbf{R}_\tau$ and turning angles $\mathbf{\Theta}_\tau$. (It should be noted that a set of these gapped values can be obtained beginning at any of the first τ points, such that the length of these subsample vectors is $N - \tau$, not significantly smaller than the original series.) Maximum likelihood estimates of the clustering coefficients $\hat{\nu}_\tau$ and step-lengths $\hat{R}_\tau$ at different intervals can be obtained using methods described in Fisher (1993). At a sufficienly high gap interval, the turning angles will be uniformly distributed. The size of that interval, τ^* and the corresponding expected step-length σ^* are the time and length scales of independence.

An example of the application of this methodology is presented in figure 6. A smooth curve is generated with constant step length $l = 1$ and clustering parameter $\nu = 0.9$ (fig. 6A). The curve is sampled at various intervals τ as described above. In order to determine the point at which any correlation is lost, I generated an empirical null-distribution of ν-estimates by simulating 1000 datasets from a uniform angular distribution ($\nu_0 = 0$) of length N/τ and obtaining 5% and 95% quantile envelopes around estimates of $\hat{\nu}_0$ (fig. 6B). In the example, the data-derived $\bar{\nu}$ crosses the envelope at $\tau^* = 21$, indicating that at that interval length the turning angles are no longer meaningfully clustered. The corresponding empirical step length is $\sigma^* = 14.4$, or, using the Bovet-Benhamou approximation, $\sigma^* = 13.7$ (fig. 6C).

I repeated this process for a range of clustering coefficient values $0 < \nu < 0.98$, simulating 20 walks at each value and obtaining estimates and scatters for τ^*. The resulting relationship is plotted in figure 7. At $\nu = 0$, i.e. the uncorrelated walk, the expected value for τ^* is 1, while at $\nu = 1$, i.e. the linear, directed movement, $\tau^* \to \infty$. An empirical equation that fits the data fairly well is

$$\tau^* = A \log \left(\frac{1}{1 - \nu^2} \right) + 1 \tag{38}$$

where A is found via regression on a linearization of the formula to be equal to about 13.71. This formula gives a rough idea of the relationship we might expect between the strength of the autocorrelation in a random walk and the expected time lag of independence.

When applying this subsampling to an true correlated movement, there is clearly some additional movement that is not accounted for in the non-correlated approximation. When calculating encounter rates, it is of some importance to know how

much of the true path length is "lost" by the subsampling procedure. Denoting the total path-length at subsampling τ as L_τ, the ratio between expected subsampled pathlength and the total true path-length after N steps is

$$\frac{L_\tau}{L_1} = \frac{\frac{N}{\tau}\langle R(n)\rangle}{N\langle r\rangle}. \tag{39}$$

For high values of ν, this quantity drops relatively slowly against τ, while for lower values of ν there is a rapid drop (see figure 7)); however, this loss is compensated for by the correspondigly much shorter time-scales of independence for less correlated walks. Superimposing the expected values for τ^* onto the distance ratio curves indicate that the amount of distance lost by the independence rescaling does not drop below a ratio of 0.6.

While this is a semi-rigorous quantification of the impact of rescaling on the total distance swept out by the true path, the main message is that we can rescale with relative impunity. As long as the time and distance scale of independence is chosen as close as possible to the autocorrelation threshold, we can be confident that the bulk of the properties of the movement will be retained despite the simplification. Only a very coarse subsampling will lead to total distances that are less than half the true distance.

4.2 Estimating encounter rates: stationary targets

The following derivations and discussions assume non correlated random walks with charactersitic time and steplength scales τ and σ in a uniform random field of predators with density ρ.

Analogously to the one-dimensional case, encounter rates in two dimensions are related to the ratio of the area swept out by a movement to the volume explored. The nature of these relationships is controlled by the relationship between the length scale of movements and the distance between targets. For uniformly distributed targets with density ρ in two dimensions, the mean distance between targets is equal to $\lambda = \frac{1}{2\sqrt{\rho}}$. If the step length $\sigma \gg \lambda$, then the encounter rate approximates the linear solution given in equation (34), with the velocity factor given approximately as σ/τ. Thus,

THIS "THUS" IS WHERE I AM STUCK AT THE MOMENT. BASICALLY,

HOW TO RELATE THIS AREA OF EXPLORATION WITH AREA OF ENCOUNTER? I HAVE PERFORMED MANY, MANY SIMULATIONS - SEE FIGURE 8 FOR AN EXAMPLE - FOR DIFFERNT DENSISTIES, VELOCITIES, ENCOUNTER RADII, ETC., AND HAVE A NICE BODY OF "DATA," BUT HAVE YET TO DIG IN AND PARSE OUT ALL OF THE PATTERNS.

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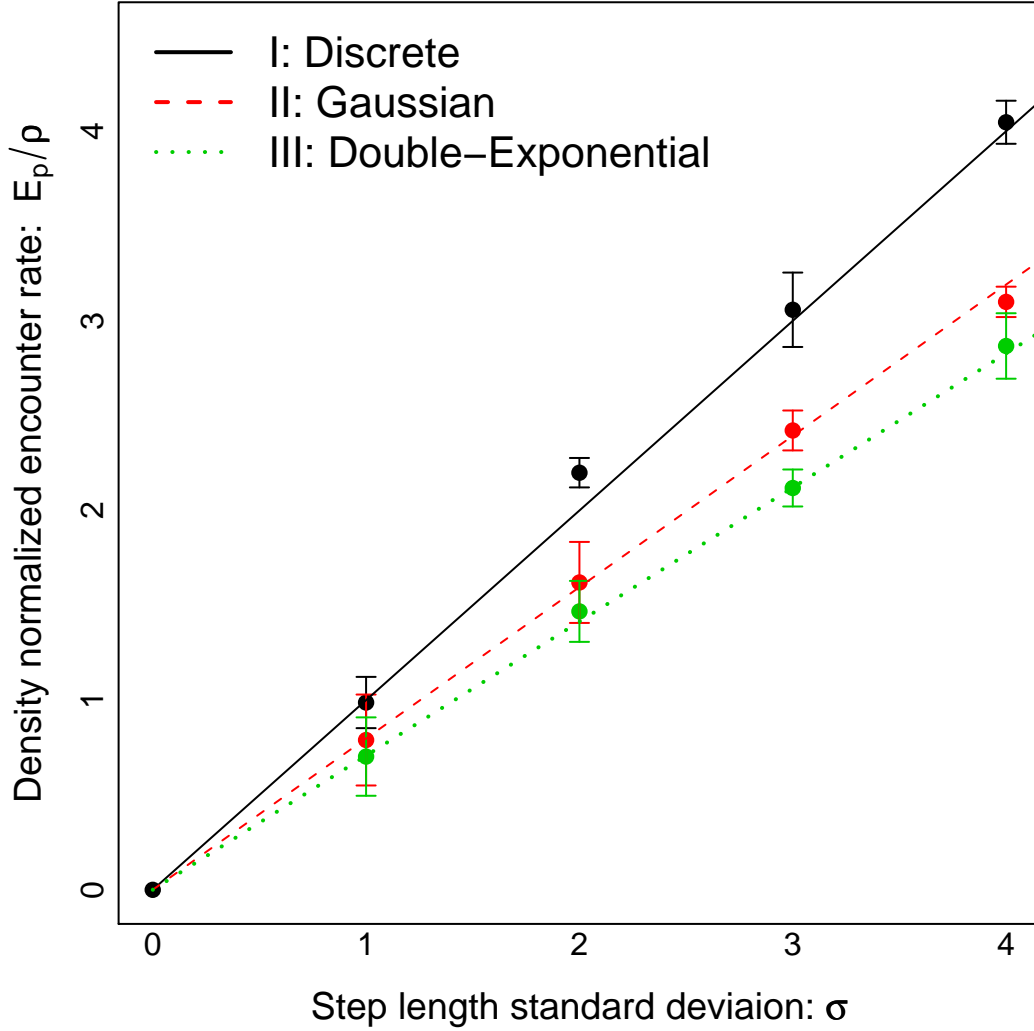
Figure 1: Results of encounter rate simulations. The number line was randomly seeded with targets in a range of densities ρ from 0.01 to 0.1. Unbiased random walks on the number line were generated and the resulting encounter rates (E_p) obtained. The slope of E_p against ρ is plotted here with the associated estimated standard deviations (error bars) for different values of σ and three different step distributions: discrete unbiased random walk (black), the Gaussian random walk (red), and the double exponential random walk (green). The lines represent the theoretically predicted slopes: 1, $\sqrt{2/\pi}$ and $1/\sqrt{2}$ respectively.
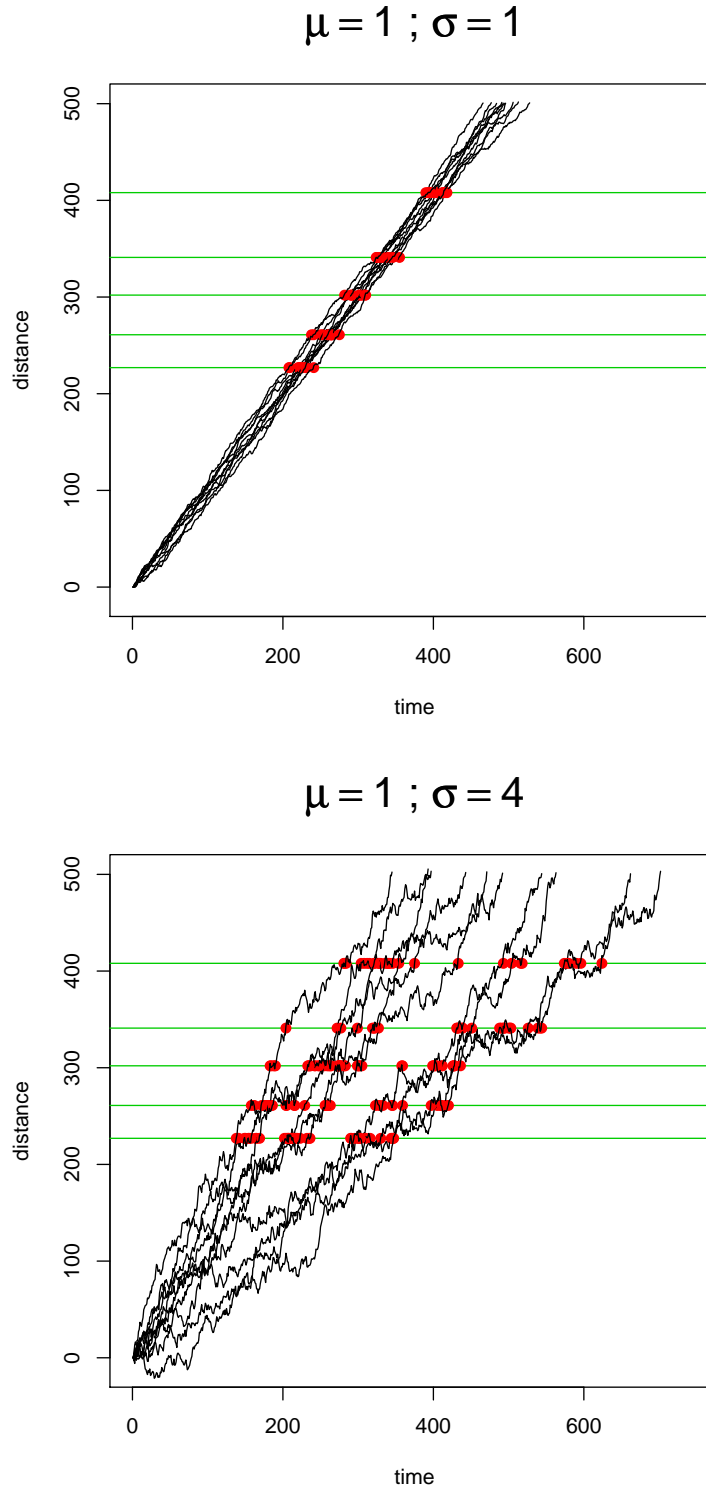
Figure 2: Trajectories of 10 simulated 1-D Gaussian MST walkers moving with $\mu = 1$ and (A) $\sigma = 1$ and (B) $\sigma = 4$. Green lines represent the location of stationary targets; red dots represent encounters. In these realizations, the number of encounters per walker per target are (A) 1.24, compared to a predicted value (27) of $\sqrt{\frac{2}{\pi} \left(\frac{\sigma}{\mu} \right)^2 + 1} = 1.28$ and (B) 2.72, compared to a predicted value of 2.47.
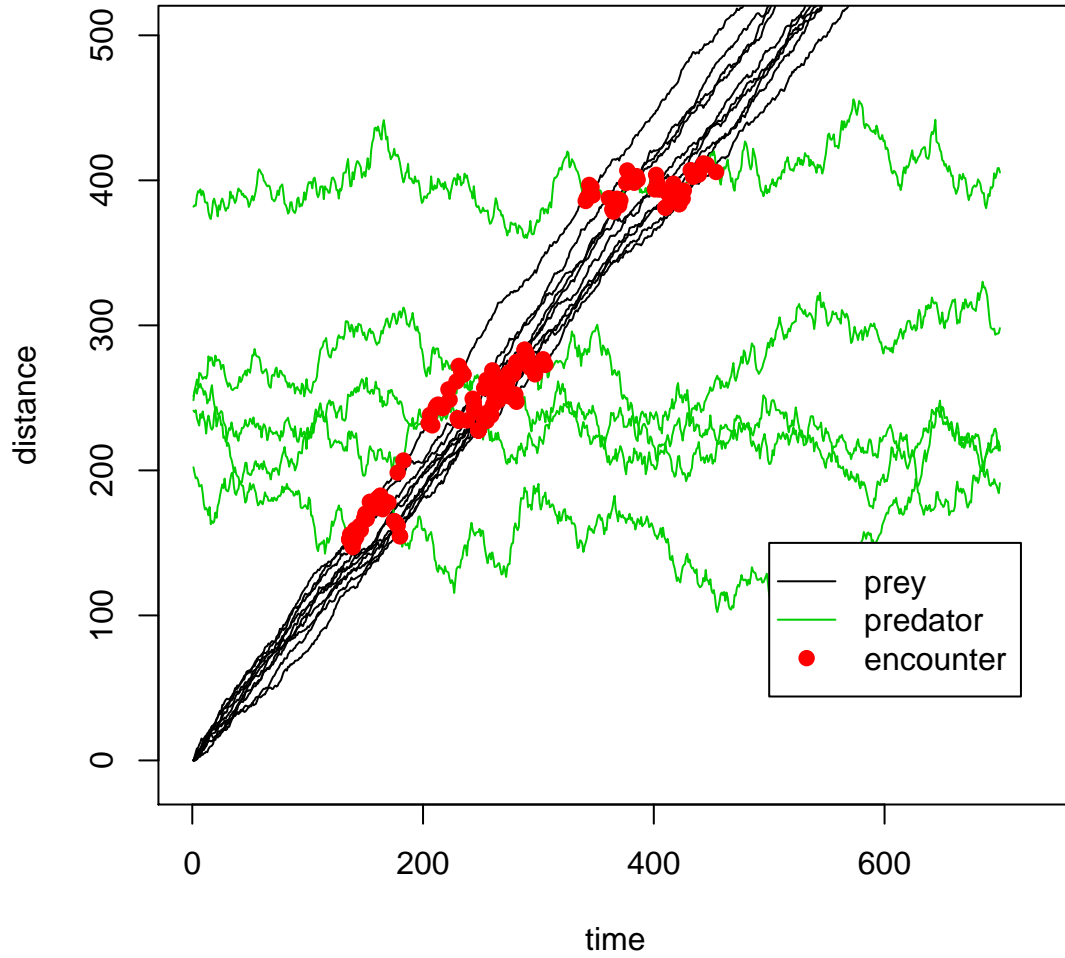
Figure 3: Motions of 10 simulated one-dimensional walkers moving as low-randomness a Gaussian MST-walkers with $\mu = 1$ and $\sigma = 1$ through a field of randomly moving targets with $\sigma_d = 4$. The number of encounters per walker per target in this simulation is 3.4 compared to a theoretically predicted value of $\sqrt{\frac{2}{\pi}\left(\frac{\sigma^2 + \sigma_d^2}{\mu^2}\right) + 1} = 3.44$ from equation 33.
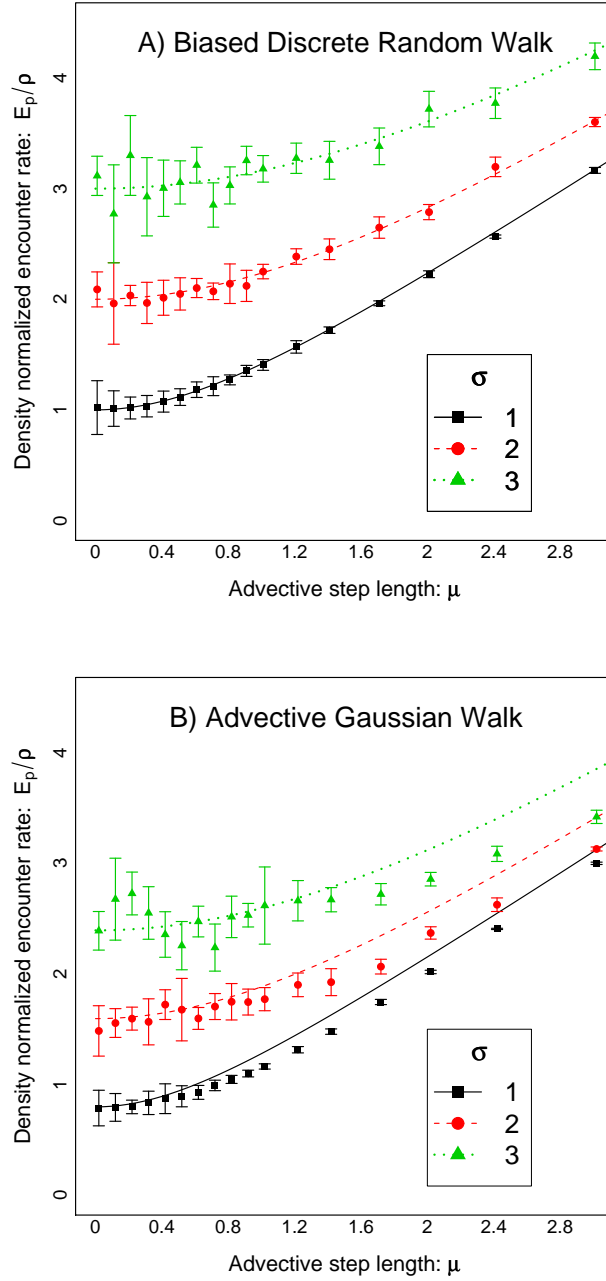
Figure 4: Results of encounter rate simulations. The numberline was randomly seeded with targets in a range of densities ρ from 0.01 to 0.1. Random walks on the number line were generated and the resulting encounter rates (E_p) obtained. The slope of E_p against ρ with the associated estimated standard deviation is plotted here against advective component mu for three values of σ. The solid lines represent the predicted encounter rates according to equation 31: $E_r = \rho\sqrt{(\kappa\sigma)^2 + \mu^2}$, where $\kappa = 1$ for (A) biased discrete random walk and $\sqrt{\frac{2}{\pi}}$ for (B) the Gaussian random walk.
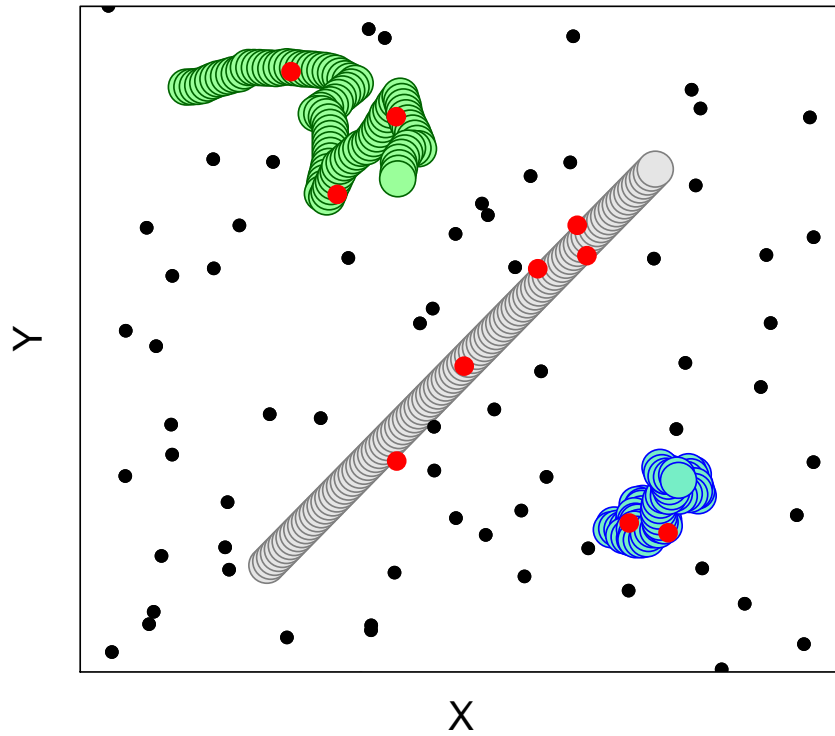
Figure 5: Three trajectories showing the effect of randomness on encounter rates. All three movements consist of 100 steps of length 1. The grey walker is moving linearly, and has the highest encounter rate. The green walker is walking with relatively high correlation between turning angles, and the blue walk displays very low auto-correlation.
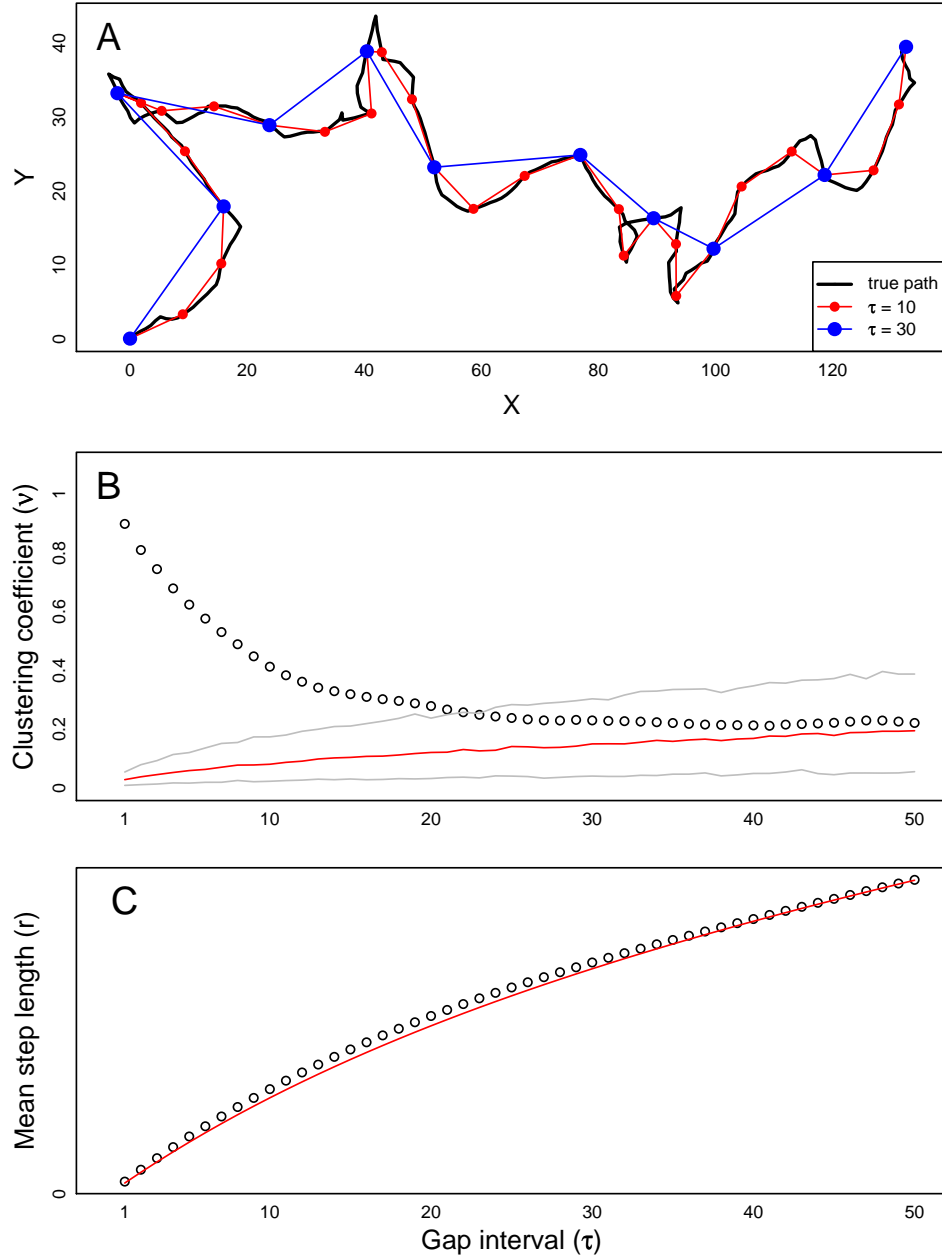
Figure 6: Example of decomposition of smooth track. (A) represents a smooth CRW trajectory, with wrapped Cauchy turning angles with clustering coefficient $\nu = 0.9$ and step lengths equal to one. Subsamplings of the data at intervals $\tau = 10$ and 30 are illustrated in red and blue respectively. While the first subsample still shows correlation, at $\tau = 30$ the walk can be considered truly random. Maximum likelihood estimates of ν against τ are shown in plot (B). The red and grey lines at the bottom are the median and 5% and 95% quantile envelopes of estimates of ν for data generated with no clustering ($\nu = 0$). At the point where the ν estimates enters the envelope (approximately $\tau = 21$), the estimate cannot be considered significantly different than zero. Plot (C) shows the mean step length at each τ along with the Bovet-Benhamou prediction. At $\tau^* = 21$, the step length of independence $\sigma^* \sim 14.4$.
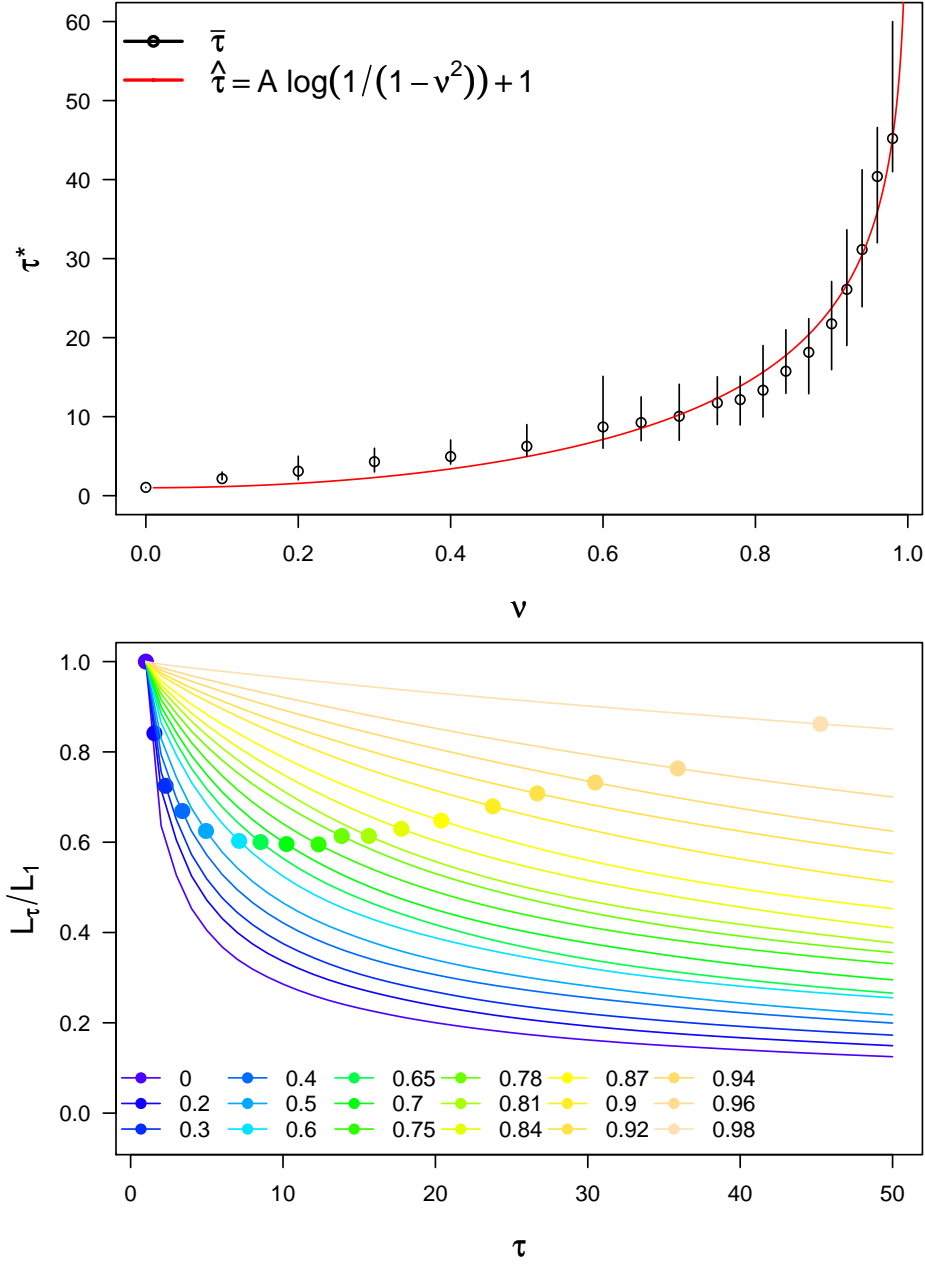
Figure 7: Simulation results exploring the relationship between clustering coefficient ν, estimated independence time-scale τ^* and the length ratio L_τ/L_1. In the plot, 20 trajectories were generated for each value of ν and values of τ^* were estimated using the method described in the text. The median values and 5 and 95% quantile values are plotted, as well as an empirically fit curve (in red). The lower plot shows the ratio of the subsampled path lengths (L_τ) compared to total path length for different values of ν, based on simulated paths of length 10000. The bold points represent the expected values of τ^* for each of the curves based on the results of the simulation above.
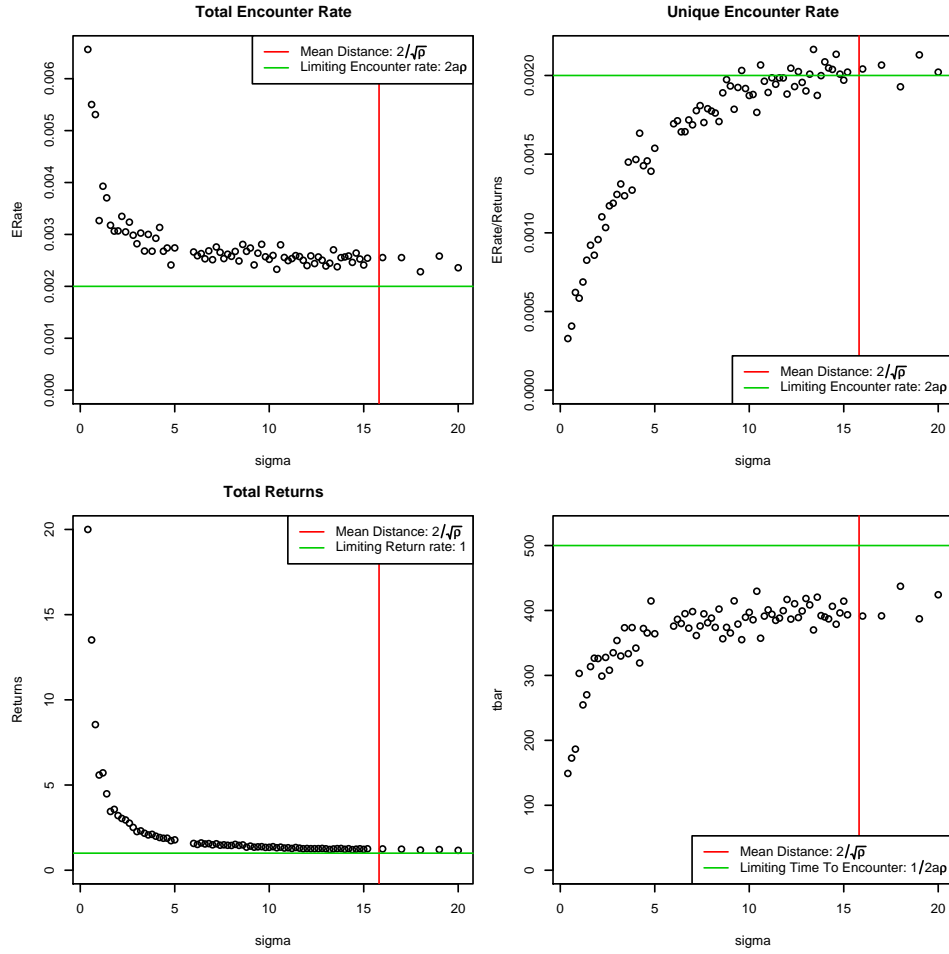
Figure 8: Simulation results of 2D encounter with a Gaussian walker moving through a field of targets with density .001 and encounter radius 1.