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Appendix A. Simulating biased random walks.

To illustrate and validate the spatial distributions corresponding to the predicted expressions for the diffusion coefficients in Table 2 of the main paper, biased random walks are simulated as follows. Each random walker starts at the origin $(x_0, y_0) = (0, 0)$. At each time step, τ, a direction of movement, θ, is chosen from the relevant angular distribution (see below). The new position is given by $(x_{n+1}, y_{n+1}) = (x_n, y_n) + \delta(\cos\theta, \sin\theta)$ (where δ is a fixed constant in the basic 'fixed-speed' model, and an exponentially distributed random variable with mean $\bar{\delta}$ and variance $\sigma_\delta^2(\bar{\delta})^2$ in the 'variable speed' model). This random walk process continues for n steps and the final position is recorded. Finally, a number of random walks, m, of this type are simulated (typically at least m >10,000) and the average diffusion coefficients and the final spatial distribution are found. Simulations are completed in the R environment (R Development Core Team 2009).

The direction of movement at each step is drawn from a specified angular distribution. To simulate the von Mises, wrapped normal and wrapped Cauchy we respectively use the *rvm*, *rwrpnorm* and *rwrpcauchy* functions from the *CircStats* package in R (R Development Core Team 2009). To simulate the truncated normal distribution we set up

a simple algorithm based on a standard acceptance-rejection method (e.g., Press et al. 1992). This program code is available from the authors as an R function on request.

The estimates of the diffusion coefficients from the simulation results are calculated from the observed mean squared displacement of m >10,000 walkers: $\overline{D}_x = \frac{2}{mn}\sum_m (x-\overline{x})^2$ and $\overline{D}_y = \frac{2}{mn}\sum_m (y-\overline{y})^2$, after the long-time steady state is reached. This includes the rescaling $4\tau/(\overline{\delta})^2$ so that in the basic 'fixed-speed' model we typically have $0 \leq D_x, D_y \leq 1$. The number of time steps required to reach `steady-state' (so that the spatial distribution is Gaussian) is inversely proportional to ρ, so simulations were not all run for the same length of time or with the same number of walkers. Simulations for small ρ reach the steady state quickly so were run for a short number of time steps ($n \geq 100$), but are very noisy so a larger number of walkers were used (up to $m = 10^6$ for $\rho \approx 0$). Conversely, simulations with large ρ are not very noisy but require a long time to reach the steady state (see Figs. 2c and d in the main paper). As $\rho \rightarrow 1$ we used a minimum of m = 10,000 walkers but ran simulations for as many as $n = 10^6$ time steps.

LITERATURE CITED

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