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, \(\tau\), a direction of movement, \(\theta\), 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 \(\delta\) is a fixed constant in the basic ‘fixed-speed’ model, and an exponentially distributed random variable with mean \(\bar{\delta}\) and variance \(\sigma^2 \bar{\delta}^2\) 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 \texttt{rvm}, \texttt{rwrpnorm} and \texttt{rwrpcauchy} functions from the \texttt{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:

$$D_x = \frac{2}{mn} \sum_m (x - \bar{x})^2$$

and

$$D_y = \frac{2}{mn} \sum_m (y - \bar{y})^2,$$

after the long-time steady state is reached. This includes the rescaling $4\sigma^2(\delta)^2$ 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 $\rho$, so simulations were not all run for the same length of time or with the same number of walkers. Simulations for small $\rho$ 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 $\rho$ 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