Appendix A from P. Nouvellet et al., "Fundamental Insights into the Random Movement of Animals from a Single Distance-Related Statistic"

(Am. Nat., vol. 174, no. 4, p. 506)

Mathematical Model

In this appendix, we give details of the mathematical model introduced in this article. The model describes properties of the "displacement" at time *t*, namely, the position of an animal at time *t* relative to its position at time t = 0. Because an animal moves in two dimensions, displacement involves two coordinates and is written $\mathbf{R}(t) = (X(t), Y(t))$, and by definition it vanishes at time t = 0: $\mathbf{R}(0) = (0, 0)$.

We take the displacement, $\mathbf{R}(t)$, to obey the simplest equation governing its continuous changes over time, namely, a linear differential equation. A degree of randomness is incorporated into this equation to represent random aspects of the biology of the problem that results in random changes of displacement. We take this randomness to be a Gaussian random function of time. For the purposes of this appendix and appendix C, we use a physical analogy that allows us to refer to the random function as a force, because forces drive movement in physics. We then allow the force to be correlated with itself over time. This is a very simple and natural way to incorporate the tendency of animals to move with some persistence of direction. Because animals move in two dimensions, the force, denoted $\eta(t)$, has two components, and we write $\eta(t) = (\eta_X(t), \eta_Y(t))$. Because the force is random in character, the equation obeyed by the displacement $\mathbf{R}(t)$ is the stochastic differential equation

$$\frac{d\mathbf{R}(t)}{dt} = \eta(t). \tag{A1}$$

The mathematical formulation of the problem requires a degree of flexibility that allows an efficient parameterization of a range of observed behaviors. We accommodate this flexibility by allowing the correlations of the force to be arbitrarily specified.

The statistical properties of the two components of the force, $\eta_x(t)$ and $\eta_y(t)$, are fully characterized by their mean values and their correlations. The assumption of foraging means there are no preferred directions of movement. We enforce this by taking $\eta_x(t)$ and $\eta_y(t)$ to be statistically independent and to vanish, when averaged over many animals. This results in X(t) and Y(t) also being statistically independent (for earlier work that employed related ideas, see Tchen 1952; Flory 1969). With E[. . .] denoting an average or expected value, the correlations of the force, namely $E[\eta_x(t_1)\eta_x(t_2)]$ and $E[\eta_y(t_1)\eta_y(t_2)]$, are taken to be equal and are given by the function $\Delta(t_1 - t_2)$, where t_1 and t_2 are arbitrary times. The dependence of correlations on only the time interval $t_1 - t_2$ means there is no preferred time in the problem.

We term $\Delta(t)$ the correlation function; this function encapsulates all unknown determinants of movement in the model. Conventional Brownian motion adopts a form for $\Delta(t)$ that is an infinitely narrow spike of finite area (in which case $\Delta(t)$ is proportional to a Dirac delta function). In this study we consider more general forms for $\Delta(t)$.

The mean square displacement that is established after time t is $E[X^2(t) + Y^2(t)]$, and we write this as $\sigma^2(t)$. From the model, the mean square displacement $\sigma^2(t)$ can be explicitly expressed in terms of the correlation function $\Delta(t)$ (see app. B). By exploiting this, we shift emphasis from $\Delta(t)$ to $\sigma^2(t)$. Thus, $\sigma^2(t)$ is the object containing all unknown determinants of movement of the model, and flexibility of the model corresponds to the different possible choices that may be made for the dependence of $\sigma^2(t)$ on time t.

Literature Cited Only in Appendix A

Flory, P. J. 1969. Statistical mechanics of chain molecules. Wiley, New York. Tchen, C. M. 1952. Random flight with multiple partial correlations. Journal of Chemical Physics 20:214–217.