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

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Detailed Mathematical Analysis of the Model

In this appendix, we describe the model of a persistent random walk introduced in this article, and we present details of calculations. This appendix contains material that may be omitted by readers who do not require an in-depth knowledge of the technical details of this study.

The displacement $\mathbf{R}(t) = (X(t), Y(t))$ is the position of an animal at time t relative to its position at time $t = 0$, and it obeys equation (A1): $d\mathbf{R}(t)/dt = \eta(t)$. The random force $\eta(t) = (\eta_X(t), \eta_Y(t))$ represents the tendency of displacements to change randomly but with some persistence of direction. The two components of the random force are taken to be independent and identically distributed Gaussian random processes (functions of time) with vanishing expected values, $\mathrm{E}[\eta_X(t)] = \mathrm{E}[\eta_Y(t)] = 0$. Statistical independence yields $\mathrm{E}[\eta_X(t_1)\eta_Y(t_2)] = 0$, and this is necessary for a rotationally symmetric description where no direction in the environment is distinguished. The correlations of the random force, $\mathrm{E}[\eta_X(t_1)\eta_X(t_2)]$ and $\mathrm{E}[\eta_Y(t_1)\eta_Y(t_2)]$, are equal and given by the function $\Delta(t_1 - t_2)$, which is termed the correlation function. This is symmetric ($\Delta(-t) = \Delta(t)$), and it is taken to have a finite area: $\int_{-\infty}^{\infty}\Delta(t)dt < \infty$.

To gain some intuition about the nature of the correlations of the random force, we state without proof the property that the probability density of $\eta_X(t_2)$, conditional that the force at some other time t_1 has the value $\eta_X(t_1) = e_1$, is a normal distribution with mean $\Delta(t_2 - t_1) \times e_1/\Delta(0)$ and variance $[\Delta^2(0) - \Delta^2(t_2 - t_1)]/\Delta(0)$. These results confirm the way that $\Delta(t)$ characterizes correlations. In particular, such a conditional probability density deviates considerably from the unconditional distribution when $\Delta(t_2 - t_1)$ is close to $\Delta(0)$, and it approaches the unconditional distribution when $\Delta(t_2 - t_1) \ll \Delta(0)$.

The solution of equation (A1) for $\mathbf{R}(t)$ subject to $\mathbf{R}(0) = (0, 0)$ is $\mathbf{R}(t) = \int_0^t \eta(s)ds$. Explicitly, this means that $X(t) = \int_0^t \eta_X(s)ds$ and $Y(t) = \int_0^t \eta_Y(s)ds$. These are integrals (equivalent to sums) of independent normal random processes. It follows that, at fixed t, both $X(t)$ and $Y(t)$ are independent and identically distributed normal random variables. Furthermore, given the statistical properties of η, it follows that $X(t)$ and $Y(t)$ have means of 0 and equal variances $\mathrm{E}[X^2(t)] = \mathrm{E}[Y^2(t)]$, which we write as $\sigma^2(t)/2$. In appendix B it is shown that $\sigma^2(t) = 4\int_0^t (t - s)\Delta(s)ds$; this last result means that the information contained in $\Delta(t)$ is also contained in the mean square displacement $\mathrm{E}[X^2(t) + Y^2(t)] = \sigma^2(t)$.

Even incomplete information about $\Delta(t)$, such as the value of its area, has implications for the behavior of $\sigma^2(t)$. For example, if $\Delta(t)$ has a nonzero area, $\int_{-\infty}^{\infty}\Delta(s)ds \neq 0$, then there is diffusive behavior at sufficiently long times and the mean square displacement ultimately becomes proportional to time t. By contrast, if $\Delta(t)$ has a vanishing area, $\int_{-\infty}^{\infty}\Delta(s)ds = 0$, then the mean square displacement $\sigma^2(t)$ exhibits some form of subdiffusive behavior at long times.

We note that normality of $X(t)$ and $Y(t)$ has a direct implication: in terms of the quantity $\|\mathbf{R}(t)\| = (X^2(t) + Y^2(t))^{1/2}$ (the magnitude of the displacement at time t), there is a unique time independent value for the ratio $\mathrm{E}\big[\|\mathbf{R}(t)\|\big]/\big\{\mathrm{E}\big[\|\mathbf{R}(t)\|^2\big]\big\}^{1/2}$ (Bovet and Benhamou 1988). We calculate the ratio using the normal probability density of $X(t)$ and $Y(t)$, which we write as $\phi(X, Y) = \{\exp[-(X^2 + Y^2)/(2\sigma^2(t))]\}/(2\pi\sigma^2(t))$. We can express $\mathrm{E}\big[\|\mathbf{R}(t)\|\big]$ and $\mathrm{E}\big[\|\mathbf{R}(t)\|^2\big]$ as integrals that can be evaluated by direct calculation using polar coordinates. We have $\mathrm{E}\big[\|\mathbf{R}(t)\|\big] = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty}(X^2 + Y^2)^{1/2}\phi(X, Y)dXdY = (\pi/2)^{1/2}\sigma(t)$ and $\mathrm{E}\big[\|\mathbf{R}(t)\|^2\big] = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty}(X^2 + Y^2)\phi(X, Y)dXdY = 2\sigma^2(t)$. Thus, $\mathrm{E}\big[\|\mathbf{R}(t)\|\big]/\big\{\mathrm{E}\big[\|\mathbf{R}(t)\|^2\big]\big\}^{1/2}$ has the value $(\pi/4)^{1/2} \approx 0.8862$ (Bovet and Benhamou 1988).

An illustrative example of the mean square displacement $\sigma^2(t)$ follows from the correlation function $\Delta(t) = D\exp(-|t|/T)/(2T)$, where T is a constant representing a single timescale in the problem and D is a constant associated with the magnitude of fluctuations of the random force. This correlation function leads to $\sigma^2(t) =$

$2D[t - T + T\exp(-t/T)]$. When the time t is large compared with the timescale T, we have $\sigma^2(t) \approx 2Dt$, which is typical of standard diffusion. We consider two special cases of the correlation function $\Delta(t) = D\exp(-|t|/T)/(2T)$:

1. The first special case is when $\Delta(t)$ has all variation contained in the shortest possible range, which arises when the timescale T approaches 0. In this limit, $\Delta(t)$ becomes a zero-width, infinite-height spike of area D that is concentrated at $t = 0$. It follows that $\Delta(t)$ is proportional to a Dirac delta function $\delta(t)$, that is, $\Delta(t) = D \times \delta(t)$. In this case, the resulting variance is proportional to time t for all times, $\sigma^2(t) = 2Dt \propto t$, and the displacement takes the form $\mathbf{R}(t) = D^{1/2}(W_X(t), W_Y(t))$ where $W_X(t)$ and $W_Y(t)$ are independent Wiener processes (e.g., see Haigh 2002). This is two-dimensional Brownian motion, which has no persistence of direction.

2. The second special case is when $\Delta(t)$ changes extremely slowly, such that over the time interval of interest it may be treated as a constant, independent of time t. This occurs when the timescale T has a very large value compared with t. An expansion of $\sigma^2(t) = 2D[t - T + T\exp(-t/T)]$ in powers of the small quantity $1/T$ yields, to leading order, a variance that is proportional to the square of time $\sigma^2(t) = Dt^2/T \propto t^2$. This behavior is characteristic of ballistic motion, and the displacement takes the form $\mathbf{R}(t) = \sigma(t) \times (Z_X, Z_Y)/2^{1/2}$, where Z_X and Z_Y are independent normal random variables with mean 0 and variance 1. When ballistic motion occurs, the movement of any animal is in a straight line at constant speed, but different animals have different realizations of Z_X and Z_Y and therefore in general move at different constant speeds in different directions.

In the case of general correlations, that is, general forms of $\Delta(t)$, an animal path exhibits a level of persistence of direction and corresponds to a continuous version of a correlated (or persistent) random walk. When we sample animal paths at time intervals of τ and consider the angle made between two straight line segments joining the displacement $\mathbf{R}(t)$ at three adjacent times (e.g., τ, 2τ, and 3τ), the distribution of angles can be expressed in terms of a single parameter $\zeta(\tau)$, which is determined solely by the mean square displacement $\sigma^2(t)$ evaluated at the times τ and 2τ. This is explicitly shown below, and the results are given in equations (2) and (3) in the main text.

Derivation of a Property of Discretely Sampled Paths

The normality and correlations of $\eta(t)$ determine the distribution of angles associated with discretely sampled paths. Sampling at time intervals of τ, a piecewise linear approximation of a path $\mathbf{R}(t)$ is obtained by joining the positions on the path at the times $t = 0, \tau, 2\tau, 3\tau, \ldots$ with straight lines (see fig. 1). The angles characterizing such a path are between adjacent straight-line segments. With $j = 0, 1, 2, \ldots$, adjacent straight-line segments are defined by the two vectors $\mathbf{A} = \mathbf{R}[(j+1)\tau] - \mathbf{R}(j\tau) = \int_{j\tau}^{(j+1)\tau}\eta(s)ds$ and $\mathbf{B} = \mathbf{R}[(j+2)\tau] - \mathbf{R}[(j+1)\tau] = \int_{(j+1)\tau}^{(j+2)\tau}\eta(s)ds$, and these differ in direction by the angle α. The joint probability density (i.e., distribution) of $\mathbf{A}$ and $\mathbf{B}$ factorizes into the product $\psi(a_X, b_X) \times \psi(a_Y, b_Y)$, where $\psi(a_X, b_X)$ is the joint distribution of the X components of $\mathbf{A}$ and $\mathbf{B}$ and is identical to the corresponding distribution of Y components. The factorization occurs because of statistical independence of the X and Y components of η. We adopt the convention that angles α lie in the range $-\pi$ to π. The distribution of angles is then given by $\phi(\alpha) = \int\delta(\alpha - \mathrm{atan2}(a_Xb_Y - a_Yb_X, a_Xb_X + a_Yb_Y))\psi(a_X, b_X)\psi(a_Y, b_Y)da_Xda_Ydb_Xdb_Y$, where all integrals range from $-\infty$ to ∞, the quantity $\delta(x)$ denotes a Dirac delta function, and $\mathrm{atan2}(Y, X)$ is the four-sector arctangent function. This returns a unique angle in the range $-\pi$ to π that has the property $\mathrm{atan2}(k\sin\theta, k\cos\theta) = \mathrm{atan2}(\sin\theta, \cos\theta)$ for all positive k. Using polar coordinates, we can write $a_X = \rho\cos\beta$, $a_Y = \rho\sin\beta$, $b_X = \lambda\cos\gamma$, and $b_Y = \lambda\sin\gamma$, where ρ and λ range from 0 to ∞ and the angles β and γ can cover any interval with width 2π. For multiple integrals with different limits of integration, we write the integration measures (such as $d\rho$) immediately to the right of the integral sign so no ambiguity exists about the range of each integral. We then find the distribution of angles to be $\phi(\alpha) = \int_0^\infty d\rho\int_0^\infty d\lambda\int_0^{2\pi}d\beta\rho\lambda\psi(\rho\cos\beta, \lambda\cos(\alpha+\beta))\psi(\rho\sin\beta, \lambda\sin(\alpha+\beta))$. The distribution $\psi(a, b)$ appearing in this expression is, because of normality of η, bivariate normal, with vanishing means $\mathrm{E}[A_x] = \mathrm{E}[B_x] = 0$, equal variances denoted $P = \mathrm{E}[A_x^2] = \mathrm{E}[B_x^2]$, and a covariance $Q = \mathrm{E}[A_xB_x]$. With $S = P^2 - Q^2$, it may be verified that $\psi(a, b)$ has the form $\psi(a, b) = [2\pi(S)^{1/2}]^{-1}\exp\{-[(a^2 + b^2)P - 2abQ]/(2S)\}$. This then yields $\phi(\alpha) = (2\pi S)^{-1}\int_0^\infty d\rho\int_0^\infty d\lambda\rho\lambda\exp\{-[(\rho^2 + \lambda^2)P - 2\rho\lambda Q\cos\alpha]/2S\}$. Changing the variable from λ to $y = \lambda/\rho$ first yields a ρ integral and then a y integral, and both may be evaluated in closed form. The result is equation (3) of the main text, with $\zeta = Q/P$.

Finally, we establish the relation between $\zeta \equiv Q/P$ and the mean square displacement $\sigma^2(t)$. We have $P = \mathrm{E}[\{X[(j+1)\tau] - X(j\tau)\}^2]$. This can also be written in the form $\int_{j\tau}^{(j+1)\tau}\int_{j\tau}^{(j+1)\tau}\Delta(t_1 - t_2)dt_1dt_2$, and by shifting integration variables $t_1 \to t_1 - j\tau$ and $t_2 \to t_2 - j\tau$, it follows that P is independent of j. Similarly, we can show that $Q = \mathrm{E}[\{X[(j+2)\tau] - X[(j+1)\tau]\}\{X[(j+1)\tau] - X(j\tau)\}]$ is also independent of j. Setting $j = 0$ and $j = 1$ in the expression for P yields (1) $P = \sigma^2(\tau)/2$ and (2) $P = \sigma^2(2\tau)/2 + \sigma^2(\tau)/2-2\mathrm{E}[X(2\tau)X(\tau)]$, and setting $j = 0$ in the expression for Q yields (3) $Q = \mathrm{E}[X(2\tau)X(\tau)] - \sigma^2(\tau)/2$. Combining (1), (2), and (3) allows us to obtain $\zeta = Q/P = \sigma^2(2\tau)/[2\sigma^2(\tau)] - 1$, which is equation (2) of the main text.

Literature Cited Only in Appendix C

Haigh, J. 2002. Probability models. Springer, London.