

Fundamental Insights into the Random Movement of Animals from a Single Distance-Related Statistic

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ABSTRACT: Statistical theories of animal movement have often been based on models of random walks, where movements take place in discrete steps and occur at discrete times. The multiplicity of distributions required in these approaches to describe animal movement (i.e., the distributions of angles, discrete steps, and times) have effects that cannot be simply disentangled, and hence they cannot be unambiguously determined. Here we present a mathematical formulation of continuous animal movements. In this new framework, it is shown that a single time-dependent distance statistic, the mean square displacement, which may be directly measured or mathematically modeled, is a central determinant of such random walks and encapsulates key information about the statistical properties of animal movements. The model and methodology presented here not only allow the determination of what were previously viewed as independent aspects of animal movements, such as the distribution of angular changes in direction, but also, because of the new emphasis on the mean square displacement, they may open up a new set of questions concerning animal movement and related phenomena. The results established in this work are directly applied to the foraging behavior of Pharaoh's ants, and very close agreement is found between observation and theory.

Keywords: correlated random walk, animal movement, foraging, Pharaoh's ants.

Introduction

Establishing the rules underlying the movement of animals (Kareiva and Shigesada 1983; McCulloch and Cain 1989) and cells (Nossal and Weiss 1974; Zygourakis 1996) is of fundamental interest in biology and related disciplines. A concept that has proved indispensable in this area is that of a correlated random walk, where the direction of a single step of the walk is statistically related to the direction of previous steps (Nossal and Weiss 1974; Kareiva and Shigesada 1983; Bovet and Benhamou 1988; McCulloch and Cain 1989; Zygourakis 1996; Codling et al. 2008).

Generally, a correlated random walk of animals is understood to describe movements that take place in two dimensions and occur at discrete times. Such walks typically rely on three distinct distributions: (1) the distribution of times between discrete steps, (2) the distribution of step lengths, and (3) the distribution of turning angles at each step (Patalak 1953; Nossal and Weiss 1974; Kareiva and Shigesada 1983; McCulloch and Cain 1989; Turchin 1991; Zygourakis 1996; Byers 2001; Codling et al. 2008). Other models of movement have been constructed where time is initially taken as continuous, but it is subsequently approximated as being discrete, in order to facilitate analysis (Bovet and Benhamou 1988; Codling and Hill 2005). These previous studies have focused on estimating parameters, such as the mean distance moved in a single step and the mean cosine of turning angles between subsequent steps (Kareiva and Shigesada 1983). This is in order to predict the mean square displacement and to compare predictions of the models with the behavior of real organisms.

In this study we introduce and analyze what we believe is a new model for the movement of animals in an unstructured territory. Crucially, our model describes the continuous movement of animals. Our model follows from a minimal modification of Brownian motion and incorporates correlations between the direction of movements at different times. The resulting random walks are short-tailed in character, in the sense that the distances traveled in a finite time have a finite variance. Random walks with infinite variances (long-tailed Levy walks) have been considered elsewhere in a related context (Viswanathan et al. 1996; Edwards et al. 2007).

The mean square distance associated with animal movement (also known as the mean square displacement) has long been recognized as an important aspect of animal behavior (Kareiva and Shigesada 1983; McCulloch and Cain 1989). This quantity also plays a particularly prominent role in our study. We present here what we believe to be the simplest model of continuous animal movement in which correlations are included. We show that essen-

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tially all results for the model can be derived, once we have determined the relationship between mean square displacement and the time taken for the displacement to occur. The central role of mean square displacement as a function of time is an exact feature of the model; it arises from the intimate way the mean square displacement is determined from correlations between directional changes. More generally, it is plausible that a substantial amount of information of direct relevance to animal movement is contained in the dependence of the mean square displacement on the time for the displacement to occur.

We have applied the model presented here to a significant biological problem: the foraging behavior of Pharaoh's ants. The quality and quantity of data from the observations of the ants provide a stringent test of the model. The following list summarizes key findings of our model and the results presented here:

1. The displacements, which are achieved over a given time interval, have a distribution that is determined solely by the mean square displacement over this time interval. The resulting distribution of displacements has an isotropic Gaussian form. These properties hold for any random-walk model with a distribution that obeys a simple diffusion equation; however, our model generally encompasses nondiffusive behavior.

2. Our model is applicable to animal positions that have been recorded at a set of equally spaced times (data of this form follow from filming as well as from other methods of recording positions). From the data, a piecewise linear approximation of each animal's path is constructed by joining the positions recorded at adjacent times by straight lines. The set of directional changes of all lines of the paths of many animals yields a distribution of angular changes. With τ denoting the time interval between recordings of position, the model predicts that the distribution of angular changes is determined solely from the ratio of mean square displacements that are established over time intervals of τ and 2τ . In particular, there are no parameters that require fitting in order to determine this distribution.

3. Mean square displacements, which are established over the times τ and 2τ , generally change when either the time interval of data sampling τ is changed or the data set is resampled, so the effective time interval of sampling is changed. The model predicts that the changed mean square displacements will change the angular distribution in a predictable manner. In general, the angular distribution is not a robust quantity but one that varies according to the precise value adopted for the sampling time interval; the angular distribution can thus be viewed as an object that is created entirely by the mode of data recording. The impact of resampling on angular distribution was the subject of previous detailed studies (see Bovet and Benhamou 1988; Codling and Hill 2005).

4. Application of the model to the foraging behavior of Pharaoh's ants by a detailed analysis of digital video recordings of their movements indicates that the mean square displacement of the ants' paths deviates considerably from being directly proportional to time. This is the characteristic of an anomalous form of diffusion (Codling et al. 2008), which is a phenomenon that has been observed in a number of theoretical models (Bartumeus et al. 2008). In the context of our study, this anomalous diffusive behavior is theoretically predicted and is empirically found to be directly manifested in the distribution of angles associated with ant paths. This anomalous diffusive behavior allows us to very simply estimate an important timescale in the problem that concisely characterizes the correlations underlying the random walk.

Model of a Persistent Random Walk

In this article we introduce a model of animal movement with the aim of applying it to real organisms to further our understanding of their behavior. The model describes properties of the displacement of an animal. The displacement of an animal at time t is its position at this time relative to its position at time $t = 0$. Because the animal moves in two dimensions, the displacement involves two coordinates and is written $\mathbf{R}(t) = (X(t), Y(t))$. By definition, the displacement vanishes at time $t = 0$.

When constructing the model, we restricted ourselves to the very simplest piece of mathematics capable of governing continuous changes of the displacement over time (a linear differential equation). Such an equation must incorporate the observed tendencies of animals to have some level of persistence in their direction of movement. These tendencies presumably arise from a combination of neuronal activity and the biomechanics of movement. In the absence of a detailed knowledge of these factors, and by recognizing that there are effectively (or genuinely) random aspects of the problem, we incorporated a degree of randomness into the equation that governs the displacement (full details of the model are given in app. A in the online edition of the *American Naturalist*). The random components in the equation that govern the displacement (and that represent random tendencies to move and change direction) are allowed to be arbitrarily correlated with themselves over time. This is a very simple and natural way to incorporate the tendency of animals to move with some persistence of direction. We encapsulate all unknown determinants of movement in the model in a specification of the correlations.

As with any modeling in biology, assumptions do need to be made. Here we assume that the animals are foraging but not purposefully heading in a particular direction (which, e.g., occurs when they are migrating). The validity

of this assumption can be observed in real data sets, by the absence of a directional preference, and this assumption makes our study a possible starting point for further studies where additional assumptions about the general patterns of movement may be included in the equation governing the displacement (see app. A and eq. [A1]).

The mean square displacement established after time t is $E[X^2(t) + Y^2(t)]$, where $E[\dots]$ denotes an average or expected value. We write the mean square displacement, $\sigma^2(t)$, as

$$\sigma^2(t) = E[X^2(t) + Y^2(t)]. \quad (1)$$

The model allows the mean square displacement, $\sigma^2(t)$, to be explicitly expressed in terms of correlations of the random tendencies to move, as is shown in appendix B in the online edition of the *American Naturalist*. Thus, all emphasis can be shifted from correlations to the mean square displacement, $\sigma^2(t)$. We adopt the view that $\sigma^2(t)$ is the object containing all unknown determinants of movement of the model. This model exhibits considerable flexibility, since many different possible choices can be made for the dependence of $\sigma^2(t)$ on time t . We note three special cases of the dependence of the mean square displacement on time:

1. $\sigma^2(t)$ is a constant, independent of time t . This is the extreme limit of so-called subdiffusive behavior (Codling et al. 2008), which generally corresponds to $\sigma^2(t)$ having a slower-than-linear growth with time t . Subdiffusion is a feature found in some models of animal movement (Codling et al. 2008). It can arise when there are negative correlations in directional changes and the animals' paths have the tendency to backtrack on themselves.

2. $\sigma^2(t)$ is proportional to time t . This corresponds to conventional diffusion and is a feature seen in many models of animal movement at long times (Kareiva and Shigesada 1983). If $\sigma^2(t)$ is proportional to t for all times, then we have Brownian motion (Brown 1828); this arises when correlations in directional changes exist over only the very shortest of timescales.

3. $\sigma^2(t)$ is proportional to t^2 . This occurs when an animal moves at a constant speed in a fixed direction (but different individuals generally have different speeds and different directions). This can be described as ballistic motion and can arise when correlations in directional changes are positive and exist over very long timescales. Ballistic motion is the extreme limit of superdiffusive behavior (e.g., see Codling et al. 2008), and it generally corresponds to $\sigma^2(t)$ having a faster-than-linear growth with time t .

Theoretical Results

All results given in this section are derived from a detailed mathematical analysis of the model, which is provided in

appendix C in the online edition of the *American Naturalist*. We begin the presentation of these results by noting that, within the framework of the model, both the X - and Y -coordinates of the displacement of an animal at time t have very simple statistical descriptions. They are each independent normal random variables with mean of 0 and variance $\sigma^2(t)/2$, and equation (1) follows from this. Despite the extreme simplicity of the distributions of X and Y (normal distributions), there are highly nontrivial characteristics of the paths of individual organisms because of the presence of correlations, as will become apparent in the distribution of angles (see below).

Although our model is fully continuous, it may be applied to situations where the positions of animals are sampled/recorded at only the discrete times $0, \tau, 2\tau, 3\tau, \dots$. Such sampling would result, for example, from a film or video recording of the animals' positions or from telemetry.

Given this sampling, we construct the piecewise linear approximation of a path by joining the adjacent positions of an animal at the discrete times $0, \tau, 2\tau, 3\tau, \dots$ via straight lines. The angular changes of the adjacent straight lines allow a definition of the turning angles. Figure 1 illustrates a piece-

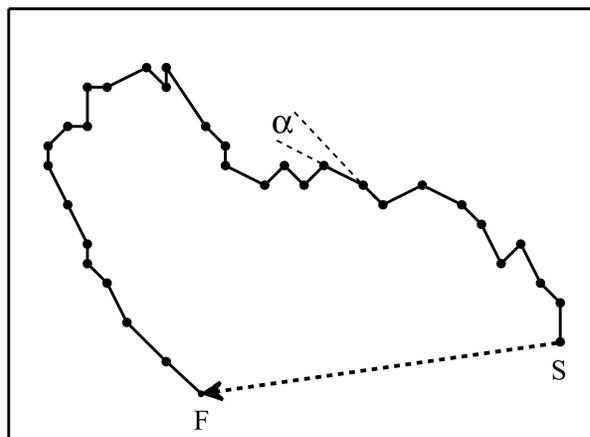


Figure 1: Plot of the piecewise linear approximation of the continuous path of a single animal (an ant from experiments described later) when its position was sampled at time intervals of $\tau = 0.125$ s. The filled dots represent the sampled positions, while the straight solid lines connecting the dots constitute the piecewise linear construction of the path. The particular path illustrated is of a 4-s duration, and thus it contains 33 positions. The path starts at position S and finishes at position F. From one time step to the next, the directions of the linear segments generally change. One angle, α , is illustrated between the adjacent linear segments joining the positions of the animal at times 1.000, 1.125, and 1.250 s. We adopt the convention that angles are positive (negative) if made in a counterclockwise (clockwise) direction. The angle illustrated corresponds to a counterclockwise change and hence is positive. The dashed arrow shows the displacement of the animal from its starting point after 4 s of movement.

wise linear path that was constructed from movements of a single animal (an ant) that was recorded at discrete times.

The distribution of turning angles for discretely sampled paths is, remarkably, found to depend on only a single parameter $\zeta \equiv \zeta(\tau)$, which is completely determined from the mean square displacement, $\sigma^2(t)$, via

$$\zeta \equiv \zeta(\tau) = \frac{1}{2} \frac{\sigma^2(2\tau)}{\sigma^2(\tau)} - 1. \quad (2)$$

The parameter ζ can vary from $-1/2$ to 1. The lower limit of this range follows from the mean square displacement having behavior associated with the extreme limit of subdiffusion (i.e., $\sigma^2(t) = \text{constant}$, independent of t). The upper limit follows from the extreme limit of superdiffusion, which is ballistic motion ($\sigma^2(t) \propto t^2$). Brownian motion ($\sigma^2(t) \propto t$) leads to the intermediate value $\zeta = 0$.

Under a reasonable approximation, the parameter ζ is proportional to the mean value of the cosine of the turning angles, $E[\cos \alpha]$, namely $\zeta \approx (4/\pi) \times E[\cos \alpha]$ (the exact relation between ζ and $E[\cos \alpha]$ is given in eq. [4], below). With angles α lying in the range of $-\pi$ to π radians, the distribution of turning angles for a given value of ζ is written $\phi(\alpha; \zeta)$ and is found to take the exact form

$$\phi(\alpha; \zeta) = \frac{1 - \zeta^2}{2\pi} \frac{(1 - Z^2)^{1/2} + \{\arctan[Z(1 - Z^2)^{1/2}] + \pi/2\}Z}{(1 - Z^2)^{3/2}}, \quad (3)$$

$$Z = \zeta \cos \alpha.$$

This distribution is illustrated in figure 2.

As shown above, the distribution of angles depends on just a single parameter, $\zeta \equiv \zeta(\tau)$, which therefore has an exceptional status in the theory. The value of ζ is a defining characteristic of paths that have been sampled at discrete time intervals of τ . All statistics of paths that provide direct measures of correlations in directional changes depend only on ζ . For example, the mean (i.e., expected) value of $\cos \alpha$, namely $E[\cos \alpha]$, is explicitly given by

$$E[\cos \alpha] = \frac{E(\zeta) - (1 - \zeta^2)K(\zeta)}{\zeta} \\ = \frac{\pi}{4}\zeta + \frac{\pi}{32}\zeta^3 + O(\zeta^5), \quad (4)$$

where $K(\zeta)$ and $E(\zeta)$ denote complete elliptic integrals of the first and second kind, respectively (Abramowitz and Stegun 1970). The smallness of the coefficient of ζ^3 in equation (4) allows the mean value of $\cos \alpha$ to be quite reasonably approximated by just the leading term in ζ , namely $E[\cos \alpha] \approx (\pi/4)\zeta$, with all higher-order terms omitted (as indicated above).

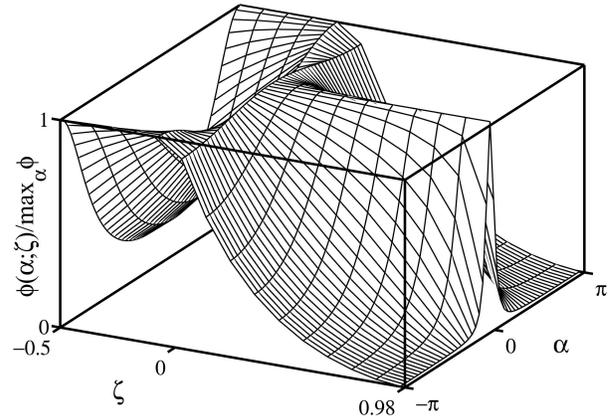


Figure 2: Plot of the ratio $\phi(\alpha; \zeta) / \max_{\alpha} \phi$ against angle α and parameter ζ , where $\phi(\alpha; \zeta)$ is the distribution of angles for a given value of ζ and $\max_{\alpha} \phi$ is the maximum value of $\phi(\alpha; \zeta)$ over all angles. Angles are measured in radians. The distribution $\phi(\alpha; \zeta)$ takes various forms depending on the value of ζ . When ζ is negative, the distribution is a U-shaped function of α (due to the presence of negative correlations). When $\zeta = 0$, the distribution is uniform in α (as would occur in Brownian motion). When ζ is close to 1 (which corresponds to near-ballistic motion), the distribution is a sharply peaked function of α . The maximum value of $\phi(\alpha; \zeta)$ varies strongly with the value of ζ . For example, when $\zeta = 0$, the maximum value is $(2\pi)^{-1}$, and when ζ tends to 1, the maximum value tends to infinity. Plotting the ratio $\phi(\alpha; \zeta) / \max_{\alpha} \phi$ allows a direct comparison of the shape of the distribution for different values of ζ , without being confounded by the very different maximum heights. If the angular distribution is required for a given value of ζ , the complete result for the distribution is given in equation (3).

Within the model, the time interval of sampling, τ , can be arbitrarily chosen. We can exploit this feature to provide an estimate of an important timescale in the problem that concisely characterizes the decay of correlations of the random tendencies that give rise to the random walk, and that we have assumed arise from neuronal activity and the biomechanics of movement. The existence of such a timescale, say T , is also equivalent to the assumption that the mean square displacement, $\sigma^2(t)$, depends on time t only in the combination t/T . We have considered correlations that decay as $\exp(-|t|/T)$ or $\exp[-t^2/(2T^2)]$. The resulting forms of $\zeta(\tau)$ that follow from these have common features. In particular, they both decrease as the sampling time τ is increased, and they have a largest value $\zeta(0)$ of unity. When the value of the sampling time is close to the timescale T , that is, when $\tau \approx T$, we find that the value of $\zeta(\tau)$ is close to $1/2$. This suggests a simple but practical estimate of the correlation time associated with movement: namely it is the choice of sampling time, τ , that leads to $\zeta(\tau) = 1/2$.

Some authors have introduced a statistic termed “sinuosity” (Bovet and Benhamou 1988, 1991; Benhamou 2004) as an alternative method of characterizing correlated

random walks. This statistic has been primarily defined for random walks with discrete step lengths, and as such it is not obviously directly relevant to the fully continuous random walks considered in our study. We note, however, that a formulation has been provided that relates sinuosity to mean square displacement at long times (Benhamou 2004). We plan to investigate elsewhere the relationship between these different approaches.

Data Analysis Procedure

To complement the theoretical results, it is necessary to have a practical means of extracting information from the data. We work on the assumption that we have a number of distinct animal paths, where animal positions are known at the times $0, \tau, 2\tau, 3\tau, \dots$. The results we require are estimates of quantities, such as the mean square displacement at the times τ and 2τ (namely, $\sigma^2(\tau)$ and $\sigma^2(2\tau)$), and the distribution of angular changes of direction along paths. Our procedure is to extract and use the maximum number of independent positions/displacements, and hence the maximum information, from the positional data in our possession. We adopted the following procedure to achieve this. By focusing on a single animal path, we extracted all X - and Y -coordinates of the animals at the times $2j \times \tau$ and $(2j + 1) \times \tau$ (where $j = 0, 1, 2, \dots$). This information allows us to directly determine a set of squared displacements of data sampled at time intervals of τ along a single path. Pooling the data over all paths allows for a good estimate of $\sigma^2(\tau)$. Next, extracting all X - and Y -coordinates of the animals on a path at the times $2j \times \tau$ and $(2j + 2) \times \tau$ allows us, in a similar way, to estimate $\sigma^2(2\tau)$. In an analogous way, all angular changes in direction can be determined from the X - and Y -coordinates that were extracted from the positional data, and an empirical distribution can be determined.

Application of the Theory to Pharaoh's Ants

We applied the theoretical results to the foraging paths taken by individual ants of the highly invasive, pheromone-laying, multiqueen species *Monomorium pharaonis* (Pharaoh's ants). These ants were allowed access, via a bridge from their nest, to a previously inaccessible area (henceforth termed the arena) and were filmed at the rate of 8 frames per second. Each frame was stored in a digital format and analyzed to determine the mean position (i.e., the mean values of the X - and Y -coordinates) of every ant that had left the nest and was exploring the arena (see app. D in the online edition of the *American Naturalist* for details of the experimental setup). This gave the positions of each ant in the arena every 0.125 s, but it did not identify which of the positions in different frames

correspond to a given ant. To make such an identification, we adopted the procedure where, given the position of a particular ant in one frame, the position of the ant closest to it in the next frame is taken as the actual position of the ant in that frame. We estimate that, over a path lasting up to 120 s (i.e., $\sim 10^3$ frames) and for the density of ants observed in our experiments ($\sim 10^3$ ants m^{-2}), this simple procedure correctly identifies 98% of the positions visited by a single ant (see app. E in the online edition of the *American Naturalist* for details of the accuracy of path identification). Having determined the positions of one ant at different times, we performed a piecewise linear reconstruction of its path.

In order to have a balanced data set and to avoid any edge effects associated with ants entering or leaving the arena, we restricted our analyses to paths of 30-s duration that were located near the center of the arena. In this time interval, Pharaoh's ants can move a significant distance (on the order of 200 body lengths).

We performed an analysis of the pixels (picture elements) of the digital video recordings of the ants in the arena. This allowed us to determine the time that ants spent in each pixel. Putative ant trails may be defined as regions of the arena in which ants spent an appreciable time. We estimate that appreciable changes in occupancy of such putative trails occurred on the timescale of tens of minutes. Thus, during any 30-s time interval at any time throughout a 70-min experiment, there was negligible excess usage of a trail compared with that of any other region. Thus, during the 30-s time intervals where ant movements were analyzed for this work, the ants effectively acted as independent agents that were not following trails. This motivates modeling the movements of individual ants as continuous random walks that are independent of the random walks of other ants.

Digital video recordings yielded the positions of the ants every 0.125 s. Figure 1 contains the actual piecewise linear path constructed for one particular ant over a 4-s time interval. From the digital video recordings, we determined the distributions of displacements of the ants over a number of 30-s time intervals during the course of the experiment.

We verified (using the Kolmogorov-Smirnov test) that $>95\%$ of these distributions were not significantly different from a normal distribution. We note that, if the distribution of displacements over a given time interval t is normally distributed and has a variance $\sigma^2(t)$, then a direct consequence of normality is that the ratio of mean displacement to root mean square displacement is independent of the variance $\sigma^2(t)$ (Bovet and Benhamou 1988) and, hence, of the choice of time interval t . With the magnitude of displacement, written as $\|\mathbf{R}(t)\| = (X^2(t) + Y^2(t))^{1/2}$, this ratio has the value

$$\frac{E[\|\mathbf{R}(t)\|]}{\sqrt{E[\|\mathbf{R}(t)\|^2]}} = \sqrt{\pi/4} \approx 0.8862, \quad (5)$$

(Bovet and Benhamou 1988; also see the discussions about this in Codling et al. 2008). The intuitive explanation of equation (5) is that, in an isotropic normal distribution, there is only a single length present, namely $\sigma(t)$. As a consequence, both $E[\|\mathbf{R}(t)\|]$ and $\{E[\|\mathbf{R}(t)\|^2]\}^{1/2}$ are directly proportional to $\sigma(t)$ such that their ratio is a constant, independent of $\sigma(t)$. Direct calculation verifies this explanation (see app. C for an explicit derivation of eq. [5]).

The result of equation (5) may be used to check the normality of the distribution of displacements without requiring any knowledge about the time dependence of $\sigma^2(t)$. Results for the actual numerical value of the ratio $E[\|\mathbf{R}(t)\|]/\{E[\|\mathbf{R}(t)\|^2]\}^{1/2}$, calculated from our ant data, are provided in table 1.

In the theory presented here, the ratio $E[\|\mathbf{R}(t)\|]/\{E[\|\mathbf{R}(t)\|^2]\}^{1/2}$ is predicted to take a fixed value of $(\pi/4)^{1/2}$ (see eq. [5]), which is completely independent of the way the mean square displacement $\sigma^2(t)$ varies with time t . By contrast, the distribution of angular changes is predicted to explicitly depend on the way $\sigma^2(t)$ varies with time t (since the angular distribution depends on $\sigma(2\tau)$ and $\sigma(\tau)$; see eqq. [2] and [3]). To investigate the angular distributions associated with the Pharaoh's ants, we first investigated the mean square displacement, $\sigma^2(t)$. A typical form for the observed time dependence of $\sigma^2(t)$ is provided in figure 3.

Previously we introduced the sampling time interval τ . This quantity can, in theory, be freely chosen. However, with our data there is a restriction: because of the mode of data recording we adopted, τ must be an integer multiple of 0.125 s (there will be a similar restriction with any positional data that is recorded at discrete times). With our data it is possible, for example, to make a choice for

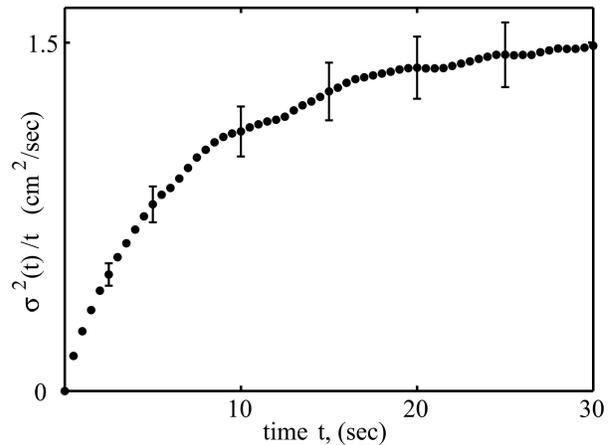


Figure 3: Ratio $\sigma^2(t)/t$ is plotted against t using data collected from Pharaoh's ants. The error bars represent the standard deviation of $\sigma^2(t)/t$. For n normally distributed displacements with a sample mean square displacement of σ_s^2 , the standard deviation is estimated as $[2/(n-1)]^{1/2}\sigma_s^2/t$. With σ_p^2 the population variance, this estimate follows from $(n-1)\sigma_s^2/\sigma_p^2$ having a χ_{n-1}^2 distribution. The plot suggests that, at relatively long times, the ratio $\sigma^2(t)/t$ approaches a constant value. An approach of the ratio to a constant value indicates an approach to conventional diffusion behavior, with $\sigma^2(t) \propto t$. It is evident that $\sigma^2(t)/t$ does not have a constant value for short times. This indicates a substantial deviation of $\sigma^2(t)$ from being proportional to t . Such behavior is termed anomalous diffusion (e.g., see Codling et al. 2008).

τ such that $\tau = 1$ s. After this choice has been made, the mean square displacements for the times τ and 2τ can be found and, using these, the value of the parameter $\zeta(\tau)$ (eq. [2]) may be established. The resulting value of $\zeta(\tau)$ allows us, via equation (3), to determine the angular distribution that is predicted by the theory. No additional information or parameters are required to determine the angular distribution.

Table 1: Ratios of the mean displacement to root mean square displacement of foraging ants, as a function of time interval

Ratio	Time interval, t (s)							
	1	2	4	6	10	15	20	30
$E(\ \mathbf{R}(t)\)/\{E[\ \mathbf{R}(t)\ ^2]\}^{1/2}$.880	.887	.892	.890	.888	.882	.883	.883
$\sigma^2(t)/\sigma^2(1)$	1	3.3	9.7	17.3	34.4	56.9	78.5	121.3

Note: When the displacement that occurs over a time interval of t , namely $\mathbf{R}(t)$, follows a normal distribution with variance $\sigma^2(t)$, the ratio $E(\|\mathbf{R}(t)\|)/\{E[\|\mathbf{R}(t)\|^2]\}^{1/2}$ is independent of $\sigma^2(t)$ (and, hence, time), and it takes the constant value $(\pi/4)^{1/2} \approx 0.8862$ (see Bovet and Benhamou 1988; app. C in the online edition of the *American Naturalist*). This relationship was tested for paths of 30-s duration that were observed at various points throughout a 70-min experiment. We present the ratio that was calculated from data for the 30-s paths that were observed during a period of the experiment that was between 40 and 42 min. This illustrates the close agreement of the experimental result of this ratio with the prediction of a normal distribution. A similar close agreement was found for 30-s paths observed at different times throughout the duration of the experiment (results not shown). The bottom row gives the ratio of mean square displacement of the ants that was established over a time interval of t to the mean square displacement for a time interval of $t = 1$, and it indicates the substantial degree of broadening of the distribution that occurs for a period of up to 30 s.

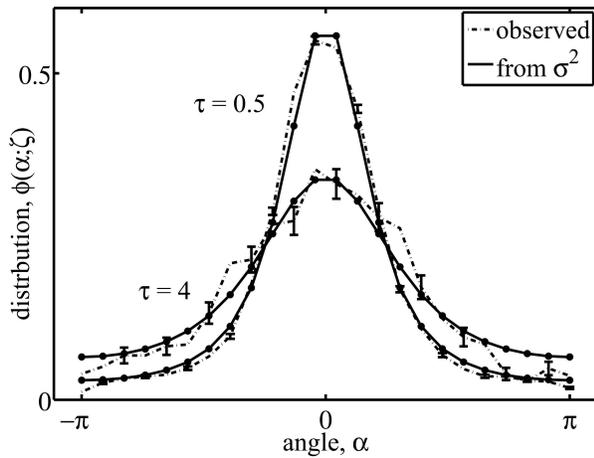


Figure 4: Analysis of the piecewise linear construction of recorded ant paths. The paths, sampled at time intervals of τ , allow for the determination of the distribution of turning angles by directly measuring angles as, for example, would be possible from figure 1. Two separate choices for τ were adopted here. The resulting angular distributions are marked with broken lines, and the error bars give the standard deviation in the distributions. From the same paths, determining the mean square displacements at times τ and 2τ and then using equations (2) and (3) allows the theoretical angular distribution to be calculated without knowledge of the observed angles (see “Data Analysis Procedure” for the method of determining $\zeta(\tau)$). The theoretical formulation applies for an arbitrary value of the sampling time. The theoretical curves are marked with dots connected by solid lines. There is very good quantitative and qualitative agreement between the angular distributions predicted by the theory (from measured mean square displacements) and the actual distributions obtained from measuring all angles. This lends strong support to the key role played by the mean square displacement, $\sigma^2(t)$.

We extracted the maximum possible information from our data to calculate $\zeta(\tau)$ using all nonoverlapping displacements that make up a path, as described above in “Data Analysis Procedure.” We note that a path of just a single ant that is observed for t s may contain a considerable amount of relevant information, since it consists of $t/(2\tau)$ nonoverlapping displacements that may be used in the calculation of $\zeta(\tau)$.

The above process can be repeated for different choices of the sampling time interval τ . The theory makes explicit predictions for the qualitative and quantitative shape of the angular distribution, for different values of τ , given knowledge of the mean square displacement $\sigma^2(t)$. The angular distributions, so predicted, can be directly compared with the angular distributions that are arrived at by directly measuring angular changes of direction. Some illustrative findings are given in figure 4.

Under a model of a correlated random walk, increasing the sampling time interval is intuitively expected to cause the distribution of turning angles to become more Brown-

ian-like, since correlations in the direction of movement are expected to decay over time. Equivalently, the distribution of turning angles, derived from just the mean square displacement $\sigma^2(t)$, is expected to broaden when the sampling time interval is increased given the observed behavior of $\sigma^2(t)$ (fig. 3). This is indeed what is seen in figure 4 (see also specific studies on this effect: Bovet and Benhamou 1988; Codling and Hill 2005).

A quantity that is widely used to describe the angular distribution, namely the mean cosine of angles $E[\cos \alpha]$ (Kareiva and Shigesada 1983), can be determined by directly measuring angles or, alternatively, by using the observed mean square displacement and equations (2) and (4). To assess the effect the size of the sample has on the predictions of our study, we resampled the data by randomly choosing a smaller sample (i.e., a subset of all the ants we observed). For 100 samples of N ant paths ($N = 10, 20, \dots, 150$), we determined the standard deviation of $\cos \alpha$ from direct calculation of angles that we measured directly, using the value of $\zeta(\tau)$ for each sample and the distribution of angles (equation [3]). It has been suggested (Bovet and Benhamou 1988) that the angular distribution contains less noise than the mean displacement, and thus the former should be preferentially used in calculations. Comparing the standard deviation of $\cos \alpha$ from the two approaches, however, yields broadly comparable results (see table 2).

We showed above that, when the sampling time τ takes a value such that $\zeta(\tau) = 1/2$, it is close to an assumed unique correlation time T associated with the random movement of the animals. Generally, we find that the correlation time, estimated from $\zeta(\tau) = 1/2$, depends on the density of ants in the arena and hence varies during the course of an experiment. The average of the correlation times that were estimated in this way, throughout a 70-min experiment, yielded a mean value of 2.3 s. This result is thus an estimate of the correlation time, T , associated

Table 2: An estimate of the standard deviation of $\cos \alpha$ from samples of data of size N

N	$T = .5$					$T = 4$				
	10	20	50	100	150	10	20	50	100	150
$SD_1 \times 10^2$	4.1	2.4	1.5	.9	.6	7.4	4.7	3.0	1.7	1.1
$SD_2 \times 10^2$	7.1	4.1	2.4	1.6	1.0	12.5	7.8	4.8	3.3	2.0

Note: The standard deviation of $\cos \alpha$, when calculated from the directly measured angles, is denoted SD_1 . The standard deviation when calculated from equation (3) (i.e., just using knowledge of the mean square displacement) is denoted SD_2 . The standard deviation of $\cos \alpha$ was estimated by randomly choosing, without replacement, a subset of 100 ant paths of size N . The original data set contained 216 paths. The values of SD_2 are slightly higher than the corresponding values of SD_1 , reflecting the fact that when n angles can be extracted from a path, $\zeta(\tau)$ is determined from $n/2$ values (see “Data Analysis Procedure,” above).

with the correlated random movements of the population of ants under investigation and originates in the underlying mechanisms that drive the ant movements.

Discussion

In previous studies it has been asserted that when it is required “to describe in detail the spatial structure of animals’ actual paths, it is indispensable to specify the distribution of changes of direction” (p. 421, Bovet and Benhamou 1988). Most theoretical studies (Othmer et al. 1988; Bovet and Benhamou 1991; Benhamou 2004; Bartumeus et al. 2005, 2008) and empirical studies (Crist and MacMahon 1991; Crist et al. 1992; Challet et al. 2005; Garcia et al. 2007) have consequently used a description of animal movement that is based on a characterization of the distributions of turning angles and step lengths. Early work on kinesis (Gunn et al. 1937), where motion was described in terms of speed (*O*-kinesis) and path sinuosity (*K*-kinesis), has been the most likely influence of the present formulation of correlated random walks.

Here we present a mathematical model, along with associated theoretical results, that relates directly to observations of the continuous movements of animals. Constructs such as step length do not appear in our theoretical description. However, any recording technique that captures images at discrete times by its fundamental nature produces a discrete time description of the data, and our analyses and modeling have accommodated data with this basic feature.

The mean square displacement of moving animals plays a central role in our theory, since it contains information that is necessary for an essentially complete description of a continuous correlated random walk. In particular, from the piecewise linear approximation of animal paths derived from a discrete time description, an angular distribution can be produced, and it is apparent that this distribution is created by the mode of recording and does not have a fundamental significance or existence in its own right. This is emphasized in figure 4 by the change in the angular distribution, which results when the discrete time of sampling of the data is changed. The change of shape of the distribution, derived from direct experimental observation of real organisms (Pharaoh’s ants), is well explained in terms of the mean square displacement, as predicted by the theory. We hold the view that the robust quantity underlying animal movement is a particular function that characterizes the statistics of the problem, namely a correlation function or, equivalently, the mean square displacement $\sigma^2(t)$. Any model that can be cast in the form of equation (A1) and that has a correlation function that depends only on the time interval $t_1 - t_2$ (see app. A) will be fully characterized by $\sigma^2(t)$.

The issue of resampling and its implication for the an-

gular distribution has been explored previously (Bovet and Benhamou 1988; Hill and Hader 1997; Codling and Hill 2005), while Bartumeus et al. (2008) considered angular distributions and the effect on resulting simulated movement paths. Here we presented an alternative approach, where the time dependence of $\sigma^2(t)$ contains key information needed to characterize the angular distribution, and we showed that knowledge of this quantity predicts angular statistics with an accuracy that is broadly comparable to those statistics derived directly from measuring angles of directional change within paths. Hence, properties that have been discussed previously, such as smoothing of angular distributions due to resampling, also hold in this study.

An additional feature of our model is that it uses information from the mean square displacement, $\sigma^2(t)$, and so it covers different regimes of time, including behavior at long times, where the motion is close to that of Brownian motion, as well as in the short-time regime, where the effects of correlations play a significant role. This leads to a full formulation of the probability distribution of the displacements of animals and their mean distances traveled at any time after starting (for a discussion on the short-time regime, see Wu et al. 2000). This is of special interest when making the comparison with discrete-step, discrete-time models. In many of these models, many quantities of interest are really defined only for the long-time regime, where the number of discrete steps is used as an approximation of time (Bovet and Benhamou 1988). By contrast, the continuous-time description presented here allows us to characterize the behavior and implications of correlations over relatively short timescales and to derive the correlation time that is directly related to the actual level of correlation in the observed paths.

We note that the model presented here relaxes some assumptions commonly made for the sake of mathematical simplicity (rather than for direct biological relevance). These include (1) the assumption of constant velocity (see Codling et al. 2008) and (2) the assumption of independence of step length and angular changes in direction (Kareiva and Shigesada 1983). Furthermore, because the angular distribution of a piecewise linear discrete path appears as a by-product of changes in the mean square displacement, as shown in this study, the need for characterizing and using complicated angular distributions (Byers 2001; Bartumeus et al. 2008; Codling et al. 2008) may be avoided.

The results presented here are designed to accommodate the most common methods of data collection, namely filming/digital video recording and telemetry (radio tracking, GPS, radio frequency identification). On a practical side, and probably of particular interest for ecological studies, knowing the mean value of the displacement in the asymptotic long-time regime, where $\sigma^2(t)/t$ is independent of time t , can yield an estimate of the diffusion coefficient and

hence allow a quantitative description of the dispersal of organisms. This can be done without knowledge of particular paths of individuals but with an average over all displacements at a given time, provided this time is suitably large. An estimate of the correlation time T gives an indication of the minimum time at which to sample the population's mean square displacement, because when $t \gg T$, the quantity $\sigma^2(t)/t$ is expected to approach a constant value (see fig. 3).

The work presented here provides a new perspective on the description and, hence, the study of animal movement via a statistical model that is centered on the mean square displacement $\sigma^2(t)$. This quantity encapsulates key features of animal movement with a number of other characteristics subordinate to it. We suggest that future progress, along the lines of our work, may lie in two directions. The first direction is measuring how the mean square displacement, $\sigma^2(t)$, varies with time t . It would be natural to consider a variety of different organisms, in different contexts, and then proceed to produce plausible models and explanations of the observed forms of $\sigma^2(t)$. The second direction would lie in investigating the optimization of resource discovery in an evolutionary ecological context. Our results suggest that modifying the nature of the search paths is equivalent to modifying a single function, namely $\sigma^2(t)$. A mathematical formulation of search strategy in terms of $\sigma^2(t)$ may thus be possible.

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