Spatial Analysis of Animals' Movements Using a Correlated Random Walk Model

Pierre Bovet and Simon Benhamou

Laboratoire de Neurosciences Fonctionnelles, Centre National de la Recherche Scientifique, 13402 Marseille cedex 9, France

A probabilistic model was developed that applies to the analysis of erratic movements made by animals foraging in a stochastic environment. This model is a first order correlated random walk model in which the following two biological constraints are integrated into the Brownian motion model: bilateral symmetry and the cephalo-caudal polarization that leads to a tendency to go forward. The main properties of the model were studied by numerical simulations using a pseudo-random generator. It was found that the spatial pattern of search paths could be quantified by a single numerical index of sinuosity. Some advice on the concrete use of this model is given. Correlated random walk diffusion was studied in relation to the sinuosity by analysing the probabilistic distribution of the bee-line distance between the first and last points of a path. Some theoretical applications of this model are developed.

1. Introduction

Animals' movements do not fit the simple deterministic kinematic equations used in classical physics. Indeed, their paths have a random pattern, which has been remarked upon for a long time (Pearson, 1906; Furth, 1920), so that they are not easy to describe with continuous mathematical functions. Probabilistic discrete step models therefore provide a useful means of representing animals' paths. Several authors, making an analogy with Brownian motion, have used the 2-dimensional random walk model to represent animals' movements (Wilkinson, 1952; Holgate, 1969; Morrison, 1978; Hoffmann, 1983). The original random walk model is too simple to represent animals' paths reasonably accurately, however, because the cephalo–caudal polarization and the bilateral symmetry observed in most animals cause a tendency to go forward that it does not account for.

Analysis of animals' movements has been shown to be worthwhile in the framework of Optimal Foraging Theory. Here, the need to quantify animals' search paths arose (Pyke *et al.*, 1977; Krebs, 1978, 1979; Krebs *et al.*, 1983; Pyke, 1983, 1984). The randomness of search paths might reflect the adaptation of animals' foraging behaviour to the stochasticity of the environment (Bovet, 1979). The aim of the present study was to quantify this randomness using a numerical index of sinuosity.

An informative way of characterizing animals' search paths consists of establishing the statistical distribution of changes of direction on the one hand, and the statistical distribution of step lengths between successive changes of direction on the other hand (Siniff & Jessen, 1969; Smith, 1974*a,b*; Murdie & Hassel, 1973; Pyke, 1978*a*;

MacDonald, 1980). It should be stressed, however, that the transformation of a recorded path into a broken line is bound to be arbitrary: in particular, the values of changes of direction obtained by this approach will depend greatly on the step lengths. In practice, the discretizations are frequently performed by plotting an animal's position at regular time intervals. In this case, the rate of change of direction, defined by Fraenkel & Gunn (1961) as the mean amount of turning per unit of time, constitutes a simple means of combining the changes of direction and the step lengths. From a theoretical point of view, Dunn (1983) has shown that the mean square of the amount of turning per unit of time is a more appropriate index. In both of the latter indices, however, time and space are amalgamated, so that it is not possible to distinguish between the component representing the structural properties of an animal's path and that giving the animal's velocity. This blending of temporal and spatial components is particularly inconvenient in cases where a correlation is thought to exist between the structure of an animal's path and the animal's velocity. This is probably so, for instance, with foraging animals which show an area-restricted searching behaviour after encountering a prey item (e.g. Knoppien & Reddingius, 1985).

A purely spatial index of sinuosity, which expresses the amount of turning associated with a given path length, would therefore be a useful means of quantifying the structure of animals' paths. It would become easy to describe animals' movements in spatio-temporal terms using the velocity in addition to the sinuosity. A purely spatial index of directionality (which varies as the inverse of the sinuosity) has been proposed by Levin et al. (1971) and Pyke (1978a). This index, however, is based solely on the distribution of changes of direction and does not take the step length into account. In this paper, a first order correlated random walk model is developed in order to define a reliable numerical sinuosity index integrating both the changes of direction and the step lengths between them. This should make it possible to make quantitative comparisons between paths and to predict the diffusion of animals' movements. We will see that this sinuosity index constitutes a behavioural parameter which can be integrated into more complex models.

2. The Model

As mentioned above, the original random walk model is too simple to formalize the search paths of animals with sufficient accuracy, because it does not take into account the cephalo-caudal polarization and the bilateral symmetry leading to a tendency to go forward. An additional correlation between the directions of the successive steps suffices, however, to express these basic properties. The simplest means of introducing this type of first order correlation consists of taking the distribution of changes of direction from one step to another, assuming the changes of direction to be independent of each other. This is a discrete version of a first order continuous Markovian process called the Ornstein–Uhlenbeck process. To use continuous mathematical formulation here would be very difficult however, because the variable (an orientation) is circular, and can therefore be defined as mod 2π, unlike the linear variables classically used; moreover, we would be dealing

with a degenerate case of the Ornstein–Uhlenbeck process, where the differential does not depend on any systematic factor and would therefore only correspond to white noise.

As shown in Fig. 1, a path can be represented by a sequence of $(N+1)$ points $(X_0, Y_0), (X_1, Y_1), \ldots, (X_N, Y_N)$ such that, for any i (integer, $1 \le i \le N$), $\vec{P}_i = (X_i - X_{i-1}, Y_i - Y_{i-1})$, representing the ith step, is a vector with the length P_i, and the value of the change of direction between the vectors $\vec{P}_i$ and $\vec{P}_{i+1}$ is measured algebraically by the turning angle α_i ($1 \le i \le N-1$). Like any angular distribution, the distribution of changes of direction is characterized by a mean vector (Mardia, 1972; Batschelet, 1981). Its orientation, $\Phi = \operatorname{arctg}(\sum \sin \alpha_i / \sum \cos \alpha_i)$, defines the angular mean of the distribution, and its length $r = (\sum^2 \cos \alpha_i + \sum^2 \sin \alpha_i)^{1/2}/(N-1)$, ranging between 0 and 1, expresses the concentration of the distribution around Φ. In order to take into account the forward tendency of the locomotion of most animals, the distribution of changes of direction is taken to be symmetrical and to have an angular mean $\Phi = 0$. The mean vector length r is then equal to the mean cosine of changes of direction and constitutes a measure of the correlation between the directions of successive steps (Tchen, 1952). When this correlation is null ($r = 0$), one again obtains the original random walk model; when the correlation is perfect ($r = 1$), one obtains a straight line movement.
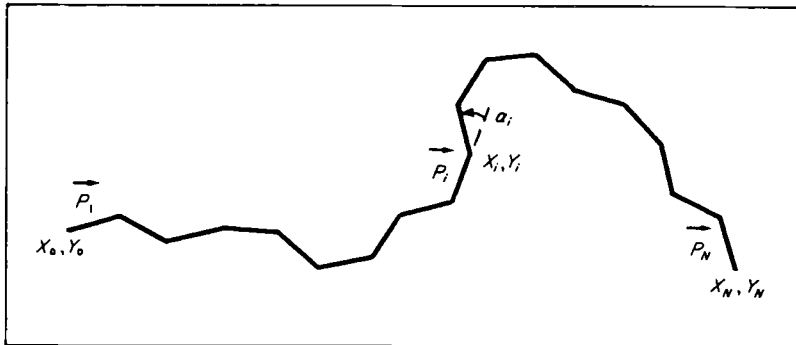

FIG. 1. Example of an N-step path. The turning angles α_i were measured between the vectors $\vec{P}_i$ and $\vec{P}_{i+1}$.

Some authors have attempted to develop correlated random walk models without taking the distribution pattern of the changes of direction into account (Tchen, 1952; Patlak, 1953a,b; Skellam, 1973; Hall, 1977; Dunn, 1983; Doucet & Wilschut, 1987). As we shall see in section 5, this approach can be used to account for the diffusion of animals' movements. Whenever it is required, however, to describe in detail the spatial structure of animals' actual paths, it is indispensable to specify the distribution of changes of direction.

The simplest means of representing a path which takes into account the distribution of changes of direction is to take a walk on a square lattice (Rohlf & Davenport, 1969; Cody, 1971, 1974; Pyke, 1978b; Deangelis & Yeh, 1984). In this very schematic model, the animal's choice at each step is restricted to one of four possibilities: to

move ahead (A), turn right (R), turn left (L), or move back (B), with probabilities as in $P_A < P_R = P_L < P_B$. With these conventions, the correlation between the directions of successive steps is $r = P_A - P_B$. The best formulation of the distribution of changes of direction is that used by Siniff & Jessen (1969), which consists of taking a circular normal (von Mises) distribution with a mean angle equal to 0 and a parameter of concentration k ranging between 0 (corresponding to $r = 0$) and infinity (corresponding to $r = 1$). The von Mises distribution is difficult to compute, however. The linear normal distribution, wrapped around the trigonometrical circle, constitutes a suitable approximation (Mardia, 1972; Batschelet, 1981). Like Kitching (1971), Murdie & Hassel (1973), and Doucet & Drost (1985), we proceed by drawing turning angles α_i between successive steps at random, independently from each other, from a normal distribution centred on 0 with a standard deviation σ. The mean vector length r of the distribution of turning angles can then be expressed as a function of σ (Mardia, 1972; Batschelet, 1981):

$$r = \exp(-\sigma^2/2). \qquad (1)$$

In some of the above models, the step length is constant, whereas in others it is variable. Since step length is mostly arbitrary and has a purely formal function, there is no need to adopt a variable step length on biological grounds. Consequently, from now on, we mainly consider paths to consist of sequences of N steps with constant length P. A generalization which is applicable to cases where step lengths are biologically relevant is given in section 4. There is obviously a direct relationship between the sinuosity of the path and the standard deviation σ of the distribution of the changes of direction used in the model (Fig. 2). On the other hand, when σ remains unchanged, any increase in the step length P will result in a decrease in the sinuosity, since the amount of turning involved in a given path length will decrease.
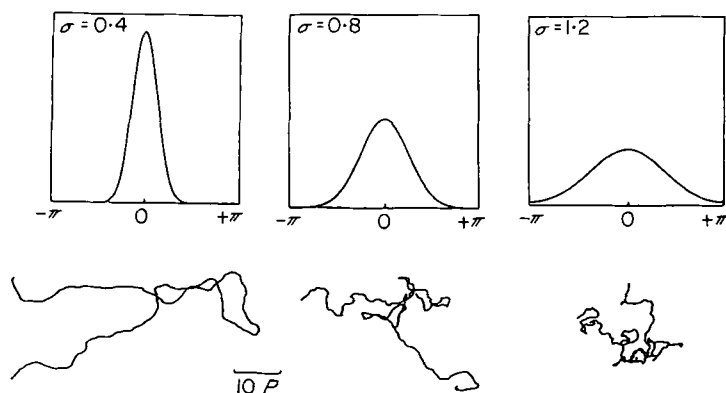

FIG. 2. Examples of 200-step paths obtained with various values of the standard deviation σ of the distribution of changes of direction between successive steps. The parent distribution is represented above each path. P = length of a step.

3. Definition of the Sinuosity

The aim of our study was to provide a means of expressing the sinuosity of animals' actual movements with a single, purely spatial index. Now, as we have just seen, the sinuosity of a path is determined both by the distribution of changes in direction and by the step length. When dealing with actual paths, however, the data recording generally involves a discretization with an arbitrary step length which influences the distribution of changes of direction obtained. It is therefore indispensable to quantify the function linking the step length, which depends on the data recording, to the observed distribution of changes of direction. The problem set by this function has not been dealt with by any of the previous authors, who have used correlated random walk models to analyse animals' movements, with the exception of Dunn (1983). For this purpose, let us consider a path which obeys our model: the step length is P, and the distribution of changes of direction is normal, centred on 0, with a standard deviation σ. This path can be rediscretized with a step with a constant length R different from P. The principle of this spatial rediscretization (which is obtained by a computer algorithm) is shown in Fig. 3: we look for the first point lying distance R away from the starting point of the original path; we then look for the next point lying distance R away from the first, and so on. By analysing the effect of the step length on the distribution of the changes of direction, it is then possible to define a reliable index of sinuosity, i.e. one which is independent of the step length (R) used in the rediscretization.
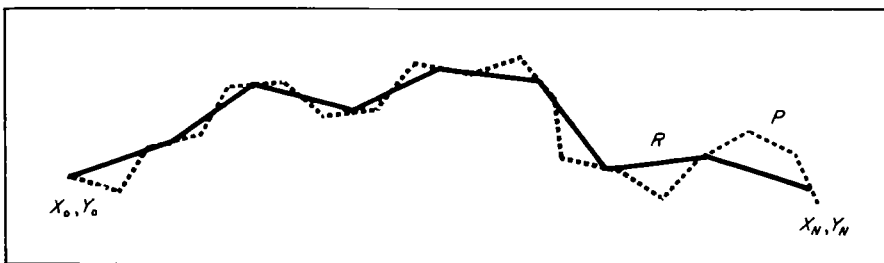

FIG. 3. Rediscretization of an N-step path (dotted line) with $R = 2P$. P: simulation step length; R: rediscretization step length.

Our approach to this analysis involves numerical simulations, since the algebraic approach seems to be too complex to be practicable. By using a pseudo-random Gaussian generator, it is possible to obtain continuous values from a normal distribution with a mean of 0 and a standard deviation σ (Bovet et al., 1986). Various values of σ were used. A path can then be simulated as follows: after each step with length P, the value of the change of direction (turning angle α_i) is determined by the pseudo-random Gaussian generator for a given value of σ, which is constant along the path. The animal then makes a step in the next direction, and so on. Technically, the simulation of a path with N steps consists of obtaining a sequence of $(N+1)$ points $(X_0, Y_0), (X_1, Y_1), \ldots, (X_N, Y_N)$ by an iterative procedure such

that:

$$\alpha_i \sim N(0, \sigma)$$

$$\theta_{i+1} = \theta_i + \alpha_i$$

$$X_{i+1} = X_i + P \cos \theta_{i+1}$$

$$Y_{i+1} = Y_i + P \sin \theta_{i+1}$$

where θ_i represents the direction of the ith step. The direction of the first step, θ_1, is chosen at random according to a uniform angular distribution by a pseudo-random uniform generator.

In this way, 500 paths each consisting of 1000 steps were simulated for each of the 12 values of σ adopted, ranging between 0·1 and 1·2 rad. We thus obtained 12 families of 500 paths, each characterized by a given value of σ. For reasons which will be explained below, no value of σ greater than 1·2 rad was used. These simulated paths were rediscretized successively with various values of step length R ranging between 0·6P and 10P. No rediscretization step length smaller than or equal to 0·5P was used, because this would have led to artefactual alignments of points. The turning angles obtained after rediscretization are expressed as lying between $-\pi$ and $+\pi$ radians (rad).

In each of the 12 families of path and for each value of R, we are dealing with 500 angular distributions. All these distributions show a mean approximately equal to 0 and a standard deviation (σ_R) which varies as an increasing function of the simulation standard deviation (σ) and of the ratio of the rediscretization step length over the simulation step length (R/P). For each family of paths, and for each value of R, we consider the distributions obtained to be samples taken from a parent distribution, with a null mean, and with a standard deviation σ_R^* estimated from the mean of the 500 standard deviations (σ_R) obtained. For each value of σ_R^* less than 1·2 rad, we observe that the shape of the distributions looks normal, and that σ_R^* is directly proportional both to the simulation standard deviation σ and to the square root of the ratio R/P (Fig. 4). This relation can easily be obtained when
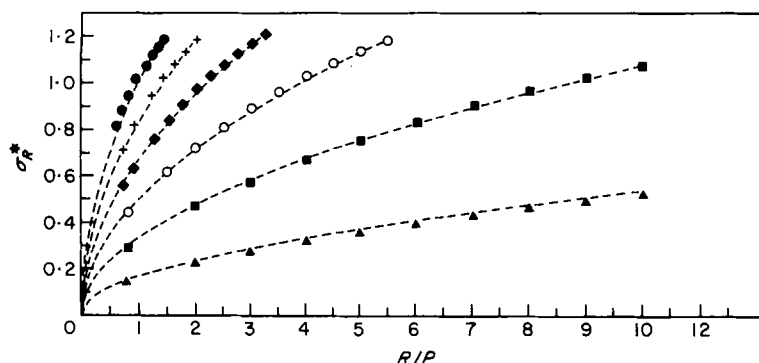

FIG. 4. Values of the standard deviation σ_R^* of the change of direction distributions obtained after rediscretization as a function of the ratio R/P for various values of the simulation standard deviation σ: ▲ 0·2; ■ 0·4; ○ 0·6; ◆ 0·8; + 1·0; ● 1·2. For clarity, only half of the computed values are shown in the figure.

adjusting the function $f = a . \sigma (R/P)^{1/2}$ to the values of σ_R^*, by the least square method. We then obtain: $a = 0.85$. The fact that this empirical value of 'a' differs from 1 is rather unexpected, since when $R/P = 1$, $\sigma_R = \sigma$ by definition. Actually, when R differs even very slightly from P (e.g., $R = 0.9P$ or $R = 1.1P$), the rediscretization introduces a smoothing of the path, which gives the value: $a = 0.85$.

In Fig. 4, the dotted curves were given this value of 'a'. It can be seen that these curves come very close to the observed values σ_R^*. In fact, the relative errors are always less than 5%, and, in most cases, less than 3%. We then have

$$\sigma_R^* = 0.85\sigma(R/P)^{1/2}.$$

Taking this formula and separating what belongs to the model (P and σ) from what has been introduced by the rediscretization (R and σ_R^*), we define "sinuosity" as follows

$$S^* = \sigma/\sqrt{P} = 1.18\sigma_R^*/\sqrt{R} \qquad (2)$$

expressed in rad $. u^{-1/2}$, where u is the unit of step length. S^* constitutes a reliable index since it can be used to characterize any family of paths, regardless of the rediscretization step length (R) used. Note that the first part of formula (2) is a theoretical expression for the sinuosity. This relation has also been established by Dunn (1983), whose definition of the rate of change of direction can be written σ^2/P, taking P to be the step duration in a constant velocity movement. The second part of formula (2) can be used to quantify the sinuosity of an actual animal's path by taking the observed distribution of changes of direction, after rediscretizing the path with a step length R. This method is based on the algorithm given in the appendix, which can easily be programmed on a computer. As a means of performing a purely spatial analysis of a path, our method seems preferable to that of Dunn (1983), which, on the one hand, involves the speed of movement, and on the other hand, relies on estimations of the observed diffusion: as we shall see below, in a correlated random walk, the diffusion is subject to very considerable random fluctuations.

Since each simulated path is generated by a probabilistic process, its computed sinuosity $S = 1.18\sigma_R/\sqrt{R}$ can be considered to be a random variable with the mean S^*. Its standard deviation, s.d.(S), can be estimated. In fact, since the angular distribution does not differ from a normal one, the standard deviation of σ_R is given by $\sigma_R^*/(2N_R)^{1/2}$, where N_R is the number of angular values after rediscretization. It follows immediately that: s.d.$(S) = S^*/(2N_R)^{1/2}$. The values of s.d.(S) obtained by simulation for each of the 12 families of 500 paths and for each value of R, come close to these theoretical values.

However, when paths are rediscretized with large values of R such that σ_R^* becomes larger than 1.2 rad, σ_R^* no longer increases proportionally to the square root of R and the sinuosity cannot be calculated. The distribution of the changes of direction then tends to become uniform, whatever the value of the simulation standard deviation σ used. It is not surprising that many animal paths which have not been recorded in sufficient detail (with too large distances between successive locations) approximately fit the random walk model. This provides no information

about the paths. It is also for these reasons that we did not take any σ values larger than 1·2 rad for our simulations.

4. Application to Data

In what follows, we distinguish between two types of data, depending on whether the path is of the continuous or the discrete type. Discrete paths have undergone a natural process of segmentation for behavioural reasons: for example, the path of a travelling animal can be broken due to its making periodical pauses, as was the case with the thrushes studied by Smith (1974a,b) and the foxes studied by MacDonald (1980), or because of some specific behaviour such as that of bees foraging for nectar from one inflorescence to another (Pyke, 1978a). In the case of continuous paths, any discretization is bound to be arbitrary because it is not based on any actual behavioural feature. Of course, some discretization of the paths is automatically introduced by the recording itself. This discretization leads to unequal step lengths which do not correspond to any biological parameter specific to the animal under study but result from a combination between the animal's velocity and the sampling frequency of the recording apparatus.

CONTINUOUS PATHS

Since the initial recording discretization is arbitrary, a rediscretization with a constant step length (R) makes it possible to give recorded paths a suitable form, which is independent of the recording apparatus and conforms to that of the paths described by the model (here the effect of the step length on the distribution of angles is known). It is then possible to determine the characteristics of the distribution of changes of direction. It must be ensured that this distribution does not differ significantly from a normal one centred on 0. Let us call σ_R the standard deviation of this distribution. On condition $0·1 \leq \sigma_R \leq 1·2$ rad, the sinuosity of the path can be estimated, substituting from equation (2), by:

$$S = 1·18\sigma_R/\sqrt{R}.$$

In recording animals' paths, it is of utmost importance to use the highest sampling frequency of which the recording system is capable. Too low a sampling frequency entails the need for such a large rediscretization step length that the distribution of changes of direction tends towards uniformity: the sinuosity of the path can thus no longer be calculated. Furthermore, the smaller the rediscretization step length, the larger the number of angular values, and the smaller the standard deviation of the sinuosity (s.d.$(S) = S/(2N_R)^{1/2}$), the more accurate the estimation of the sinuosity index. Note, however, that the size of the rediscretization step R chosen should not be shorter than half of the longest recorded step, so as to avoid artefactual alignments of points. Furthermore the rediscretization step must be large enough to prevent any correlation from emerging between successive changes of direction.

To illustrate the above considerations, a concrete example is given in Fig. 5a, which shows the central place foraging path of a *Serrastruma lujae* ant as recorded
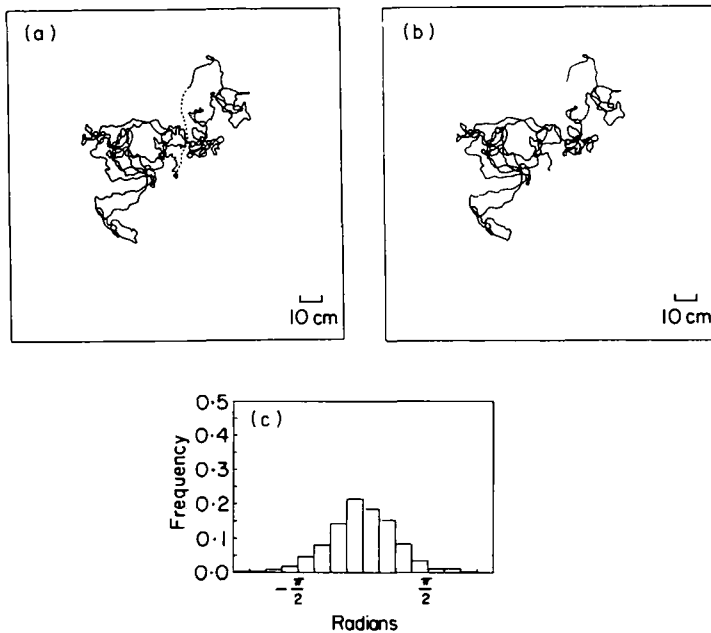
FIG. 5. (a) Foraging path of a *Serrastruma lujae* ant observed for 45 minutes. (b) The same path rediscretized with a step length $R = 1\cdot5$ cm. (c) Distribution of changes of direction corresponding to this rediscretization: $n = 664$, $m = -0\cdot04$ rad, $\sigma = 0\cdot82$ rad.

by A. Dejean in Central Africa in 1984. The small circle in the centre represents the nest entrance hole, the full line the ant's path before capturing an item of prey, and the dotted line its return path after capturing the prey. Here we shall take only the outward path: this is shown in Fig. 5b after rediscretization with a step-length of $1\cdot5$ cm. Let us check whether the distribution of changes of direction here is compatible with a normal distribution centred on 0, as stated by our model. Figure 5c gives the distribution of changes of direction corresponding to the rediscretized path in Fig. 5b. Kuiper's test (see Batschelet, 1981) shows that this distribution does not differ significantly from a normal distribution centred on 0 with a standard deviation equal to that found here, i.e. $\sigma_{1\cdot5} = 0\cdot82$ rad ($k = 1\cdot43$, $P > \cdot20$).

This confirms that we are justified in calculating the sinuosity of this path after rediscretization with the step-length $R = 1\cdot5$ cm. We then obtain:

$$S = 1\cdot18 * 0\cdot82/\sqrt{1\cdot5} = 0\cdot79 \text{ rad . cm}^{-1/2}.$$

Note that with $N_{1\cdot5} = 664$, one obtains s.d.$(S) = 0\cdot02$ rad . cm$^{-1/2}$. This means that the actual sinuosity lies within the 95% confidence interval $(0\cdot75-0\cdot83)$ rad . cm$^{-1/2}$.

DISCRETE PATHS

Some animals' movements are naturally discrete. Such animals choose their direction after each step and move straight in this direction up to the next choice

point. A rediscretization of this kind of path would lead to a loss of information because the step lengths are not arbitrary, but correspond to actual features of the animal's path.

Our model is still applicable in such cases, however, if we assume that the changes of direction made by the animal between successive steps with variable length P_i independently obey a normal law whereby the mean $= 0$ and standard deviation $0 \cdot 1 \leq \sigma \leq 1 \cdot 2$ rad. Indeed, it can be shown by the process of simulation and rediscretization presented in section 3, above, that the sinuosity of the path can be calculated—regardless of the step length distribution—by:

$$S = \sigma / \sqrt{m}(P) \tag{3}$$

where σ represents the standard deviation of observed changes of direction, and $m(P)$ the mean step length.

An example of discrete paths is given by Pyke (1978a) in his study on bumblebees (*Bombus flavifrons*) flying from one inflorescence to another to gather nectar. From this author's data it is possible to calculate the mean length of the bees' movements between flowers ($m(P) = 36 \cdot 7$ cm) and the standard deviation of the distribution of changes of direction ($\sigma = 1 \cdot 11$ rad). According to equation (3), this gives the sinuosity $S = 0 \cdot 18$ rad . $cm^{-1/2}$. Note that the sinuosity was obtained here with a group of animals, and not with a single animal as in the previous example.

5. Diffusion

An important property of animals' movements is their diffusion in the environment. This property has been studied by numerous authors, generally using random walk models (see review in Okubo, 1980). The diffusion is characterized by the probability distribution of the beeline distance D between the first and the last points of a path. With our model, it can be said intuitively that the greater the sinuosity of a path, the smaller its diffusion. This relation needs to be explained.

In a first order correlated random walk, the expected value of the square of the beeline distance $E(D^2)$ is given as a function of the step number N (Tchen, 1952; see also Barber & Ninham, 1970; Skellam, 1973; Hall, 1977; Okubo, 1980; Dunn, 1983) by:

$$E(D^2) = P^2(N(1+r)/(1-r) - 2r(1-r^N)/(1-r)^2)$$

where r, according to equation (1), expresses the correlation between the direction of successive steps with length P. When N is large, this equation can be reduced to

$$E(D^2) = N \cdot P^2(1+r)/(1-r). \tag{4}$$

Let us now determine the expected value $E(D)$ of the actual beeline distance D. Given that the distance D of an N-step path has two components, X_N and Y_N, on the X and Y axes respectively, one obtains:

$$D^2 = X_N^2 + Y_N^2.$$

Tchen (1952) has stated that when N is large, the two components X_N and Y_N are normally distributed and statistically independent. A correlated random walk model

does not lead to any preferential orientation in space, so one obtains:

$$E(X_N) = E(Y_N) = 0$$

$$\text{s.d.}(X_N) = \text{s.d.}(Y_N) = \delta.$$

From this, it follows that

$$E(X_N^2) = E(Y_N^2) = \delta^2.$$

We then obtain

$$E(D^2) = E(X_N^2) + E(Y_N^2) = 2\delta^2$$

or

$$\delta = (E(D^2)/2)^{1/2}.$$

Let $u = X_N/\delta$ and $v = Y_N/\delta$. Thus, u and v are two independent random variables distributed according to the normal law $N(0, 1)$. Then $d = D/\delta = (u^2 + v^2)^{1/2}$ is a random variable distributed according to a χ law with two degrees of freedom. The expected value of a χ law with n degrees of freedom is given by $\sqrt{2}\Gamma((n+1)/2)/\Gamma(n/2)$ with $\Gamma(x) = \int_0^\infty t^{x-1} \exp(-t)\, dt$. In particular, for $n = 2$, one obtains

$$E(d) = (\pi/2)^{1/2}.$$

From this, it follows that

$$E(D) = \delta E(d) = (\pi E(D^2)/4)^{1/2}$$

i.e., substituting from equation (4):

$$E(D) = P(0\cdot79 N(1+r)/(1-r))^{1/2}. \tag{5}$$

One might be tempted to use the beeline distance to estimate the sinuosity of the path. It is not a good index for this purpose, however, because it is too variable: the standard deviation of the distance is given by

$$\text{s.d.}(D) = (E(D^2) - E(D)^2)^{1/2} = 0\cdot52 E(D). \tag{6}$$

This means that the coefficient of variation of the beeline distance, $\text{s.d.}(D)/E(D)$, is greater than $1/2$ and does not decrease with increasing values of N. Let us compare this result with that obtained in section 3 in connection with our index of sinuosity S. There we had $\text{s.d.}(S) = E(S)/(2N_R)^{1/2}$, where N_R is the number of angles obtained after rediscretization. This means that the coefficient of variation of the sinuosity, $1/(2N_R)^{1/2}$, is bound to be lower than $1/2$ and that it decreases as N_R increases. This is because the distance D is calculated on the basis of only two points on the animal's path (the point of departure and the point of arrival), whereas the index S is based on all the points on the rediscretized path. Thus, in the example of an ant's foraging path given above (see Fig. 5), where we have $N_R = 664$, the coefficient

of variation of the sinuosity S is equal to 0·03, which is much less than 0·52 i.e. the value corresponding to the beeline distance D. This comparison between the coefficients of variation of D and S shows that S constitutes a much steadier index than any of those that can be calculated from D, such as the popular index of straightness D/L (Batschelet, 1981), where L is the total length of the path.

Equations (5) and (6) are general ones for any random walk with a correlation between the direction of successive steps, whatever the actual value r ($\neq 1$) of the correlation. In particular, they are still valid when r tends to 0 (original random walk model). In our model, where σ is less than 1·2 rad (i.e. $r \geq 0·5$), $2/\sigma$ constitutes a good approximation of the expression $((1+r)/(1-r))^{1/2}$. The beeline distance of a path with sinuosity S and length L ($L = N \cdot P$; with large N) is a random variable, the expected value and the standard deviation of which—from equations (2), (5) and (6)—are:

$$E(D) = 1·77\sqrt{L}/S \tag{7}$$

$$\text{s.d.}(D) = 0·92\sqrt{L}/S. \tag{8}$$

The results obtained by simulation for $E(D)$ and s.d.(D) come very close to the theoretical values. Figure 6 shows, for various sinuosity values, the mean distance $\bar{D}$ of the simulated correlated random walks vs. the path length L. The dotted lines were based on equation (7). Here one can see that the beeline distance is on average proportional to the square root of the path length and inversely proportional to its sinuosity.
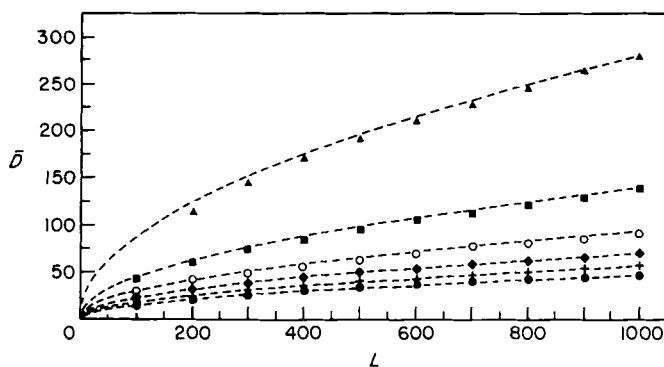

FIG. 6. Mean beeline distance $\bar{D}$ as a function of the length L and the sinuosity S of the paths. $\bar{D}$ and L are expressed in the unit of length u, and S in rad . $u^{-0·5}$. As in Fig. 4, only half of the computed values are shown in the figure. Values of S: ▲ 0·2, ■ 0·4, ○ 0·6, ◆ 0·8, +1·0, ● 1·2.

The diffusion process can be defined in purely spatial terms, depending only upon the path length and its sinuosity. It is often more interesting, however, to think of it as a time-dependent dynamic process. This is the classical approach to the diffusion based on physical models. A dynamic expression of the diffusion can always be

obtained by taking into account the mean velocity: so that the path length can be replaced by the duration of the movement multiplied by its mean velocity. In this expression, the mean and the standard deviation of the beeline distance are proportional to the square root of the duration of the movement and inversely proportional to the sinuosity of the path.

6. Discussion

The main advantage of our model is the fact that it can be used to describe any erratic path by means of a single numerical index. This is an extremely valuable feature since, with this index, it is possible to compare various paths in quantitative terms, from the point of view of their sinuosity. It could be used in particular to compare the sinuosity of paths taken by animals of the same species moving in environments which differ, for example, with regard to the density of prey, or to compare the sinuosity of different species inhabiting the same environment.

Our model is more than just a simple means of measuring the sinuosity of paths under investigation, however it is also a means of establishing the statistical properties of these paths, from which predictions can be made as to their fitness. This model can thus be used to directly establish the diffusion expectancy of paths having a given sinuosity. At present, the diffusion expectancy of a path is an extremely instructive parameter from the adaptive point of view and can be encountered in a wide range of biological problems, such as that of the pollination of flowers by insects.

In the framework of Optimal Foraging Theory, assumptions can be made about search paths when antagonistic constraints affecting sinuosity arise. This happens when the animal, in order to increase its search efficiency, needs to both reduce its beeline distance by increasing the sinuosity of its path, and reduce the likelihood of overlap by decreasing it. In particular, optimal sinuosity can be determined for an animal searching for a prey item from a central place and homing straight back after finding it (Bovet, 1983).

Hitherto, we have been assuming that the animals moved with a constant sinuosity throughout their foraging bouts, because we were dealing with foraging search paths in a homogeneous stochastic environment, i.e. one where the prey items are randomly distributed (according to Poisson's law). Improvements to our model can be made, in which the path sinuosity is regulated by certain environmental features. For instance, an animal may increase its sinuosity when it encounters a prey item. This behaviour leads the animal to an area-restricted search (Krebs, 1973) and thus decreases its beeline distance. Hence it becomes more efficient when foraging in a patchy environment. Knoppien & Reddingius (1985) have shown that a similar effect can be produced by reducing the animal's velocity. Another case where an improvement can be made is that of an animal living in an environment with a stimulus gradient which it uses to orientate itself. This kinokinetic behaviour can be described by a model in which the sinuosity varies as a function of the increase or decrease in the stimulus intensity during the movement (Bovet, 1984; Bovet & Benhamou, 1984; Bovet et al., 1986). The effects of behavioural factors of this kind on sinuosity can be taken into account in devising probabilistic cybernetic models.

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APPENDIX

Computing Changes of Direction After Rediscretization

The original sequence of points $(x_0, y_0), (x_1, y_1), \ldots, (x_n, y_n)$ must first be replaced by a new sequence of points $(X_0, Y_0), (X_1, Y_1), \ldots, (X_N, Y_N)$ such that, for any I, one has $((X_I - X_{I-1})^2 + (Y_I - Y_{I-1})^2)^{1/2} = R$, R being the rediscretization step length. For this purpose, one starts with $(X_0 = x_0, Y_0 = y_0)$. Then $(X_1, Y_1), \ldots, (X_N, Y_N)$ are computed using the following iterative procedure. Let us call $((x_{j-1}, y_{j-1}), (x_j, y_j))$ the segment on which the point (X_I, Y_I) lies; the distance

$$D = ((X_I - x_i)^2 + (Y_I - y_i)^2)^{1/2} \quad \text{for } i = j, j+1, \ldots$$

is then computed until obtaining $D > R$. Let us call k the first value of i with which this condition holds. The point (X_{I+1}, Y_{I+1}) will be on the segment $((x_{k-1}, y_{k-1}), (x_k, y_k))$. Let us call

$$U = (X_I - x_{k-1}) \cdot \cos \lambda + (Y_I - y_{k-1}) \cdot \sin \lambda$$

and

$$V = (Y_I - y_{k-1}) \cdot \cos \lambda - (X_I - x_{k-1}) \cdot \sin \lambda$$

where

$$\lambda = \text{arctg} \, ((y_k - y_{k-1})/(x_k - x_{k-1})) + a \cdot \pi,$$

with $a = 0$ when $(x_k - x_{k-1}) > 0$ and $a = 1$ otherwise. U and V are the co-ordinates of the point (X_I, Y_I) in the following reference system: U-axis deviates from X-axis with the angle λ; it originates from (x_{k-1}, y_{k-1}) and runs through (x_k, y_k); V-axis is orthogonal to U-axis and has the same origin. The distance between (X_{I+1}, Y_{I+1}) and (x_{k-1}, y_{k-1}) is then computed:

$$H = U + (R^2 - V^2)^{1/2}.$$

Finally, we obtain:

$$X_{I+1} = H \cdot \cos \lambda + x_{k-1}$$

$$Y_{I+1} = H \cdot \sin \lambda + y_{k-1}.$$

The orientation of the segment $((X_I, Y_I), (X_{I+1}, Y_{I+1}))$ is then computed

$$\theta_{I+1} = \text{arctg} \, (Y_{I+1} - Y_I)/(X_{I+1} - X_I)) + a \cdot \pi,$$

with $a = 0$ when $(X_{I+1} - X_I) > 0$ and $a = 1$ otherwise. The value of the change of direction at the point (X_I, Y_I) is then given by

$$\alpha_I = \theta_{I+1} - \theta_I$$

which must lie between $-\pi$ and $+\pi$ before the angular distribution can be determined.