SHORT COMMUNICATION

**M. Challet · V. Fourcassié · S. Blanco · R. Fournier ·
G. Theraulaz · C. Jost**

A new test of random walks in heterogeneous environments

Abstract Environmental heterogeneities can change animal movement in two different manners. First, they can modify movement characteristics (move lengths or turning angles), in which case the movement remains of the diffusive kind. Second, they can bias displacement towards a particular direction in which case it becomes non-diffusive. We propose in this paper a simple method that only requires computing the mean length of a sample of trajectories in some bounded area to distinguish between these two kinds of movement. We show through simulations that the method allows to detect the presence of heterogeneities that orient animal movement. We apply it to experimental trajectories of *Messor sancta* ants engaged in corpse aggregation to show that their displacement is oriented at the contact of the formed corpse piles and that their trajectories become non-diffusive.

Introduction

The analysis of animal pathways is often important to better understand the dynamics of the spread of a population of organisms in a given environment (Turchin 1991; Parrish and Hamner 1997; Turchin 1998). The individual movement of an animal can be approximated in a discrete fashion by a series of straight moves separated by turning angles and it is often described as a correlated random walk (Kareiva and Shigesada 1983; Root and Kareiva 1984; Bovet and

M. Challet · V. Fourcassié · G. Theraulaz · C. Jost (✉)
Centre de Recherches sur la Cognition Animale,
CNRS UMR 5169, Université Paul Sabatier,
Bât 4R3, 118 route de Narbonne,
31062 Toulouse Cedex 4, France
e-mail: jost@cict.fr
Tel.: +33-5-61556437
Fax: +33-5-61556154

S. Blanco · R. Fournier
Laboratoire d'énergétique, Université Paul Sabatier,
118 route de Narbonne,
31062 Toulouse Cedex 4, France

Benhamou 1988; McCulloch and Cain 1989; Turchin 1991). The term "correlated" refers to the fact that, due to the bilateral symmetry of most organisms, animals have a strong tendency to move forward and thus that the direction of travel at step i depends on the direction at step i-1. In homogeneous environments, Kareiva and Shigesada (1983) have proposed a model, based on the evolution of the net-squared displacement of organisms, to test the correlated random walk assumption (see also McCulloch and Cain 1989; Wu et al. 2000): given the observed mean turning angles and move lengths of the organisms under study, the expected net-squared displacement as a function of the number of consecutive moves for a correlated random walk is compared with the observed mean net-squared displacement computed for the population. If the observed curve departs too much from the expected curve, this should indicate some directional bias in the movement of the organisms and the correlated random walk assumption should be rejected (see Crist and McMahon 1991, for an example of application in ants). This method is also used to test whether the spread of a population in an homogeneous environment obeys a diffusion process.

In nature, animals generally move in environments characterized by the presence of many spatial heterogeneities at different scales. These heterogeneities can affect the diffusive character of their movement and influence it in several manners. First, they can locally modify their movement characteristics: move lengths can shorten and/or turning angles increase when animals engage in area-restricted search (Benhamou and Bovet 1989; Bell 1990) after encountering e.g. a patch of high-resource density (Root and Kareiva 1984; Crist et al. 1992), a patch of high humidity (Dejean and Benhamou 1993; Durou et al. 2001), or when they experience a decrease in ambient temperature (Challet et al., in press). Such modulated movements still remain diffusive. Second, environmental heterogeneities can also bias their movement towards a particular direction: animals can use guidelines such as forest boundaries or pheromone trails, or they can be attracted by several types of stimuli, e.g. odours, sound or light (Fraenkel and Gunn 1961; Schöne 1984). Such a modification can render movement non-diffusive.

In this paper we provide a test that allows to distinguish between diffusive (with modification of movement characteristics only) and non-diffusive (with oriented displacement) correlated random walks in heterogeneous environments. It is of particular interest when the experimenter does not easily perceive spatial environmental heterogeneities. The test is based on a recent result from physics that shows that the average length of a random walk trajectory in a bounded area is independent of its characteristics and depends only on the geometry of the area (Blanco and Fournier 2003). This result is valid for many types of random walks, in particular the ones characterized by an exponential move length distribution and a symmetric distribution of the turning angles around zero (i.e. an equal probability to turn right or left), which applies to the movements of most organisms and that will be used in this paper. We first illustrate the method through a series of simulations and then apply it to a sample of ant pathways collected in a heterogeneous environment.

Material and methods

Simulations

To represent heterogeneous environments, the simulated trajectories were all inscribed in a rectangular area (40×10 arbitrary distance units) divided into two adjacent zones within which movement characteristics remain constant (Fig. 1a and b). These trajectories were correlated random walks with a symmetric turning angle distribution around zero (with mean cosine=0.5) and a negative exponential distribution of move lengths with parameter λ corresponding to the rate of directional change. $1/\lambda$ thus represents the mean distance travelled before a directional change occurs.

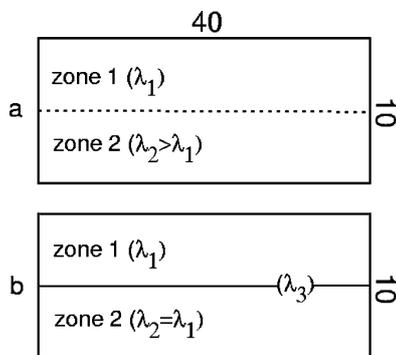The simulations were run in two conditions. In the first condition (Fig.1a), the distribution of move lengths of the

Fig. 1 The simulated trajectories are inscribed in a rectangular area (40 × 10 arbitrary units) divided into two adjacent zones, each with its own mean move length $1/\lambda$ and a symmetric distribution of turning angles around zero. (**a**) In the first condition, the mean distance travelled before changing direction is lower in zone 2 than in zone 1 > $1/\lambda_1$ ($1/\lambda_2$) (**b**) In the second condition, this distance is the same in the two zones but the organisms have a tendency to follow the boundary between the two zones (straight line) and to leave it after travelling on average a distance $1/\lambda_3$

organisms varies in space: the mean distance travelled before a change of direction is higher in zone 1 than in zone 2 ($1/\lambda_1 = 2$ unit distance for zone 1 and $1/\lambda_2 = 1$ unit distance for zone 2 in the first set of simulations, $1/\lambda_1=10$ and $1/\lambda_2 = 1$ in the second set of simulations). Two hundred trajectories were simulated for each set of simulations, which corresponds to a reasonable sample size in biological experiments. In the second condition (Fig.1b), a directional bias is introduced in the movement of the organisms: the mean distance travelled before the change in direction is identical in the two zones ($1/\lambda_1=1/\lambda_2=1$), but when the organisms reach the common boundary of the two zones, they walk along this boundary for an average distance $1/\lambda_3$ that varies from 0 (no following behaviour) to 5 units distance. Two hundred simulations were run for each value of $1/\lambda_3$. In both conditions the organisms in the simulations enter the rectangular area at a random location on its perimeter with an angle of incidence distributed according to a cosine function (highest probability for angles perpendicular to the area perimeter, see Blanco and Fournier 2003 for details).

Path analyses

According to Blanco and Fournier (2003) the expected trajectory length L_{th} from any entry point into a bounded area to the first exit point is given by the formula:

$$L_{th} = \frac{\pi S}{P},\qquad(1)$$

where S is the surface and P the perimeter of the studied area. For the area we used in our simulations we get $L_{th}=12.57$.

To test this prediction, we simply need to compute the arithmetic mean length $<L>$ of N trajectories of length L across the area:

$$<L> = \frac{\sum_{i=1}^{N} L_i}{N}\qquad(2)$$

If the values of $<L_1>$ (for the simulations in the first condition) and $<L_2>$ (for the simulations in the second condition) are significantly different from L_{th}, then the trajectories do not correspond to a diffusion process. The variance of L_{th} has to be computed by simulations, no theoretical results are available yet.

All simulations and statistical analyses were done with the R statistical software (http://www.r-project.org/, version 1.7, the R code can be requested from the authors).

Results and discussion

In the first condition, when only the average distance travelled before changing direction varied between the two adjacent zones, we found that the average lengths of
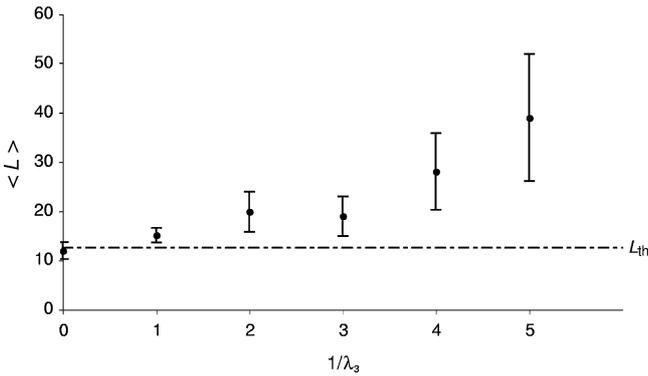
Fig. 2 Mean length of simulated trajectories $<L_2>$ as a function of the average length travelled by the organisms along the zone boundary $(1/\lambda_3)$. The bars represent the 95% confidence interval of the mean $(n=200)$ to illustrate the power of the test

the 200 simulated paths did not differ significantly from the theoretical value $L_{th} = 12.57$ predicted by Eq. (1): $<L_1>=12.63\pm0.87$ (mean$\pm$SE, SD = 12.3) and $<L_1> = 12.27\pm0.71$ (mean$\pm$SE, SD = 10.1), for $1/\lambda_1 = 2$ and $1/\lambda_1=10$, respectively. This illustrates that the trajectories of the organisms can still be considered as the result of a diffusion process, in spite of the fact that the characteristics of the trajectories in the second set of simulations were very different between the two zones.

In the second condition, when the organisms had a tendency to follow the boundary between the two zones, we found that the average length of the simulated paths $<L_2>$ increased with increasing $1/\lambda_3$ (Fig. 2). Two hundred trajectories were sufficient to detect the difference from $L_{th} = 12.57$ for values of $1/\lambda_3 \geq 1$ (95% CI do not overlap the prediction), thus confirming that following a trail or edge renders the movement non-diffusive.

Illustration of the method with a biological example

The tendency of ants to evacuate dead corpses from their nest and to pile them at some distance from it to form "cemeteries" is well known to myrmecologists (Hölldobler and Wilson 1990). In the framework of another research project (Theraulaz et al. 2002) we have successfully modelled the dynamics of corpse aggregation in the seed harvesting ant *Messor sancta* as a one-dimensional reaction–diffusion process. Our aim is now to extend our model in two dimensions. As a prerequisite however we needed to know whether the movement of ants engaged in the formation of cemeteries could be considered as diffusive. We were interested, in particular, to apply our method to test whether ants had a tendency to follow the periphery of corpse piles.

The trajectories of single ants moving on and around a circular pile of 2000 dead corpses artificially assembled (radius of the pile: $r_1 = 4$cm) in an arena were videotaped and digitized as a series of Cartesian coordinates once every second by using a a GrafBar GP-7 sonic digitizer (Science Accessories Corporation,

Southport, USA). To avoid any directional bias in the movement of the ants, the arena was surrounded by white sheets that homogenized the light and masked any potential visual landmarks. First, 97 trajectories of ants walking on the corpse pile were recorded. Second, 66 trajectories of ants walking within a zone encompassing the corpse pile and an annular ring of 1cm width (radius of the zone: $r_2= 5$cm) were recorded. Equation (1) predicts the average length of the trajectories to be $L_{th, r1} = 6.28$cm and $L_{th, r2} =7.85$cm, for ants walking on the corpse pile and within the zone encompassing the corpse pile and the annular ring, respectively.

The mean length of the trajectories was compared with a *t*-test to the theoretical values computed from Eq. (1). Note that path length distributions on a closed surface can be highly skewed, but the size and skewness of our samples allowed nevertheless to use a *t*-test (Boos and Hughes-Oliver 2000). We found that the mean length of the trajectories on the corpse pile, $<L>_{r1}=6.74$cm, did not differ significantly from the prediction $L_{th,r1} =6.28$cm ($t=1.24$, df=96, p=0.22). The movements of ants on the corpse pile had thus a diffusive character. For the trajectories of ants moving within the zone encompassing the corpse pile and the annular ring however, the observed mean length $<L>_{r2} =5.33$cm was significantly different from the prediction $L_{th,r2} =7.85$cm (t=2.96, df=65, p=0.004). The movement of ants thus ceases to be diffusive when a peripheral zone is considered around the corpse pile. Indeed, additional examination of the trajectories shows that ants have a strong tendency to follow the periphery of the pile when entering into contact with the latter.

Conclusion

The method presented here can be used to distinguish between diffusive and non-diffusive movements and it is particularly adapted to the detection of directional biases that could be induced by spatial heterogeneities. It complements that proposed by Kareiva and Shigesada (1983) but it is the only one that can be used in particular situations commonly encountered in experiments. First, our method can be applied to short trajectories inscribed within a small area and made of a low number of moves. Second, it works even if the characteristics of the trajectories (e.g. mean move length) vary in space as in the first condition of our simulations, in which case the linear relationship between the net-squared displacement and time (Kareiva and Shigesada 1983) would not hold. In conclusion, the method we propose in this paper is able to detect non-diffusive movements on the basis of the sole calculation of the lengths of a sample of trajectories in a bounded area.

References

Bell WJ (1990) Searching behavior patterns in insects. Annu Rev Entomol 35:447–467

Benhamou S, Bovet P (1989) How animals use their environment: a new look of kinesis. Anim Behav 38:375–383

Blanco S, Fournier R (2003) An invariance property of diffusive random walks. Europhys Lett 61:168–173

Boos DD, Hughes-Oliver JM (2000) How large does n have to be for Z and t intervals? Am Statistician 54:121–128

Bovet P, Benhamou S (1988) Spatial analysis of animals' movements using a correlated random walk model. J Theoretical Biol 131:419–433

Challet M, Jost C, Grimal A, Lluc J, Theraulaz G (in press) How temperature influences displacements and corpse aggregation behaviours in the ant *Messor sancta*. Insectes Sociaux

Crist TO, McMahon JA (1991) Individual foraging components of harvester ants: movement patterns and seed patch fidelity. Insectes Sociaux 38:379–396

Crist TO, Guertin DS, Wiens JA, Milne BT (1992) Animal movement in heterogeneous landscapes: An experiment with *Eleodes* beetles in shortgrass prairie. Funct Ecol 6:536–544

Dejean A, Benhamou S (1993) Orientation and foraging movements in a patchy environment by the ant *Serrastruma lujae* (Formicidae—Myrmicinae). Behav Process 30:233–244

Durou S, Lauga J, Dejean A (2001) Intensive food searching in humid patches: adaptation of a Myrmicine ant to environmental constraints. Behaviour 138:251–259

Fraenkel GS, Gunn DL (1961) The orientation of animals. Dover Publications, New York

Hölldobler B, Wilson EO (1990) The Ants. The Belknap press of Harvard University Press, Cambridge

Kareiva PM, Shigesada N (1983) Analyzing insect movement as a correlated random walk. Oecologia 56:234–238

McCulloch CE, Cain ML (1989) Analyzing discrete movement data as a correlated random walk. Ecology 70:383–388

Parrish JK, Hamner WM (1997) Animal groups in three dimensions. Cambridge University press, Cambridge

Root BR, Kareiva PM (1984) The search for resources by cabbage butterflies (*Pierisrapae*): Ecological consequences and adaptative significance of Markovian movements in a patchy environment. Ecology 65:147–165

Schöne H (1984) Spatial orientation. Princeton University Press, Guildford, Surrey

Theraulaz G, Bonabeau E, Nicolis SC, Solé RV, Fourcassié V, Blanco S, Fournier R, Joly JL, Fernandez P, Grimal A, Dalle P, Deneubourg JL (2002). Spatial patterns in ants colonies. Proc Natl Acad Sci USA 15:9645–9649

Turchin P (1991) Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. Ecology 72:1253–1266

Turchin P (1998) Quantitative analysis of movement: Measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, Massachusetts

Wu H, Li B, Springer TA, Neill WH (2000) Modelling animal movement as a persistent random walk in two dimensions: expected magnitude of net displacement. Ecol Model 132:115–124

ERRATUM

M. Challet · V. Fourcassié · S. Blanco · R. Fournier ·
G. Theraulaz · C. Jost

A new test of random walks in heterogeneous environments

Published online: 20 October 2005
© Springer-Verlag 2005

Unfortunately, Fig. 1 has been printed with errors, hence the correct version is given here.
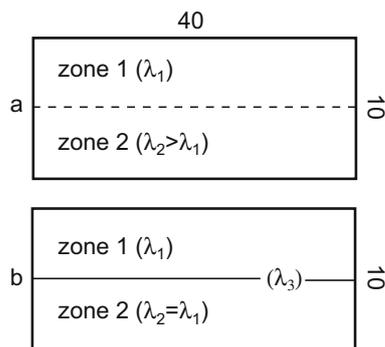

Fig. 1 The simulated trajectories are inscribed in a rectangular area (40×10 arbitrary units) divided into two adjacent zones, each with its own mean move length $1/\lambda$ and a symmetric distribution of turning angles around zero. **a** In the first condition, the mean distance travelled before changing direction is lower in zone 2 than in zone 1 ($1/\lambda_1 > 1/\lambda_2$). **b** In the second condition, this distance is the same in the two zones, but the organisms have a tendency to follow the boundary between the two zones (*straight line*) and to leave it after travelling on average distance $1/\lambda_3$

M. Challet · V. Fourcassié · G. Theraulaz · C. Jost (✉)
Centre de Recherches sur la Cognition Animale,
CNRS UMR 5169, Université Paul Sabatier,
Bât 4R3, 118 route de Narbonne,
31062 Toulouse Cedex 9, France
e-mail: jost@cict.fr
Tel.: +33-5-61556437
Fax: +33-5-61556154

S. Blanco · R. Fournier
Laboratoire d'énergétique, Université Paul Sabatier,
118 route de Narbonne,
31062 Toulouse Cedex 4, France