Ecological Complexity 22 (2015) 86–92

Contents lists available at ScienceDirect

Ecological Complexity

journal homepage: www.elsevier.com/locate/ecocom

Original Research Article

Statistical mechanics of animal movement: Animals's decision-making can result in superdiffusive spread

Paulo F.C. Tilles [1], Sergei V. Petrovskii [*]

Department of Mathematics, University of Leicester, Leicester LE1 7RH, UK

A R T I C L E I N F O

Article history:
Received 21 January 2015
Received in revised form 17 February 2015
Accepted 17 February 2015
Available online 13 March 2015

Keywords:
Composite random walk
Environmental stochasticity
Fat tails
Movement behavior
Anomalous diffusion

A B S T R A C T

Peculiarities of individual animal movement and dispersal have been a major focus of recent research as they are thought to hold the key to the understanding of many phenomena in spatial ecology. Superdiffusive spread and long-distance dispersal have been observed in different species but the underlying biological mechanisms often remain obscure. In particular, the effect of relevant animal behavior has been largely unaddressed. In this paper, we show that a superdiffusive spread can arise naturally as a result of animal behavioral response to small-scale environmental stochasticity. Surprisingly, the emerging fast spread does not require the standard assumption about the fat tail of the dispersal kernel.

1. Introduction

Statistical mechanics of ecological processes have been identified as a promising direction of research that can create a unifying framework for many diverse applications (Levin, 2012). Animal dispersal is a key factor that underlies a variety of phenomena in spatial ecology (Bullock et al., 2002; Clobert et al., 2001) where application of concepts and tools of statistical mechanics has proved to be especially useful and insightful (Bartumeus et al., 2008; Viswanathan et al., 2011; Lewis et al., 2013). A major focus of research has been on understanding of how far individual animals can travel over a given time or, equivalently, how fast the mean squared displacement (MSD), $\delta^2(t) = \langle(\mathbf{r}(t) - \mathbf{r}(0))^2\rangle$ (where $\mathbf{r}(t)$ is the position of the animal at time t), can grow with time (Viswanathan et al., 2011, 1996). Whilst $\delta^2 \sim t$ corresponds to the standard diffusion and to the Brownian motion as the underlying stochastic process (Chorin and Hald, 2006; Kareiva, 1983; Turchin, 1998), the case $\delta^2 \sim t^\gamma$ with $\gamma > 1$ is conventionally referred to as the "superdiffusion" and is linked to Levy flights and Levy walks (Viswanathan et al., 2011; Klafter and Sokolov, 2005; Shlesinger et al., 1993).

In field observations or laboratory experiments, for technical reasons the position of individual animal(s) is usually recorded not continuously but with a finite time-resolution or time-step, say Δt (Viswanathan et al., 1996; Turchin, 1998; Mashanova et al., 2010). In the corresponding time-discrete framework, individual animal movement is described by the dispersal kernel $\rho(l)$ that gives the probability distribution of the distance l traveled by an animal during the time Δt. In the case of Δt being sufficiently small, the distance l can be regarded as a step made along the movement path over the given time. The product $\rho(l)dl$ gives the probability that an individual released at $t = 0$ will, after the time Δt, be found at a distance between l and $l + dl$ from the point of its release. A 'thin-tailed' dispersal kernel with the rate of decay at large l being exponential or faster corresponds to the Brownian motion; a 'fat-tailed' kernel with the power-law rate of decay at large distances, $\rho(l) \sim l^{-1-\mu}$ where $0 < \mu < 2$, is associated with the Levy flight (Viswanathan et al., 2011, 1996; Shlesinger et al., 1993; Sornette, 2004). In the intermediate case $\mu \geq 2$, the random walk slowly converges to the Brownian motion in the multi-step limit. Because of the lower rate of decay, a fingerprint of the Levy flight is a much higher frequency of the long-distance travel compared to the Brownian motion. Understanding of the fat-tailed/long-distance dispersal is important as it may significantly affect the rate of biological invasions (Kot et al., 1996; Shigesada and Kawasaki, 2002), the rate of pathogens spread (Brockmann et al., 2006), conditions of species persistence in fragmented landscapes (Baguette, 2003; Levin et al., 1984), etc. This is one of the reasons

---

[*] Corresponding author. Tel.: +44 116 252 3916; fax: +44 116 252 3915.
E-mail address: sp237@le.ac.uk (S.V. Petrovskii).

[1] On leave from: Instituto de Física de Sao Carlos, Universidade de Sao Paulo, Sao Carlos, Brazil.

http://dx.doi.org/10.1016/j.ecocom.2015.02.006
1476-945X/

why patterns of individual animal movement have been a focus of considerable interest (Benhamou, 2007; Codling et al., 2008; Edwards et al., 2007; Viswanathan et al., 2008; Reynolds, 2010; Turchin, 1996).

Fat-tailed kernels correspond to animal spread at a much faster rate than that predicted by the Brownian motion; the fatter the kernel, the faster is the growth of the MSD with time. A question arises here as to whether quantification of the rate of spread in terms of the MSD can still be meaningful for the Levy flights because, in a strict mathematical sense, kernels with the power-law decay do not possess a finite variance for $\mu \le 2$. There are, however, several ways to overcome this difficulty. For instance, one can introduce a finite characteristic speed of the travel, thus turning Levy flights to Levy walks (Shlesinger et al., 1993, 1987). A similar approach is based on exclusion of very large steps (hence effectively truncating the kernel at large distances) as the probability of their occurrence in any finite sample is extremely small (Sornette, 2004). Alternatively, one can consider a pseudo-MSD by calculating the moment of a lower (fractional) order (Viswanathan et al., 2011). Interestingly, all these approaches result in the same relation between the exponent γ in the rate of spread and the exponent μ in the rate of decay in the dispersal kernel, namely, $\gamma = 2/\mu$ (where $0 < \mu \le 2$). Correspondingly, the case $\mu = 1$ results in the ballistic-like spread with $\delta^2 \sim t^2$ and the case $\mu = 2/3$ results in a turbulent-like spread with $\delta^2 \sim t^3$. Evaluating the value of γ is therefore a universal way to quantify the rate of animal dispersal across a broad range of different movement patterns.

There is now significant evidence (Ramos-Fernández et al., 2004; Reynolds, 2012; Reynolds et al., 2013, 2007; Sims et al., 2008) that animals of different taxa may employ the superdiffusive movement pattern; however, little has been done to understand the mechanisms behind the Levy walks. This evokes the classical problem of revealing the process resulting in a given pattern (Levin, 2012, 1992). The existing theoretical framework is largely descriptive and is mostly focused on the properties of the step length distribution, e.g. arguing whether it is fat-tailed or not. The animal itself is often considered quite schematically, i.e. as a particle or even as a "robot" (Gautestad, 2013), simply assuming that, at certain moments of time, the next travel distance is somehow drawn from a given distribution.

Meanwhile, one important factor that distinguish animals from particles is behavior. Particles cannot make decisions but animals can (Rankin, 2002; Sinn et al., 2001). Behavior has indeed been identified as an essential factor affecting the movement pattern (Reynolds, 2012; Owen-Smith et al., 2010) but its impact on animal movement and dispersal has only been considered on large spatial and temporal scales, e.g. as corresponds to animal movement over a large foraging area. The main objective of this paper is to show that animal behavior exhibited on a much smaller scale of a single step along the path is a crucial factor that can affect the movement pattern. Specifically, we are going to show that, in a noisy environment, animal's basic reaction to external clues can turn the movement into superdiffusion.

Our arguments are as follows. During their movement, animals receive cues or 'signals' from their environment. Such cues can be of visual, auditory or olfactory origin. Through these cues, animals become aware of the presence of predators, of the availability of food (e.g. by perceiving an odor), of the presence of a mating partner (e.g. by detecting female pheromones), etc. The cues therefore bring information that is vital for the animal's well-being. The animals respond to the cues by making decisions about their movement; in their conceptual paper, Nathan et al. (2008) referred to this situation as "why move". Exact timing of the cues is difficult or perhaps even impossible to determine though, as it is affected by many different factors, some of them being either unknown or having a large uncertainty, or being stochastic. For instance, the smell is brought in with the air flow which is often turbulent. Correspondingly, we assume that the timing of the cues' perception can be regarded as random. Altogether, the cues can be regarded as a small-scale environmental stochasticity.

The standard approach to animal movement (Viswanathan et al., 2011; Turchin, 1998; Codling et al., 2008) consider animals making 'steps' along their movement path so that, at certain moments of time, the length of the next step is drawn from a given probability distribution. It apparently implies that the moving animal makes a decision with regard to where it wants to be after a time Δt, i.e. about its next position on the movement path. Correspondingly, the animal has to possess certain cognitive powers enabling it to plan its future actions or future state (such as its next location), at least over a certain relatively small period of time. However, here we argue that this is hardly feasible. While some mammals like apes or dogs may be capable of some elementary planning, the existence of similarly complex behaviors in lower animals (e.g. invertebrates) is highly unlikely. To the best of our knowledge there is no evidence that invertebrates can exhibit a reaction more complicated than an immediate response to a stimulus. On the other hand, the response to a stimulus through an involuntary reflex action resulting in a muscle contraction is a common physiological property of animals (Purves et al., 2004). We therefore assume that the decision taken by the animal as a response to the environmental cues has *an immediate effect*. Specifically, we assume that the decision is implemented by changing the magnitude of the force that the animal exerts in order to maintain its movement.

In the next section, we translate the above assumptions into a model and undertake a comprehensive study of the properties of the corresponding movement pattern.

2. Model and results

The animal movement as a response to external signals or cues may be formally described as a sequence of bouts. A bout ends (and the next bout starts) when the animal receives a cue from the environment. We are considering the situation when the signals are distributed in time homogeneously (in the statistical sense) so that the mean number of cues received during a time interval depends only on its duration, say t, but not on its starting moment. With the further assumption that for a small t the probability of receiving more than one cue is negligible, we have a situation that coincides precisely with the one resulting in the Poisson distribution. If we denote by ω the mean number of cues per unit time, then the probability that an animal receives at least one cue during the time t is

$$P_t(\omega) = 1 - e^{-\omega t}. \tag{1}$$

Here parameter ω accounts for the properties of environmental noise but it is also related to the biology of the dispersing animals, because it depends on their perception threshold.

Eq. (1) gives the probability that the movement will be interrupted during the time interval $(0, t)$, i.e. that the duration of the given bout will not exceed t. In order to obtain the probability density of bout duration, we need to differentiate Eq. (1) with respect to t, which results in the following exponential distribution:

$$\psi(t) = \omega e^{-\omega t}. \tag{2}$$

Correspondingly, $\langle t\rangle = 1/\omega$ is the characteristic time between the subsequent cues.

Upon receiving a cue, the animal changes its movement by exerting a force, i.e. by changing its acceleration. It is reasonable to expect that the animal tries to optimize its energy expense, and hence it is only accelerating for a certain time, say τ (which can be