

Conclusions

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Concluding remarks

In principle, random walk models are rough, first-order approximations to the pattern of animal movement. In this context, they might fail providing insight on the causes of the type of movement or dispersal of organisms. Basically they represent statistical characterizations of movement. The statistical features of Lévy flights and Lévy walks, i.e., intermittence, scale-invariance and super-diffusion, reproduce the statistical properties observed in the movement of organisms at large-scales. This is true both at the individual and at the population level. However, such properties not always involve Lévy-stable distributions. For example, intermittence (*sensu lato*) is a property intrinsic to any random walk model, not only the Lévy class, because all random walks are *discrete* step models of movement. Although this, the properties of Lévy processes are based, precisely, in the way intermittence (commonly related to changes of direction) and displacement are combined while moving. In other type of random walks (based on Gaussian statistics), these combinations do not generate new properties at the large-scales.

Further, another type of Markovian stochastic processes named fractional Brownian motions (Mandelbrot, 1977, 1982; Feder, 1988) can lead also to anomalous diffusion although based on a Gaussian statistics of move lengths (see Technical Appendices, Appendix B). For these reasons, the study of animal movement and dispersal as Lévy processes may be considered an extension of the existing knowledge on these issues. However, if we assume that different mathematical formulations of random walks may reflect different biological mechanisms involved in animal movement, then differences between Lévy processes and other stochastic processes may not be just a methodological issue. Instead, these differences may be

caused by different biological adaptations of organisms and populations to different ecological situations or scales.

In fractional Brownian motions, long-run correlations (scale-invariance) are obtained by particular time-scaling properties of the variance of displacements (see Feder (1988)). It is difficult to think on any biological mechanism directly responsible of such kind of scaling. Therefore, on the basis of fractional Brownian models we may assume that scale-invariance is an emergent property derived from the complexity of animal movement behavior. In contrast, Lévy statistics can be easily obtained by a simple and direct mechanism: the execution of *scale-invariant episodic reorientations* on the move. Once provided a certain degree of directional persistence during displacements, the statistical features generated by reorienting the movement with no characteristic time scales are really robust. In animal movement, directional persistence is guaranteed during displacements either by bilateral symmetry, short-range correlations originated from “local” scanning mechanisms, or certain short-memory processes (note that if large-memory processes are involved, random search assumptions are violated). In the case of dispersal, such fractal-time episodic reorientations should be related to the spatial pattern of the deposition sequence of propagules. The propagules may be produced by one or many focus.

Having identified episodic reorientations as a key element in the “organization” of optimal stochastic searches, the issue is the possible existence of selection pressures relying on some essential properties of stochastic processes at either behavioral or physiological levels of organisms. Indeed, chance is a powerful force that biologists are just beginning to understand (Peterson, 1998; Denny & Gaines, 2002). An evolutionary perspective is central in order to establish cause-effect mechanisms between the fractal nature of large-scale animal movement patterns and the stochastic properties of searching processes.

9.1 Some considerations for future experimental works

9.1.1 On the discretization procedures of animal movement data

When modelling animal movements by means of random walks, the modeler may have two main goals: i) to reproduce with the highest accuracy the movement path, and ii) to reproduce with the highest accuracy the movement statistics of turning angles and move lengths.

The main objective of the standard experimental discretization procedures of animals' path is trying to minimize the loss of information of the path recorded by the animal. Further, the discretization of the animal's path into move lengths assume that animal movement is mainly a continuous process unless evident stops are incorporated (Turchin, 1998). By assuming animal movement as continuous, it is intrinsically accepted the discretization introduced by any random walk method is artifactual. Moreover, the stochastic components derived from this "artifactual" discretization procedure (i.e., the resulting distributions of move lengths and turning angles) are believed to account for all those mechanistic processes that cannot be considered in the model for the sake of simplicity. Indeed, much of what we accept as stochastic in a biological model may well be deterministic given sufficient understanding of the mechanisms involved. This is illustrated by examples provided by the study of behavioral patterns in ant colonies (Solé et al., 1993). However, this fact does not imply that stochastic mechanisms do not exist in animal movement (Denny & Gaines, 2002). Moreover, other kind of punctuations in the movement different from stops, such as reorientation leaps, behavioral characteristic interruptions, etc. may not be so evident to direct observation, or may be evident on long time scales.

If we assume that the movement is continuous when it is not, and apply standard discretization procedures to reproduce with the maximum fidelity the movement path, we may screen the real statistics of the movement (the one based on the real discretization). Thus, it is very important to observe the animal while moving, and to previously identify whether or not the animal incorporates "reorientation leaps" or behavioral interruptions. If so, we must concentrate on obtaining the statistics of such punctuations which reflect the real discretization of the movement, and thus, the real statistics of move lengths and turning angles.

Thus, in large-scale (spatial or temporal) animal movement studies it is more appropriate to assume as a working hypothesis that animal movement is discrete (for large scales this is a very reasonable principle) and to account for the statistics of the interruptions, rather than getting a detailed record of the animal path.

9.1.2 On the evaluation of random search scenarios

Although there are pretty appealing animal movement data in the scientific literature, the search context is usually not well parameterized or even overlooked. To study possible adaptive mechanisms to random search strategies, the contextualization of available animal movement data is fun-

damental. In addition to the movement of the searcher, our models suggested that the consideration of other parameters is required for scaling the search scenario properly when designing an experiment (depending on the animal studied, this information may be more or less difficult to obtain):

- Type of encounter dynamics: non-destructive or destructive.
- Spatial distribution (e.g., degree of patchiness) and density of targets.
- Dynamics of recovery of targets after visits (only in non-destructive searches).
- Type of movement and velocity of targets (if mobile).
- Detection distances of searcher (necessary to compute the mean free path)

To turn to a behavioral ecology at the landscape-scale (Lima & Zollner, 1996), the acquisition of information not only regarding the animal movement, but also regarding the whole search scenario is essential.

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Conclusions

Animal movement and dispersal strategies have been described as Lévy processes. The effects of the statistical properties of Lévy walk and Lévy flight models have been analyzed in different contexts. The causes of such statistical features have been suggested on the basis of empirical observation. Finally, the effect of dispersal ranges on metapopulation extinction thresholds has been explored. In the following paragraphs, an outline of the main conclusions reached is provided

Part I: Lévy walks and encounter rates

Chapter 3:

- In a one dimensional model, Lévy walks confer a significant advantage for increasing encounter rates (in relation to Brownian motion) when the searcher is larger or moves rapidly relative to the target, and when the target density is low. Brownian motion is valid at high density scenarios.
- If the targets show super-diffusive movement (i.e., Lévy targets), encounter rates are governed by relative searcher to target velocities rather than relative searcher to target sizes.

Chapter 4:

- The properties of Lévy walk models (i.e., scale-invariance and super-diffusivity) are also relevant for encounter rates in spatial systems

of two- and three- dimensions, and for both destructive and non-destructive dynamics. Nevertheless, the higher is the dimension of the system, the weaker is the effect of the movement statistical properties in relation to encounter rate fluctuations (as it is predicted by mean field theory).

- In certain conditions, encounter rate fluctuations may be shaped by the diffusive properties generated by the trajectories of the interacting particles (organisms) rather than by physical aspects related to them such as velocity or size. In particular, encounter rates are more sensitive to changes in super-diffusivity at low target densities and/or low spatial dimensionalities.
- Adaptive responses of living organisms to control the statistical properties of their movement and/or to control the dimensionality of their spatial explorations are suggested.

Part II: Lévy walks as adaptive search strategies

Chapter 5:

- Flight time intervals of the dinoflagellate *Oxyrrhis marina* switched from an exponential to an inverse square power-law distribution when the prey *Rhodomonas* sp. decreased in abundance. Concomitantly, amplitude and frequency of the short-term helical path increased. The biological mechanism related to the change in the statistical properties of movement was identified as the “reorientation leaps” produced by transient arrests of the longitudinal flagellum beat.
- The generality of the mechanism involved, suggest helical Lévy walks as a wide random search strategy for microzooplankton.

Chapter 6:

- Lévy walk statistical properties (i.e., scale-invariance and super-diffusivity) allow higher efficiency in random search scenarios (destructive and non-destructive) compared to correlated random walks. The latter models can only introduce scale-finite correlations in the movement, that can be interpreted as the by-product of locally scanning mechanisms.
- Lévy walk properties are robust to any behavioral mechanism providing short-range correlations in the walk. Thus, specific biological

mechanisms related to how animals punctuate their movement with sudden reorientations in a random search would be sufficient to sustain Lévy walk properties.

- Relying on the experimental results on *O. marina* and the results of numerical simulations (quantifying encounter rate variation, and comparing Lévy walks to correlated random walks) we propose the hypothesis that some animals may have evolved the ability of performing Lévy walks as adaptive strategies in order to face search uncertainties.

Part III: Lévy-dispersal kernels and dispersal ranges

Chapter 7:

- Barro Colorado Island low-canopy maps of rainforest understory habitats, involve a percolation phenomena at a critical height of approximately 13 meters. Species living in microenvironments occurring at canopy heights below this critical height $h_c \approx 13m$ can only experience landscapes with disconnected habitat patches (i.e. fragmented habitat landscapes), while those species capable of living also above h_c will experience a fully connected landscape of suitable microenvironmental conditions.
- Below and above h_c different optimal Lévy-dispersal strategies emerged (low and high Lévy indexes, respectively). In general, optimal Lévy-dispersal strategies mainly depended on the connectivity of habitat patches and not on the quantity of habitat. Different Lévy-dispersal strategies may imply different sensitiveness of species to habitat loss and habitat fragmentation processes in the rainforest.

Chapter 8:

- In a metapopulation context, increasingly lower dispersal capacities shifted the extinction thresholds to lower values of habitat loss, and increased transient times to metapopulation-dynamic equilibrium (when dynamics is far from the extinction threshold).
- Depending on the degree of clumpiness in the dispersal process, the habitat lost *within* the dispersal domain had quantitative relevance in the equilibrium values of patch occupancy (high dispersal capacities) or not (low dispersal capacities).

- We outlined three closed-form analytical solutions. The first one for the transient time duration of metapopulations when mean-field assumptions are appropriate. The second one expresses equilibrium patch occupancy in terms of metapopulation extinction/colonization rates, habitat loss and dispersal range. And the third one relates critical habitat destruction values for metapopulation extinction to metapopulation extinction/colonization rates and dispersal ranges.