

Lévy Processes in Animal Movement and Dispersal

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Introduction

The solid ecological theory we should expect for the future generations, should bring together in a natural and easy way, the experimented naturalists intuition to the most telling conceptual abstraction. There is a necessary and urgent need to establish a conceptual bridge between the so-called autoecology (Begon et al., 1988), the ecology of individuals and populations, and the systemic view of ecological processes (Margalef, 1977, 1980, 1991). This bridge can only be established by thinking that such different perspectives, not only are complementary, but are basically the same thing.

Ecosystems are complex systems in which spatiotemporal patterns at higher levels emerge from localized interactions and selection processes acting at lower levels. Two fundamental aspects focus at present investigation: the degree to which system-level properties emerge from local, disperse and variate evolutionary contexts, and the degree to which those local processes are influenced and shaped by the effect of the continued functioning and change of ecosystems (Levin, 1998).

Animal movement and dispersal are major drivers of spatiotemporal patterns in ecosystems. Questions about animal movement and dispersal in ecology have been difficult to answer for two principal reasons. First, quantifying the precise distributions of populations interacting in time and space has been difficult. Recent technological advances have to some extent removed this barrier and will keep doing it in the future. Second, and currently perhaps more profoundly limiting, is the lack of concepts and/or technical tools for analyzing the feedbacks between macroscopic ecosystem properties and its fundamental units that are subject to selection. An evolutionary perspective and the blending of insights from behavioral ecol-

ogy (Bell, 1991; Krebs & Davis, 1993), landscape ecology (Hansson et al., 1995), and spatial ecology (Okubo, 1980; Tilman & Kareiva, 1997; Bascompte & Solé, 1998) is essential. In particular, the understanding of the evolutionary component of large-scale and long-term properties of animal movement and dispersal (therein large-scale properties of animal movement) will establish useful links across scales, from individual to ecosystems and backwards.

From an applied perspective, a poor understanding of large-scale properties of animal movement has negative consequences in practical management and conservation decisions, such as assessing potential biodiversity impacts of habitat fragmentation, designing exploitation and management strategies for fragmented populations, future planning of reserve networks, reintroduction of key species, etc. This is so because large-scale properties of movement are essential to quantify and predict many relevant ecological processes at the individual (e.g., home ranging, site fidelity, foraging, etc.), the population (e.g., metapopulations persistence, invasion spreading, etc.), the community (e.g., community assemblage, species coexistence, etc.), and the ecosystem level (e.g., ecosystem rate limitations, etc.).

2.1 Large-scale animal movement and the necessity of chance

Previous studies have stated that large-scale properties of animal movements involve two characteristic traits: i) **scale-invariance**: fractal and multifractal patterns in movement paths, and fractal dispersal processes (e.g., Fitt & McCartney (1986); Aylor & Ferrandino (1989); Kot et al. (1996); Bascompte & Vilà (1997); Seuront et al. (2004), and ii) **intermittence**: movement interruptions or active discretization of displacements due to behavioral or physiological mechanisms (Harnos et al., 2000; Kramer & McLaughlin, 2001). Fractal methods have been used to analyze both animal movement and intermittence (Dicke & Burrough, 1988; Cole, 1995; Nams, 1996; Bascompte & Vilà, 1997; Harnos et al., 2000; Schmitt & Seuront, 2001; Seuront et al., 2004). These methods highlight self-affine properties (i.e., statistical properties that are maintained across several scales) in animal paths and animal movement interruptions (see Feder (1988) for a useful review on fractals). However, no clear explanatory framework exists for scale-invariant phenomena in animal movement. Therefore, in ecology, it is common to consider fractals just in terms of their applicability as statistical descriptors, which may be powerful or criticable depending on

the authors (Frontier, 1987; Sugihara & May, 1990; Johnson et al., 1995; Turchin, 1996). Further, the benefits of intermittent locomotion remains a controversial issue which is mainly discussed in energetical terms (O'Brien et al., 1990; Kramer & McLaughlin, 2001), but no consideration is done on its statistical effects on the resulting large-scale movement. Overall, no full understanding of the role of intermittent locomotion or scale-invariance in large-scale animal displacements has been achieved yet.

Another important unsolved problem from a landscape-behavioral perspective concerns the inherent stochasticity involved in many animal large-scale/long-term search displacements and its possible adaptive value (Lima & Zollner, 1996). Several authors have explicitly addressed the possible role of randomness in animal movement and dispersal at the landscape-level by means of field experiments (Zollner & Lima, 1997, 1999a; Bullock et al., 2002). These empirical studies provide two key results: First, the ever-presence of large-scale movements in natural populations (Lima & Zollner, 1996; Bullock et al., 2002), and second the limited perceptual capacity at landscape-level by some animals under common ecological conditions (Zollner & Lima, 1997, 1999a). Moreover, environmental fluctuations in ecosystems increase the unpredictability in resource availability throughout time. Thus, environmental stochasticity together with inevitable biological constraints could introduce randomness in many relevant ecological contexts: foraging, mating, dispersal, habitat colonization, etc. Consequently, adaptive behaviors to randomness may have had an important role in animal survival, and in potentially constraining spatiotemporal ecosystem processes and patterns.

So far, in the context of animal movement and dispersal, scale-invariant phenomena, intermittence, and randomness have been studied in isolation but never synthesized into a coherent ecological and evolutionary framework, which is the goal of this thesis. Part of the problem is related to the fact that **pre-encounter constrains** (i.e., constrains due to search strategies, diffusive behaviors, encounter statistics) are commonly not explicitly considered, neither at the individual or at population-level scales. However, when large scales are considered, we should expect pre-encounter constrains to be important in the overall energetic balance of organisms' ecological interactions, and in global rate limitations of populations. There are several historical reasons why pre-encounter constrains have been understated in ecological interactions. On the one hand, short and medium-scaled experimental designs of classical behavioral ecology and optimal foraging theory (Krebs & Davis, 1993) biased the study of ecological interactions to the study of post-encounter behavioral mechanisms and costs (e.g., pursuit, capture, handling, or digestive processing) rather than pre-

encounter ones. On the other hand, the development of spatially explicit approaches in theoretical ecology have mainly focused in the relationship between *local* interactions (i.e., short-ranged animal movement and dispersal) and macroscopic spatiotemporal patterns (Tilman & Kareiva, 1997; Bascompte & Solé, 1997; Dieckmann et al., 2000). Thus, although the incorporation of space in theoretical approaches has allowed new insights in ecological dynamics, large-scale pre-encounter processes are still not thought as potential drivers of ecosystems' spatiotemporal dynamics.

The ecological and evolutionary approaches to foraging are strongly tied to scale and conceptual biases. A whole picture of the problem is thus necessarily associated to considering the problem as a multiscale phenomenon. Different questions and different answers might be expected to emerge as we move from one scale to another. How animals behave (and eventually evolve) under spatiotemporal constraints and co-evolve with other members of their biota is strongly influenced by the physical world and its statistical features (Figure 2.1).

A wide spectrum of spatial and temporal scales can be considered in principle, influencing both the problems that can be properly analysed and the approximations used. Post-encounter events are likely to be most relevant at the small scales, while pre-encounter events should be mainly understood as tied to larger scales. Optimization processes influencing each component are thus expected to be also scale-dependent. When considering post- and pre-encounter tradeoffs, they are likely to be related to mechanical and stochastic-like optimization processes. The overall fitness of an ecological interaction would require to considering an appropriate weighted sum of both. Concerning conceptual biases, classical theories of ecological interactions (such as behavioral ecology and optimal foraging theory) emphasize the role of post-encounter processes in relation to pre-encounter ones at short and intermediate scales. In contrast, the framework taken in this thesis, hereafter the Lévy framework (LF), highlights the relevance of pre-encounter phenomena in relation to post-encounter ones, particularly while looking at the large-scale ecological interactions.

2.2 The concept of a random search

Establishing such a crude dichotomy in ecological interactions (i.e., pre- and post-encounter processes), allow us to discern between animal movement **before** the encounter and animal movement **after** the encounter. The selective pressures and the ecological constraints involved before and after the encounter are different. Therefore, distinct animal abilities could have

evolved (and may be identified) to overcome possible trade-offs in both scenarios.

Animal movement **before** the encounter can be related to search processes. Dispersal and diffusive processes in general, can be considered collective search processes. By a search we mean the process of looking for the presence of real or suspected objects of interest (i.e., food, mate, shelter, etc.). By definition, a search should always involve some degree of uncertainty on the properties of the searched object (named target). When there is no search uncertainty, because both spatial and temporal behavior of targets are known or because displacements are dictated by strong external cues, the resulting animal movement (although being a pre-encounter movement) cannot be considered a search. For example, most of the optimal foraging questions related to the traveling salesman problem (Lawler & Rinooy Kan, 1985; Anderson, 1983) should not be considered a search problem as we have defined it in the present thesis. In the classical traveling salesman problem, a salesman must choose the shortest path from his home office to all cities on his itinerary and back to his home office again. It represents an important class of combinatorial problems where the underlying geometry and number of target sites (in this case cities) is known from the very first beginning. Although animals indeed face such problems, the optimization is not on *trying to locate unknown sites* but on minimizing the path that intersects all of them. These kind of problems have nothing to do with **rules of search**, but instead with **energetic rules**. Foraging strategies related to the traveling salesman problem are common in animals with high cognitive abilities (i.e., memory, cognitive spatial maps, etc.) but should not be mistaken with a search *sensu strictu*. In Garber (1988), a good biological example of a traveling salesman problem can be found.

In any ecological interaction, the search component may be more or less relevant depending on the cognitive capacities of organisms, the predictability of its environment, and the scales involved in the interaction. The optimization of a search strategy, the **general search problem**, involves the selection of a specific set of “rules of search” that enhances the probability of finding unknown located items. According to the characteristics of the “rules of search” we can classify the *continuum* of search strategies in two main types: systematic and random searches. In systematic searches, the rules to optimally cover a given area are based on deterministic algorithms (i.e., fixed and organized plans), while in random searches these rules relay on stochastic processes. Systematic search strategies only work when some *a priori* relevant (although partial) information about target characteristics or locations at “landscape-level” is available. The

Archimedean spirals represent one of the most common systematic searching rules in homing behaviors (Bell, 1991; Turchin, 1998). In military research the usage of systematic search plans is a common topic (Haley & Stone, 1980; Champagne et al., 2003). In a random search situation, animals must attempt to move in such a way so as to optimize their chances of locating resources (i.e., food, mates, shelter, breeding habitats, etc.), covering certain regions by generating certain probabilistic effects. Overall, random search or random dispersal are not totally unstructured movements. Randomness does not imply an homogeneous coverage of the space explored: instead, *random* stands for *stochastic phenomena*, that is, patterns and processes derived from probabilistic laws.

So far, animal search rules relying on stochastic processes are not considered in behavioral evolution because it is assumed that sensorial or cognitive improvements override the need of random search in nature. Indeed, sensorial or memory-processing capabilities of organisms may suggest that chance is not relevant in animal movement (even if large-scales are considered). The common underlying reasoning of a biologist is that when organisms move to find each other or to find certain ecosystem conditions they always make use of sensorial or memory-processing capabilities. Indeed, different evolutionary pathways have provided organisms with different “tools” to avoid the necessity of searching at random (i.e. by creating more and better sensory cues, by improving high-level environmental information-processing mechanisms, by synchronizing temporal and spatial variations of the abundances of searchers and targets, etc.). However, it is not possible to completely neglect the existence of chance in nature. In particular it should be taken into account that: (i) in search processes at large-scales, a certain degree of uncertainty is unavoidable, and (ii) in such scenarios, the success of the search can, indeed, be improved by means of random search strategies.

2.3 Lévy processes: Lévy flight and Lévy walk models

Lévy processes are a class of stochastic processes based on the Lévy-stable distribution. Such processes are tightly related to anomalous diffusion and fractal statistics (see Technical Appendices B i C). Lévy processes are commonly described by Lévy flight random walk models.

A random walk model is a formalization of the intuitive idea of taking successive steps, each in a random direction. Thus, they are simple stochastic processes consisting of a discrete sequence of displacement

events (i.e., move lengths) separated by successive reorientation events (i.e., turning angles). The statistical distribution of displacement lengths on the one hand, and the statistical distribution of changes of direction (i.e., turning angles) on the other hand, describe the stochastic process. In particular, Lévy flight models involve a uniform distribution for the turning angles and a power-law distribution for the move lengths (i.e., the so-called flights). More precisely, Lévy flight models exploit a broad class of move or flight length (ℓ) distributions named Lévy-stable distributions (Mandelbrot, 1977, 1982; Shlesinger et al., 1995). These distributions have relevant statistical properties related to the Generalized Central Limit Theorem. Consider variables that follow the power law $P(\ell) = \ell^{-\mu}$. Sums of such variables converge to the Lévy stable distribution, with Lévy stable index $\alpha_L = \mu - 1$. If the power law exponent μ lies in the interval $1 \leq \mu < 3$, then the Lévy stable distribution of the sums of such variables also has a power-law form. For $\mu > 3$ the form of the Lévy stable distribution of the sums converges to a Gaussian distribution due to the Central Limit Theorem. Thus we recover Brownian motion for $\mu \geq 3$. The case of $\mu \leq 1$ does not correspond to normalizable distributions. In practice, we generate Lévy flights by sampling a power-law distribution (representing the tail of the Lévy-stable distributions) in the following way (inversion method, see Technical Appendix A)

$$\ell = \ell_0 u^{(1-\mu)^{-1}}. \quad (2.1)$$

Where u is a uniformly distributed random variable ($u \in (0, 1)$), ℓ_0 is the minimum flight length, and μ the power-law exponent.

Lévy flight models involve basically two types of random walks: the Lévy flights and the Lévy walks. The main difference between both types of random walks is that in Lévy flights, the flights are instantaneous (jumping-like movement) whatever the length of the move. In Lévy walks, the flights are “walked” through a constant (or variable) cruising speed, thus the time to reach the end of a flight depends on the length of the flight. Depending on the stochastic process we want to model we may use one or the other. When the time scales are large enough in comparison to the times involved in the move lengths or flights, then the process may be modeled as a Lévy flight. The distinction is important because the statistical spatiotemporal properties of both models are not the same. In space, a Lévy flight process represents the set of points where a Lévy walker changes direction (this set of points is named a Lévy dust (Mandelbrot, 1977)). In Lévy flights and Lévy walks (therein Lévy flight models), directional persistence intrinsically occurs because of the power-law distribution of move lengths (Fig. 2.2a,b). This feature explains the existence of ultra-long straight travels. As the

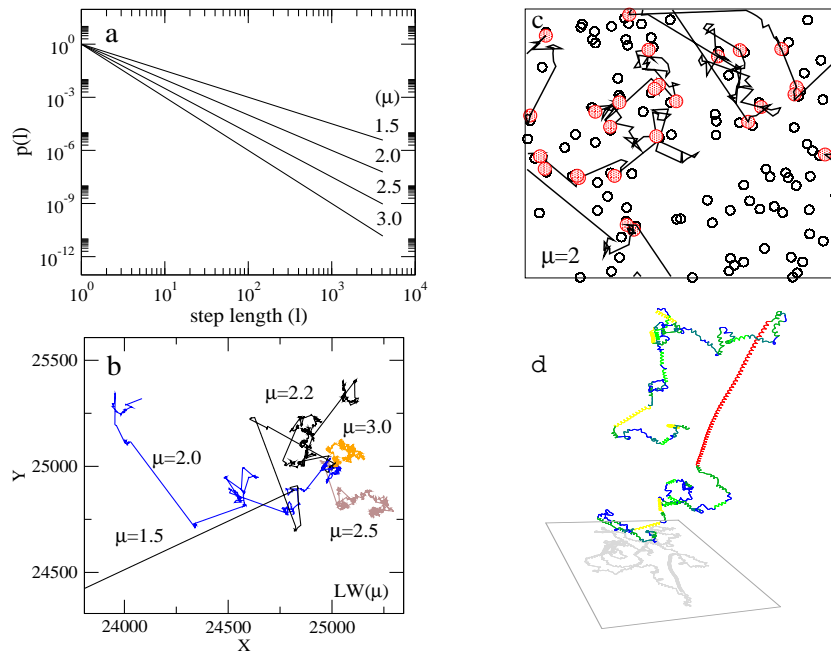


Figure 2.2: (a) Power-law probability distributions of move lengths (i.e., the so-called flights) obtained with different Lévy exponents (μ). (b) Visual aspect of Lévy flights generated with different Lévy exponents (μ). (c) Simulated path of a Lévy random searcher ($\mu = 2$) looking for non-mobile uniform distributed targets (white circles). Encountered targets are marked with filled circles. (d) A three-dimensional representation of an helical Lévy walk (HLW). Colors are related to step lengths. HLW have been observed in planktonic microorganisms (Bartumeus et al., 2003).

Lévy index μ diminishes the probability of long travels increases, thus the directional persistence in the movement also increases. Lévy flight models thus comprise a rich variety of paths ranging from Brownian motion ($\mu \geq 3$) to straight-line paths ($\mu \rightarrow 1$) (Fig. 2.2b). Fig. 2.2c, shows a simple search scenario occurring in some ecological interactions, and Fig. 2.2d shows a simulated complex search strategy observed in planktonic organisms (see Chapter 5).

Lévy flight models have their origin in the field of statistical mechanics and find wide application in physics (Shlesinger et al., 1995; Klafter et al., 1996; Weeks & Swinney, 1998) and natural sciences such as geology and biology (Metzler & Klafter, 2004). The first mention of a Lévy type of random walk as possible animal search strategies can be found in Shlesinger & Klafter (1986). After that, Lévy type of random walks were formally

considered by plankton ecologists (Levandowsky et al., 1988a,b; Klafter et al., 1989). Two pioneer studies related scale-invariant animal movement to optimal random search strategies (Viswanathan et al., 1996, 1999) by means of statistical physics methods and Lévy flights. Since then, Lévy flight models have been adjusted successfully to a wide range of animal movement data, involving large-spatial and long-term scales (Viswanathan et al., 1996; Levandowsky et al., 1997; Atkinson et al., 2002; Marell et al., 2002; Bartumeus et al., 2003; Ramos-Fernández et al., 2004; Austin et al., 2004). Animal paths turn out to be a combination of “walk clusters” with long travels between them. The heterogeneous multiscale-like sampling patterns generated by such paths are closely related to fractal geometries (Mandelbrot, 1977) and better modeled by random walks with Lévy statistics.

2.4 Why a statistical physics approach to animal movement?

Why should animal movement have anything to do with statistical physics? The central task of statistical physics is to deal with macroscopic phenomena that emerge from microscopic interactions among many individual components. Rather than “summing up” on a computer the behavior of all the individual components, we try to understand what we observe in terms of a collective phenomenon which obeys stochastic laws (Viswanathan, 1997). A statistical physics approach is expected to build up an ecological science more accordingly to the ecological reality by emphasizing: i) that ecosystems exhibit macroscopic regularities on the basis of similar statistical features arising because of many degrees of freedom (Pueyo, 2003), and ii) the recognition of the stochastic or probabilistic nature of ecological interactions (Alonso, 2003). The stochasticity may happen to appear as a consequence of large numbers or collections of entities or as a consequence of the scales considered.

Biological units are much more flexible and complex in behavior than molecules or inert particles. Thus, given the astonishing number of particularities of biological systems, a statistical physics approach could seem *a priori* too simple (Margalef, 1980, 1991). However, statistical physics offers a theoretical and technical framework which is companionable with a populational view of ecological phenomena from where a solid theory can be build up. This view is particularly straightforward applicable to animal movement issues.

2.5 Objectives and structure of the thesis

The general aim of this thesis was to develop a theoretical framework based on statistical physics (concepts and methods) and Lévy flight modeling to study the cause-effects of scale-invariance and intermittence in large-scale animal movements within the context of random search strategies. Our approach is novel not only because of the methodology used (based on statistical physics concepts and Lévy statistics), but also because it is founded on principles usually understated in animal ecology.

To achieve this objective we carried out three main studies, which define the main parts of the thesis:

2.5.1 Part I: Lévy walks and encounter rates

The objective of this part was to quantify the relevance of super-diffusive phenomena (a fundamental property of Lévy walks) in encounter rates. We carried out a series of numerical simulations in spatially explicit systems (1D, 2D, and 3D) where randomly moving particles (Lévy random walkers) must find each other. The simulations were meant to represent different encounter scenarios. The study was divided into two parts, corresponding to chapter 3 and 4.

Chapter 3 focused in the comparison between Brownian and Lévy types of motion in order to know in which situations one type of diffusion was better than the other in terms of encounter rates or search efficiency. The main goal of the study (based on 1D simulations) was to explore those scenarios where Lévy statistics were better than normal diffusion, and to show that Brownian strategies (i.e., normal diffusion) were also a valid movement strategy in certain scenarios.

Chapter 4. In this study we extended the 1D model of the previous chapter to explore the role of the type of motion in relation to encounter rates in 2D and 3D environments. The specific objective of the study was to quantify variations in encounter rates due to the super-diffusion properties provided by Lévy walking particles in spatially explicit systems. We showed that in certain scenarios encounter rate variation was shaped by the nature of the statistical properties of the movement of particles (organisms) rather than by physical aspects related to them such as size or velocity. In particular, super-diffusivity was relevant at low resource densities and/or low spatial dimensionality. We also showed how the movement trajectories of the searching particles could be optimized depending on the type of encounter dynamics (destructive or not), and the mobility of the target particles (i.e., velocity and super-diffusivity).

2.5.2 Part II: Lévy walks as adaptive search strategies

Once stated the potential relevance of super-diffusive phenomena in encounter rates, in this part, the main objective was to study the possible role of super-diffusive phenomena in real animal movement. In particular, we focused on *how* (Chapter 5) and *why* (Chapter 6) Lévy walk properties (i.e., scale-invariance, and intermittence) could be sustained by specific animal movement mechanisms.

Chapter 5. As far as we are aware, results included in this chapter are the first showing an organism capable to adjust its search statistics as a function of resource concentration. As resource decreased the heteroflagellate *Oxhyrris marina* changed from a Brownian to a Lévy search statistics. Changes in the helical behavior of the animal were also tracked and interpreted. The biological mechanism allowing the main statistical change was also identified: the transient arrests of the longitudinal flagellum provided a strong intermittent movement.

Chapter 6. Assuming random walk models as a necessary tool to understand how animals face environmental uncertainty, we analyzed the statistical differences between Lévy walks and another type of random walk models commonly used to fit animal movement data, the correlated random walks.

2.5.3 Part III: Lévy-dispersal kernels and dispersal ranges

This part intends to establish a link between the individual and the population scales, by modeling population dispersal strategies as Lévy processes. Dispersal kernels are key functions describing the dispersal process. In essence they are probability distribution functions describing the probability of finding a “propagule” at a given distance from the dispersal focus. At population scales, dispersal is modeled as Lévy flight processes, that is, scale-invariant displacements are performed instantaneously whatever the length of the move. Thus, only the set of visited points by a Lévy walker is computed. A Lévy-dispersal kernel is the one based on a Lévy distribution sampled as a Lévy flight process. Lévy-dispersal kernels can be interpreted as either individual large-scale movements (juvenile dispersal) or as random population-level colonization/invasion mechanisms. In chapter 7, we modeled (meta)population dispersal strategies by means of Lévy-dispersal kernels. And in chapter 8, we studied the role of dispersal capacity in the context of metapopulations and habitat fragmentation.

Chapter 7. A Lévy flight model was introduced to study the effect of dispersal or colonization processes in different “suitable-habitat” land-

scapes by rainforest plants or animals living in the understory (arboreal) or close-to-floor (terrestrial). A *population* dispersal efficiency was computed assuming that long-range dispersal involves a higher energetic cost or mortality risk than short-range dispersal. A unique optimal Lévy-dispersal kernel emerged for each different landscape configuration. Percolation effects, related to the connectivity of rainforest understory landscapes, influence optimal dispersal strategies.

Chapter 8. The first intention of this chapter was to study the role of Lévy-dispersal kernels in the context of metapopulation persistence and habitat fragmentation. Before that, we studied the role of dispersal ranges which is still an important gap of knowledge to be covered in metapopulation theory. The dispersal range in our model may be comparable to any empirical measure of dispersal such as mean dispersal distance or maximum dispersal capacity. The assumption of a characteristic dispersal range has nothing to do with scale-invariance. Thus, the spatially explicit model developed and the analytical solutions obtained, will be the basis for the implementation of Lévy-dispersal kernels in metapopulation models. Further, this will allow to explore the role of scale-invariance in metapopulation dispersal and extinction thresholds.

Two chapters of this thesis (chapter 3 and 5) have been already published. Other two (chapter 6 and 7) are accepted and going to be published within this year, 2005. The remaining ones (chapter 4 and 8) are still in preparation.

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