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## Review

# Lévy flights and superdiffusion in the context of biological encounters and random searches

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## Abstract

We review the general problem of random searches in the context of biological encounters. We analyze deterministic and stochastic aspects of searching in general and address the destructive and nondestructive cases specifically. We discuss the concepts of Lévy walks as adaptive strategies and explore possible examples. We also review Lévy searches in other media and spaces, including lattices and networks as opposed to continuous environments. We analyze empirical evidence supporting the Lévy flight foraging hypothesis, as well as the more general idea of superdiffusive foraging. We compare these hypothesis with alternative theories of random searches. Finally, we comment on several issues relevant to the practical application of models of Lévy and superdiffusive strategies to the general question of biological foraging.

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## 1. Biological encounters

Biological encounters typically involve a diffusive aspect, movement, as well as a reactive component, such as eating or mating. They thus represent a special case of reaction–diffusion processes with relevance not only in physics and chemistry, but also for understanding diverse phenomena in geology, biology, and even social sciences. Two-species reaction–diffusion models can be used to describe many ecological systems [1–9]. In particular, one important application relates to the general problem of regulating encounter rates between organisms. It represents a scientifically important issue of broad interest because living organisms need to interact with individuals of other species or of their own. To a large extent, biological interactions fall into two general categories: (i) inter-specific interaction, typically a trophic interaction between a consumer and a consumable, adopting the form of predation, parasite infection or mutual rewarding (e.g., flowers and pollinators); and (ii) interaction between individuals of the same species, e.g., mating or territorial competition. Thus, factors conditioning encounter rates between organisms are believed to play a crucial role in the ecological constraints important in the evolution of life [9]. These interactions can involve many potential factors and multiple ecological adaptive pathways [10].

Search strategies represent one of the most important factors that can modulate the rate of encounters. Hence, considering the above context, strategy choices can become essential in determining the fitness of a given species. This possibility is rendered further plausible because searches—and locomotion in general—require the expenditure of metabolic energy. Inefficient search could deplete energy reserves and lead to rates of encounters below a minimum acceptable threshold.

The framework of the search problem [9] distinguishes between two kinds of interacting organisms. They are either a “searcher”, e.g., forager, predator, parasite, pollinator, the active gender in the search activity involved in the mating process, or else they are a “target”, e.g., prey, food, the passive gender in the mating activity. Regarding the nature of the searching drive, in certain instances it can be guided almost entirely by external cues, either by the cognitive (memory) or detective (olfaction, vision, etc.) skills of the searcher. However, in many situations the movement is not-oriented [11], thus becoming in essence a stochastic process. Therefore, in such cases [12] (and even when a small deterministic component in the locomotion exists [12,13]) it is a random search that defines the final outcomes of biological encounters.

Generally, we can state the random search problem in terms of the following question: what is the most efficient strategy for searching randomly located objects whose exact locations are not known *a priori*? Performing efficient searches is not a trivial or straightforward task for a number of reasons. On the one hand, the searchers typically have a certain degree of “free will” to move and search according to their choice. By “free will” we refer not to contra-causal

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