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Part I

Introduction: Movement

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Empirical motivation for studying movement

1.1 How do organisms really move, and why?

Animals must move in order to eat and mate. They may also need to escape their predators. The details of their movement may depend on many factors such as climate, temperature, concentrations of pheromones, or the local density of other organisms (including humans) [172, 365]. Although such factors may affect the velocity, sinuosity, or specific trajectory taken, they do not change the primary reasons underlying the movement: the biological necessity of interactions or "encounters" with other organisms.

Given the ubiquity of moving organisms, a number of important questions arise naturally. For example, the priority in the order of driving factors that determine animal movement is not yet well understood and may even depend on the specific activity an organism is performing at a given time. However, there has been progress in understanding *how* organisms move, i.e., what patterns the trajectories follow. This is the main focus of this book. As an illustrative example, Figure 1.1 shows how spider monkeys move in the Yucatan Peninsula when they are allowed to roam freely. What factors determine the shape and the statistical properties of such trajectories? If we know the answers to these questions, we can venture beyond phenomenological descriptions and ask about causation: for a specific species of organism, why do the organisms actually move as they do? *Cui bono*,[1] i.e., what advantage or benefit do they gain from such behavior? Moreover, how did the specific biological mechanisms involved in generating the behavior evolve?

Such questions have prompted investigations in the new interdisciplinary subfield known as *movement ecology*. Because these questions are relevant in such research areas as random walk theory, stochastic processes, and anomalous

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[1] The Latin adage, suggestive of hidden motives, asks, "for whose benefit?"

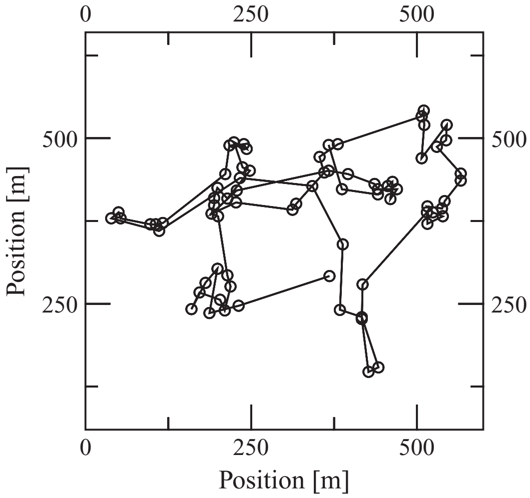


Figure 1.1 Movement patterns of spider monkeys in the Yucatan Peninsula, studied and reported by Ramos-Fernández *et al.* [292]. Patterns generated by moving animals share features with random walks studied by physicists. Compare the trajectory with those of humans, shown in Figure 7.1. The qualitative and quantitative similarities seen in the patterns of diverse animals might be because for all or most animals, the temporal and spatial organization of movement patterns serves to optimize physical quantities such as encounter rates and search efficiencies.

diffusion, they have also attracted the attention of physicists (see [18, 45, 49, 136, 159, 170, 232, 238, 247, 249, 254, 269, 274, 295, 303, 324, 340] appearing in a special issue [91] of *Journal of Physics A*, published in October 2009 and dedicated to the random search problem).

1.2 Biological encounters as a reaction-diffusion process

Biological encounters typically involve a diffusive (i.e., transport) component and a reactive (i.e., interaction) component, such as eating or mating. They thus represent a special case of reaction-diffusion processes. Typically, the diffusion process is linear in the sense that the superposition principle holds for the probability density functions of the random walkers.

In this case, the superposition principle guarantees that the probability of finding one of many random walkers at a specified position will equal the sum of the probabilities of finding each of them individually at that position. In more technical terms, the superposition principle guarantees the existence of random walk propagators.

However, for the superposition principle to hold, the random walkers must not interact among each other because such interactions will typically lead to nonlinear effects. (Noninteracting random walkers must always obey linear Fokker-Planck equations for the probability density function for the walkers [60, 193].) This linear approach to diffusion is remarkably useful. For example, Sparrevohn *et al.* [356] have found that thousands of fish released at a single point diffuse as random walkers once the movement of the water (i.e., advection) is taken into account.

In contrast, the reaction process necessarily involves one “particle” interacting with another, which can lead to nonlinear phenomena. Consider, for example, “reactions” represented by a predator wanting to eat its prey. Whereas two meals of prey may, in principle, be approximately twice as beneficial as a single meal, 10^3 meals are not approximately 10^3 times more beneficial. Reactions between predator and prey thus inherently deviate from linear behavior.

Eating, mating, and pollination represent distinct reactions. To a large extent, such biological interactions fall into two general categories. The first category includes interspecific interactions, typically, a trophic interaction between a consumer and a consumable, which can adopt the form of predation, parasite infection, or mutual rewarding (e.g., flowers and pollinators). The second category relates to interactions between individuals of the same species, e.g., mating or territorial competition. Two-species reaction-diffusion models (i.e., those with two reacting species) can thus be used to describe many ecological systems [19].

Most importantly, the diffusion (i.e., movement) that accompanies such diverse reactions remains the same, at least in a first approximation. Specifically, we do not expect the randomness seen in the movements to depend strongly on whether the organism is foraging for food or searching for a mate (or for something else), so long as such relevant search cues as the density of organisms remain comparable. This premise, to the extent that it remains approximately valid, justifies the study of the diffusive properties of biological encounter processes independently of the nature of the reactive processes. In this book, we focus mainly on the encounter rates between organisms; i.e., we address only the diffusive aspects of the underlying reaction-diffusion process.

This approach can be tailored to take into account new types of behaviors. For example, search for food may not necessarily be dominant. Avoidance of predators may also be important [115]. A predating organism may benefit from increased encounter rates with its prey, while simultaneously benefiting from lower encounter rates with its own predators.

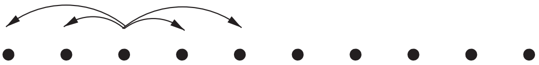
Factors conditioning encounter rates between organisms are believed to play a crucial role in the ecological constraints important in the evolution of life. These interactions can involve many potential factors and multiple ecological adaptive pathways. In this context, it is difficult to exaggerate the importance of movement. For example, locomotion and its detection go hand in hand, and therefore it has been hypothesized that the evolution of external bilateral sensory organs (e.g., eyes and ears) is partially due to the sudden increase in spatial complexity and patchiness of the marine odor landscape during the Ediacaran-Cambrian interval [289], about 542 million years ago. Foraging and search strategies represent one of the most important factors affecting encounter rates. We thus wonder whether they might even have influenced indirectly the evolution of the sensory apparatus.

We study encounter rates in a framework [19] that distinguishes between two kinds of interacting organisms. The organism is either a *searcher*, e.g., forager, predator, parasite, pollinator, or the active gender in the search activity involved in the mating process, or it is a *target*, e.g., prey, food, or the passive gender in the mating activity. Statistical models of foraging do not need to take into consideration the "microscopic" details of the process – they are essentially irrelevant to the averages. In this sense, it is important to recognize the limitations and applicability of such models. Despite this "coarse graining," these models lead to statistically robust results, precisely because they do not depend on the particular biological implementation of the search mechanisms. There is a long tradition in statistical physics in which apparently simple models lead to remarkably good agreement with experiment (e.g., the Ising model of ferromagnetic phase transitions). We will return to this topic in Section 2.5, and again in Part III.

The framework we adopt allows for considerable variation and easily generalizes to cover new cases. For example, the search could be guided almost entirely by external cues, either by the cognitive (memory) or detection (olfaction, vision, etc.) skills of the searcher, or the searches might not be oriented, thus effectively becoming stochastic processes. Even if the actual process is completely deterministic, a statistical approach is useful, or perhaps even necessary, if the environment is a disordered medium. Deterministic walks (e.g., the traveling salesman problem and the traveling tourist problem [358]) in random environments can appear indistinguishable from (genuinely stochastic) random walks, an issue we discuss in greater detail in Part IV.

One of the important questions in the random search problem can be stated as follows: what is the most efficient strategy for searching randomly located objects whose exact locations are not known *a priori*? The question is relevant because performing efficient searches is not trivial or straightforward. Typically, the searchers have a certain degree of "free will" as they move. (By free will, we refer not to contracausal behavior but rather to the degree of autonomy commonly seen in human beings and other organisms; see Section 14.3.) Nevertheless, organisms are at the same time subject to physical and biological constraints that restrict their modes of action. For example, a predator cannot search too long without finding food or it will perish. There is therefore an interplay between free will and constraints, with somewhat unpredictable consequences, including the possible emergence of complex behavior. Indeed, there is an inherent complexity and dynamical richness

(a) Short-range dispersal



(b) Long-range dispersal

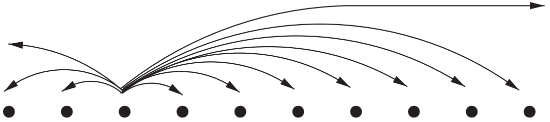


Figure 1.2 (a) The usual uncorrelated Brownian random walk assumes that the random walker can move only to neighboring sites within some limited range. In the long time limit, the mean squared displacement of such random walks grows linearly with time. (b) The behavior is qualitatively different for a random walker that can move to sites arbitrarily far away. In Lévy flights and walks, the probability of moving to a site ℓ units away decays algebraically, i.e., asymptotically, as a negative power of ℓ. The mean squared displacement for such *anomalous diffusion* (see Chapter 3) can grow superlinearly.

in the random search problem – and, by proxy, in other applications involving biological encounters.

1.3 Impact and scientific importance

Mathematical modeling of the movement and diffusion [265] of plant seeds and pollen, animals [378], micro-organisms [35], cells [230], organelles [160], and even genetic material [158] has played an important role in biology, ecology, and medicine [84]. Ignorance of how organisms actually move has motivated scientific research to a large extent, but there are a number of other reasons for the growing interest in the problem. Indeed, in a world in which we have an increasing awareness of how organisms, ecosystems, and society are intrinsically interconnected, the question of how and why organisms move becomes important even for political, economic, environmental, and health-related reasons.

Consider, for example, the seemingly "pedantic" question of how pollen diffuses [158]. The spread of organisms represents a particular case of the dispersal of genetic material. In this context, Shaw *et al.* [338] report that rapeseed pollen disperses in a manner inconsistent with exponential (e.g., Gaussian) models but consistent with the power laws associated with long-range dispersal. Figure 1.2 illustrates the difference between short- and long-range interactions. The scaling exponents for rapeseed pollen lie in the Lévy walk range [338]. Lévy walks represent a special case of superdiffusion, and a detailed description of Lévy processes appears in Chapter 3. Genetically modified (GM) crops of rapeseed resistant to herbicides

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have been engineered by a multinational biotechnology corporation.[2] In principle, the shape and weight of pollen in GM crops do not differ on any fundamental level from those in non-GM crops. For this reason, superdiffusion of genes from GM crops is possible [338], with potential policy implications. GM crops represent just one example of how the diffusive properties of biological systems can have far-reaching effects. Lévy flights may also find application in efforts to control the spread and proliferation of diseases via eradication strategies for optimal disease containment [103], e.g., vaccination [311]. Indeed, any mechanism that slows the diffusion of a disease agent or vector can be exploited; e.g., the time spent by mosquitoes in search of oviposition targets significantly reduces the reproductive rate of the malaria parasite [142].

We cite a second example, one related to environmental issues and conservation efforts. The complexity of foraging and movement patterns and the rich dynamics underlying the relationships between predator and prey render plausible, if not inevitable, a cascade of environmental impacts due to human activities. It is well known that human fishing activities negatively affect marine ecosystems [24, 276, 382]. Waugh *et al.* [400] have documented the change in behavior of royal albatrosses around fishing operations. Similarly, female leatherback turtles (*Dermochelys coriacea*) in the Atlantic appear to fine-tune their foraging behavior and daily activity patterns to take into account the local conditions [150]. In the context of such foraging flexibility, Hays *et al.* [150] have highlighted the importance of regulating whole-ocean fishing gear to minimize turtle bycatch. A quantitative description of animal movement may well allow for a more nuanced and scientifically informed approach to environmental policy. In a similar context, the diffusive properties of sheep are valuable in identifying and predicting spots of potential land degradation and for planning the distribution of flocks in the context of sustainable management in shrubby rangelands [38].

Indeed, beyond the purely theoretical interest in the movement of animals and organisms in general, awareness has grown about the potential ecological impact arising from the poorly understood interactions between anthropogenic changes in the environment, on one hand, and dispersal, on the other. We cite a third and final example of the importance of studying animal movement: Van Houtan *et al.* [383] have studied the sensitivity to landscape fragmentation of dispersal mechanisms for species of birds in the Amazon tropical forests, in the context of an intriguing problem of great concern – why species disappear from forest fragments. Their results seem to suggest a nonlinear and highly complex set of interactions, with considerable interspecific variability. Birds that disappear from fragments show a

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[2] Monsanto (NYSE: MON) has manufactured the herbicide glyphosate and has produced GM seeds that grow into plants resistant to this herbicide.

tendency to disperse over large distances in connected forest but not in fragmented forest. In contrast, species that persist in fragments do not cross gaps as often, yet disperse farther after fragmentation than before [383]. The authors conclude that *heavy-tailed* models better explain the dispersal kernels than Gaussian models and that tropical forest birds disperse more than commonly thought.

Other applications transcend biology and ecology. Biological foraging is actually a special case of random search. It can also include, for instance, searches for misplaced keys, missing children, and international criminals. Similarly, enzymes sometimes perform random searches for specific DNA sequences. In the context of operations research, Shlesinger [340] has noted the relevance of random searches to the hunt for submarines in World War II. Indeed, the physics and mathematics underlying random searches are so general, and their applications so diverse, that they became a topic of an American TV drama.[3]

1.4 Follow the data

Significant progress has been made over the last hundred years in the study of linear and nonlinear partial differential equations, nonlinear maps, and chaos [333]. These advances led to theoretical expectations that, until the 1980s, tended to bear on the empirical investigations. But the inherent stochasticity observed in movement data makes it difficult to link movement complexity with dynamical models of population processes [275], for example. Ecological theory traditionally held premises similar to those seen in the theory of equilibrium statistical mechanics for memory-free, scale-specific processes, normal diffusion, and Fickian transport [131]. Gautestad and Mysterud [131] have noted that animals from many taxa generally express strategic homing, site fidelity (i.e., memory), and same-species or conspecific attraction (with possibly non-Fickian transport due to interaction among diffusing individuals). Hence ecological systems and processes have more in common with complex systems far from equilibrium than was suspected earlier. It is no surprise that studies of nonequilibrium statistical mechanics [179, 198], scale-free Lévy processes [209, 342], fat-tailed or leptokurtic [417] dispersal kernels, and non-Markovian chains with long-range memory have contributed to the advance of theoretical ecology (Figure 1.3).

Because the basic premises of equilibrium statistical physics do not necessarily hold for biological and ecological systems, a data-centric scientific research program allows a quantitatively more correct and theoretically less biased approach. Such a program has two guiding principles that represent a break from the earlier

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[3] Lévy flight searches are discussed in the episode “Nine Wives” (episode 12 of season 3) of the TV series *Numb3rs*.

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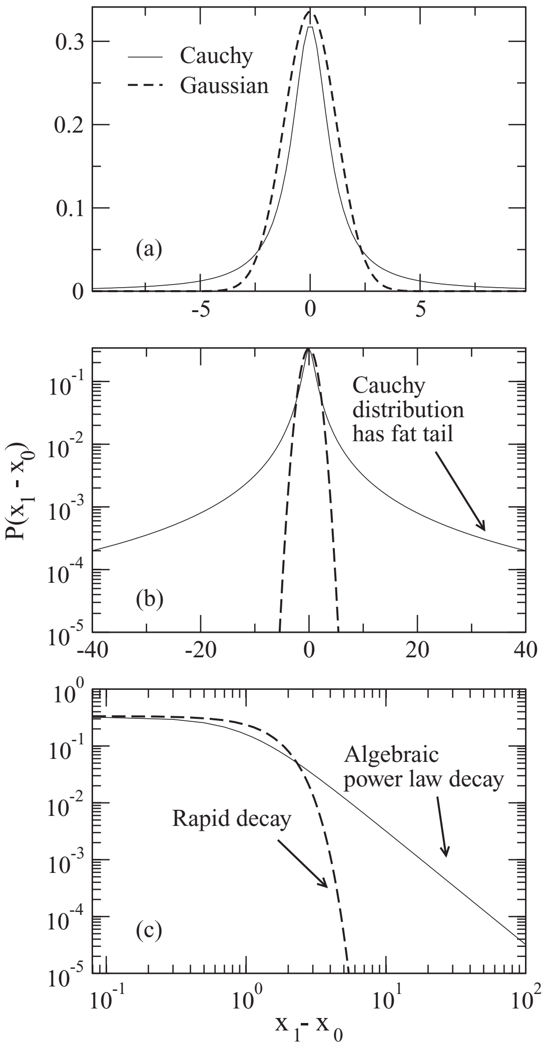

Figure 1.3 (a) Normalized probability density functions to move from position x_0 at time t_0 to position x_1 at time t_1 for a Brownian random walk and a Lévy flight, shown for some large but arbitrary value of $t_1 - t_0$. A Cauchy distribution of random walk jump lengths can be used to generate a Lévy flight. The same curves are plotted on (b) semilog and (c) log-log scales. These distributions, known as random walk propagators (see Chapter 3), are Gaussian for Brownian random walks but have asymptotic power law decay for Lévy flights. For this reason, such distributions are often described as "fat tailed" and "heavy tailed" in the literature. They also have scale-free properties (see Figure 2.1).

approach: (1) to discard preconceived expectations relating to the central limit theorem, Gaussian statistics, and Brownian motion and, instead, to expect a rich variety of behaviors; and (2) to construct a theoretical framework that, while testable (i.e., falsifiable) and amenable to model comparison, nevertheless captures the most important statistical properties of the data.

We will argue in subsequent chapters that the formalism of Wiener processes, Gaussian statistics, and the (non-fractional) Laplacian operator in the diffusion (or heat) equation does not adequately describe the experimental findings in a large number of studied cases. The discrepancy between model and data to some extent mirrors the now well-documented inadequacy of Gaussian statistics and Wiener processes to correctly model price fluctuations in financial markets [222] (notwithstanding the Black-Scholes theory of options pricing).

Historically, a major theoretical advance in the study of stochastic processes that could rival Gaussian-like statistics for describing animal movement came from the study of Lévy processes. Paul Lévy generalized the central limit theorem to cover distributions with diverging second moments [209]. The main difference between Wiener and Lévy processes stems from the fact that the probability density function of a Lévy-distributed random variable has infinite variance [209], in contrast to the usual case, for which the variance and all higher moments remain always finite. In the context of animal movement, the earliest reference to the superdiffusion of organisms is a 1986 paper by Shlesinger and Klafter [341] about Lévy random walks.

Today, advances in the experimental methodologies and the abundance of data have greatly increased, qualitatively and quantitatively, our knowledge of how animals move. In addition to very high frequency (VHS) and satellite-tracking telemetry, GPS [278], acoustic telemetry, and geolocation [319], a method known as *dead-reckoning* can also track the underwater fine-scale movement of animals [411]. Dead-reckoning involves using the position of "fix" at an earlier time and advancing it to correct for nonzero velocity.

The data confirm that organisms move with a directional persistence that is absent in Brownian motion. However, they rarely move in perfectly straight lines; hence, Lévy walks cannot perfectly describe how real organisms move. What is most important is that, over the course of two decades of study, a growing consensus among researchers in the relevant fields holds the view that many organisms diffuse anomalously: real organisms rarely have Gaussian probability functions for displacements with a variance that grows linearly in time. Rather, the motion of organisms is rich in variety and surprisingly complex. Presently, it appears that no single *universal* natural law applies across all species: animals with home ranges [135, 293], for example, behave differently from those that migrate seasonally.