THE PHYSICS OF FORAGING

An Introduction to Random Searches and Biological Encounters

Do the movements of animals, including humans, follow patterns that can be described quantitatively by simple laws of motion? If so, then why? These questions have attracted the attention of scientists in many disciplines and stimulated debates on ecological matters to queries such as, "how can there be free will if one follows a law of motion?"

This is the first book on this rapidly evolving subject, which introduces random searches and foraging in a way that can be understood by readers with no previous background on the subject. It reviews theory as well as experiments, addresses open problems and perspectives, and discusses applications ranging from the colonization of Madagascar by Austronesians to the diffusion of genetically modified crops.

The book will interest physicists working in the field of anomalous diffusion and movement ecology as well as ecologists already familiar with the concepts and methods of statistical physics.

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Dedicated to our families

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Preface

As the FBI helps a 14-year-old victim who escaped from a dangerous polygamist self-proclaimed prophet, it is faced with the question of how to search 2200 square miles of mountain desert.

"How rough is the terrain? Because the rougher the terrain, the more likely she was forced into a Lévy flight type movement. I can create a viable search pattern," says Charlie Eppes, the mathematical genius.

"It's like when you lose your keys," explains Amita Ramanujan, his girlfriend and former doctoral student. "You don't methodically search every inch of your house from front to back. You look like crazy in one area, and then jump to the next most likely area and look there."

The preceding dialogue, from the American television series *Numb3rs*, shows how far the theory of Lévy flight foraging has penetrated mainstream science. Although the term *foraging* has a biological connotation, in fact, biological foraging is a special case of random searches. Michael Shlesinger, for instance, has pointed out the relevance of random searches to operations research in World War II, involving the hunt for enemy submarines.

There are intriguing aspects of the random search problem that are peculiar to biological foraging. Why should the movements of freely moving animals follow any natural law at all? This is a fascinating question, and we find it remarkable that animals – and even humans – that possess a degree of "free will" actually move in a manner that can be described quantitatively by physical principles.

Questions such as how they move (and why) have attracted the attention of physicists for a number of other reasons as well. The trajectories of individual organisms as they forage and search closely resemble certain kinds of random walks studied by theoretical physicists. Encounter interactions of moving organisms thus have a close parallel with reaction-diffusion processes seen in nonequilibrium statistical mechanics. These mathematical similarities and the abundance of experimental

data have allowed physicists to make contributions toward the study of foraging. Hence the choice of title, *The Physics of Foraging*.

This book is an introduction to the interdisciplinary study of how organisms move in order to encounter and interact. Our goal is to bring together relevant theoretical concepts, along with a review of the experimental findings, to allow the current literature to be readable and understandable. The focus is on the statistical properties of the trajectories of single organisms. Such quantities are statistically coercive, making them useful in constraining the range of possible behaviors or in predicting the conditions under which the adoption of a given random walk strategy might confer some relative advantage, and so forth.

The statistical physics approach to the problem of foraging and random searches in many ways complements the more traditional treatment given in other disciplines. Collaboration between biologists and ecologists, on one hand, and physicists, on the other, began in earnest about two decades ago. By the early 1990s, there was enough empirical evidence to suggest that organisms do not always diffuse like particles performing Brownian motion. In collaboration with Sergey Buldyrev and Shlomo Havlin, we proposed in 1999 what has become known as the Lévy flight foraging hypothesis to try to account for the observed phenomena. Since then, a number of works coauthored by physicists have further impacted the interdisciplinary subfield of theoretical movement ecology. At present, the field is still evolving rapidly; hence we also discuss in the book a number of open problems and perspectives, both from theoretical and empirical points of view.

We are in great debt to many people with whom, along the years, we have discussed many aspects of random searches, Lévy flights, and related topics. We thank our key collaborators in the two first *Nature* papers that congealed our interest in the topic: V. Afanasyev, S. V. Buldyrev, S. Havlin, E. J. Murphy, and the late P. A. Prince. We thank Ivars Peterson for the appealing article on the first *Nature* paper that helped focus attention on statistical physics approaches to understanding the more enigmatic aspects of foraging. We also thank Mark Buchanan for drawing considerable attention to the topic in a more recent feature article in *Nature*. We have had discussions with many other people to whom we are grateful: J. S. Agnaldo, F. Bartumeus, M. W. Beims, D. Boyer, C. Carvalho, J. Catalan, S. Cavalcante, M. D. Coutinho-Filho, J. C. Cressoni, A. Davis, A. M. Edwards, C. L. Faustino, M. L. Felisberto, N. M. Freeman, U. L. Fulco, M. Gitterman, L. Giuggioli, I. M. Gléria, H. D. Jennings, V. M. Kenkre, J. Klafter, A. Y. Kasakov, L. S. Lucena, M. L. Lyra, A. Marshak, J. L. Mateos, R. Metzler, O. Miramontes, C. M. Nascimento, A. M. Nemirovsky, R. W. Nowak, E. J. Nunes-Pereira, F. S. Passos, R. A. Phillips, M. C. Santos, M. F. Shlesinger, L. R. da Silva, M. A. A. da Silva, I. M. Sokolov, C. Tsallis, T. M. Viswanathan, and N. W. Watkins. Moreover, we are in great debt for the support and encouragement provided by our families. Last,

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