An emerging movement ecology paradigm

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Movement of individual organisms, one of the most fundamental features of life on Earth, is a crucial component of almost any ecological and evolutionary process, including major problems associated with habitat fragmentation, climate change, biological invasions, and the spread of pests and diseases. The rich variety of movement modes seen among microorganisms, plants, and animals has fascinated mankind since time immemorial. The prophet Jeremiah (7th century B.C.), for instance, described the temporal consistency in migratory patterns of birds, and Aristotle (4th century B.C.) searched for common features unifying animal movements (see ref. 1).

Modern movement research, however, is characterized by a broad range of specialized scientific approaches, each developed to explore a different type of movement carried out by a specific group of organisms (2). Beyond this separation across movement types and taxonomic (or functional) groups, movement research divides into four different "paradigms," the random, biomechanical, cognitive, and optimality approaches (1), which are loosely linked to each other. Although movement research is extensive and is growing rapidly (2), specialization has its cost: measurement and analysis tools are repeatedly reinvented, and lessons learned from one line of research often do not affect others. Most importantly, we lacked a cohesive framework that would serve as a unifying theme for developing a general theory of organism movement.

This Special Feature lays the foundation for "movement ecology" as a unifying paradigm for studying all types of movement involving all organisms. The term movement ecology has been used occasionally in the literature [as of August 2008, a search of movement ecology in the title, abstract, or keywords in the ISI Web of Knowledge database (http://apps.isiknowledge.com) yielded 18 publications, the first of which was published in 1976], chiefly referring to ecological interactions associated with animal movement. However, the movement ecology concept underlying this Special Feature is markedly different. It refers to a proposed scientific paradigm that places movement itself as the focal theme, and, by providing a unifying framework and common tools, it aims at promoting the development of an integrative theory of organism movement for better understanding the causes, mechanisms, patterns, and consequences of all movement phenomena.

This Special Feature is based on an international project held at the Institute for Advanced Studies (IAS) in Jerusalem from 2006 to 2007 (3). Three of the 12 contributions, presenting a general conceptual framework (1), a literature review (2), and a framework for generating and analyzing movement paths (4), are direct products of this IAS project. Three other contributions are coauthored by IAS group members; they illustrate applications of the proposed conceptual framework for seed dispersal (5), foraging and other movements of elephants (6), and dispersal of lynx (7). The remaining six contributions were solicited from other research groups to broaden the scope of this collection. These include a theoretical paper on the link between foraging behavior and the statistical properties of movement paths (8) and five empirical studies on dispersal of plants (9) and butterflies (10), navigation of salmon and sea turtles (11), migration of vultures (12), and dispersal, foraging, and other movements of elks (13). Holyoak *et al.* (2) estimate that over the last decade (1997–2006) ≈26,000 papers referred to movement. Because of this extremely broad scope of movement ecology, the fairly diverse coverage of movement types and taxonomic groups in this Special Feature is inevitably incomplete. To foster integration, the authors were requested to place their works in the context of the proposed unifying theme (1) and discuss the pros and cons of this approach.

The general framework introduced by Nathan *et al.* (1) asserts that four basic components are needed to describe the mechanisms underlying movement of all kinds: the organism's internal state, which defines its intrinsic motivation to move; the motion and navigation capacities representing, respectively, the organism's basic ability to move and affect where and when to move; and the broad range of external factors affecting movement. At first glance, this framework appears to be primarily applicable to self-propelled sentient animals, for which the internal motivation to move and the ability to actively move while making decisions in response to information about the environment are comprehensible. However, two studies in this Special Feature (5, 9) apply this framework to investigate the movement of passively transported organisms that lack a central nervous system, such as plants.

Damschen *et al.* (9) provide the most fundamental application of movement ecology for studying plant community dynamics, classifying plant species according to a single categorical parameter depicting the dispersal mode. Such simplifications are often compulsory because urgent conservation concerns preclude detailed investigations of dispersal mechanisms for many species. Interestingly, the predicted effects of fragmentation on community dynamics were supported for bird-dispersed species that were studied in detail in this system, but not for wind-dispersed and "unassisted" species, for which dispersal has not yet been investigated. Wright *et al.* (5) parameterize a mechanistic wind dispersal model for two tropical tree species, interpreting the movement ecology from an evolutionary context. Importantly, they found that surrogates of seed fate (the potential fitness consequences of dispersal) vary in a complex manner with respect to atmospheric conditions (external factors), seed terminal velocity (motion capacity), and the timing of seed release (navigation capacity).

Linking Processes to Patterns and the Importance of Scale

The general challenge of identifying the mechanisms underlying ecological patterns (14) is particularly relevant for movement research: we need to identify phases of specific activity modes in observed movement paths (1, 4) and reveal the underlying mechanisms from their statistical properties. This Special Feature illustrates two complementary ways to address this challenge. The first, applied here to animals (4) and plants (5), explicitly depicts the underlying mechanisms and associate potential determinants of movement processes with the resulting patterns. The second takes the

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Author contributions: R.N. wrote the paper.

The author declares no conflict of interest.

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opposite approach: from patterns to processes. Bartumeus and Levin (8) quantify intermittency in movement patterns of animals that search, suggesting that the switch between scanning and reorientation could infer, for example, the effects of limited perception and/or a patchy environmental structure. Wittemyer *et al.* (6) use time-series techniques to infer about basic movement phases and formulate hypotheses about the major links, such as those between risk (human hunting) aversion, social dominance, and seasonal dynamics of the resources, that underlie elephant movements.

A major challenge in movement research is to explicitly link the statistical properties of movement patterns to specific internal traits and/or behaviors. Movement ecology facilitates this integration (1). The theoretical guidelines provided by Getz and Saltz (4) and Bartumeus and Levin (8) must be complemented by empirical studies that delve more deeply into the mechanistic determinants of movement. Lohmann *et al.* (11) suggest a novel hypothesis of how salmon and sea turtles navigate long distances back to their spawning grounds in essentially featureless oceanic landscapes. Ovaskainen *et al.* (10) apply the harmonic radar technique to quantify small-scale movements of butterflies originating from populations in continuous landscapes in China and Estonia and from fragmented landscapes in Finland. Significant differences in small-scale movements were found only between butterflies from old and newly established populations in Finland, suggesting that variation in motion capacity or internal state makes butterflies from newly established populations more mobile. Mandel *et al.* (12) analyze the effects of atmospheric factors and topography on migratory flights of vultures, emphasizing their dependence on high turbulent kinetic energy (TKE) conditions in the atmospheric boundary layer. High TKE was also critical for long-distance wind dispersal of tree seeds (5).

A related key challenge in ecological research, identifying the key processes shaping patterns at different spatial and temporal scales (14), was emphasized in many contributions to this Special Feature. Lohmann *et al.* (11) suggest scale-dependent navigation in salmon and sea turtles, in which geomagnetic and olfactory imprints of the natal areas guide a phase of large-scale navigation by the Earth's magnetic field, followed by small-scale navigation governed by chemical gradients to specific destinations. Fryxell *et al.*'s (13) analysis of elk movements across five orders of magnitude in time (minutes to years) and space (meters to hundreds of kilometers) provides one of the most comprehensive investigations of movement at multiple spatiotemporal scales. They show that elk switch among two or more movement modes at each spatiotemporal scale examined. They stress the challenge of elucidating the basic components of the movement ecology framework and their interactions to fully understand the observed movement patterns.

The Role of Movement in Determining Ecological and Evolutionary Processes

As emphasized in Damschen *et al.* (9), movement plays an important, but not exclusive, role in determining ecological and evolutionary patterns. However, we should remain mindful of Daniel Janzen's assertion (as quoted in ref. 3) that "an awful lot of biologists conveniently trim [movement] out of their way of thinking to make their problems simpler". Progress in movement ecology requires that studies of populations, communities, and ecosystems will consider movement explicitly. However, movement research needs to consider constraints and tradeoffs associated with other life history traits and should elucidate how premovement and postmovement processes such as fecundity and establishment interact with movement to shape ecological processes and patterns. Revilla and Wiegand (7) illustrate an application of the movement ecology framework to elucidate the role of dispersal in the dynamics of lynx populations in spatially structured landscapes. They propose that between-patch movement and within-patch demography cannot be considered as separate entities, because birth–death processes affect the movement behavior of individuals and vice versa.

Potential Future Directions

Introducing new concepts into any discipline is frequently met with resistance, as part of refining and clarifying emerging paradigms (15). This Special Feature aims at gearing up this process for movement ecology. There is a growing recognition of the need to understand and predict movement processes driving biological invasions, the spread of pests and diseases, and the persistence of local populations and entire species in light of ongoing global environmental changes. Combined with drastic improvements in our ability to track and analyze movement, it is hoped that movement ecology will pave the way for developing a unified theory of organismal movement. Although this Special Feature provides only a taste of a much broader scientific enterprise (2), we hope it will help accelerate scientific progress in solving our most urgent ecological problems, in further elucidating the research questions addressed here and other important issues such as collective movements of groups, large-scale connectivity, and movements of microorganisms and humans.

ACKNOWLEDGMENTS. I thank the Institute for Advanced Studies in Jerusalem for hosting and sponsoring our group, and all group members, visitors, students, Special Feature authors, reviewers, and editors Jim Brown and David Stopak for their help, insight, and inspiration.

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