Trends and missing parts in the study of movement ecology

Marcel Holyoak[a,1], Renato Casagrandi[b], Ran Nathan[c], Eloy Revilla[d], and Orr Spiegel[c]

[a]Department of Environmental Science and Policy, University of California, 1 Shields Avenue, Davis, CA 95616; [b]Dipartimento di Elettronica e Informazione, Politecnico di Milano, Via Ponzio, 34/5, 20133 Milan, Italy; [c]Movement Ecology Laboratory, Department of Evolution, Systematics, and Ecology, Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem 91904, Israel; and [d]Department of Conservation Biology, Estación Biológica de Doñana, Consejo Superior de Investigaciones Cientificas, Avenue Maria Luisa s/n, E-41013 Seville, Spain

Edited by James H. Brown, University of New Mexico, Albuquerque, NM, and approved September 9, 2008 (received for review February 21, 2008)

Movement is important to all organisms, and accordingly it is addressed in a huge number of papers in the literature. Of nearly 26,000 papers referring to movement, an estimated 34% focused on movement by measuring it or testing hypotheses about it. This enormous amount of information is difficult to review and highlights the need to assess the collective completeness of movement studies and identify gaps. We surveyed 1,000 randomly selected papers from 496 journals and compared the facets of movement studied with a suggested framework for movement ecology, consisting of internal state (motivation, physiology), motion and navigation capacities, and external factors (both the physical environment and living organisms), and links among these components. Most studies simply measured and described the movement of organisms without reference to ecological or internal factors, and the most frequently studied part of the framework was the link between external factors and motion capacity. Few studies looked at the effects on movement of navigation capacity, or internal state, and those were mainly from vertebrates. For invertebrates and plants most studies were at the population level, whereas more vertebrate studies were conducted at the individual level. Consideration of only population-level averages promulgates neglect of between-individual variation in movement, potentially hindering the study of factors controlling movement. Terminology was found to be inconsistent among taxa and subdisciplines. The gaps identified in coverage of movement studies highlight research areas that should be addressed to fully understand the ecology of movement.

dispersal | foraging | migration | navigation | physiology

Almost all organisms have to move at some point during their lives, either under their own locomotion or transported by physical processes or organic agents. Movement is beguiling in its variety and complexity. For example, why do sooty shearwaters with chicks in nests in New Zealand regularly forage in the waters off California or Alaska (1)? Why do some planktonic organisms undergo regular daily vertical migrations (2)? Why do some species show nomadic movements, and others follow fixed-route roundtrip migrations (3)? Movement is often in response to short-term goals such as reproduction, maintenance, including feeding, and survival, including escaping threats. It may also be shaped by longer-term fitness implications, such as avoidance of inbreeding and population extinction. Its importance in biology is attested to by numerous books (e.g., ref. 3).

Here, we address the movement of whole organisms or gametes as opposed to the movement of appendages, molecules, or physical entities. Terminology for movement is, at best, confusing. Some terms such as "movement" are frequently used for body parts rather than whole organisms, and others such as "orientation" have multiple meanings, some of which are relevant to movement and others not (e.g., policy orientation, or compass direction). Physical entities, such as water, sediments, or tectonic plates, also move. Therefore, only a subset of the studies referring to movement address organisms, and only a further subset really focus on it with description, measurement, or hypothesis testing. However, nearly 26,000 published articles in the last decade referred to organismal movement. It is therefore a formidable task to identify papers that focus on organismal movement and contribute importantly to our understanding. We aim to investigate the completeness of the ways in which movement is studied and variation among disciplines and taxonomic groups in how movement is studied and described. Our aim is to foster a more integrative approach and identify gaps in the literature.

There are various integrative conceptual frameworks which might aid our study of movement (e.g., refs. 3 and 4). Here we adopt the framework of Nathan *et al.* (5), which was developed by several of us before the literature review reported here. The framework is applied to movement "phases," characterized by a single set of goals. For instance a phase might be a foraging trip, or seed dispersal. Ultimately, the sequence of all movement phases set the lifetime track of an individual. The framework represents a relatively complete view of movement because all aspects of movement that we have found in the literature can be fitted somewhere within it. As illustrated in figure 2 in ref. 5, the framework contains four main components that contribute to movement, the internal state and external factors, motion and navigation capacities. Internal state includes an organism's physiological state and its short-term motivation in relation to its long-term "goals" (e.g., reproduction, maintenance, survival, learning, or more specific versions of these). An organism's movement is controlled by its motion and navigation capacities, which give the realized movement path. The motion capacity is the ability of the organism to move either under its own locomotion or by being carried by either physical means (winds, water, etc.) or other organisms (phoresy), and its choice of alternative motion mechanisms (e.g., a bird can walk or fly). The navigation capacity is the ability of organisms to orient (choose a heading direction) and navigate (to orient and know their location relative to their destination) including the implied use of memory or inherited capacity. All three of the preceding factors can be modified by external environmental factors, including the landscape, meteorological and other physical factors (e.g., variation in oceanic currents or river flow), the distribution of resources and different environmental conditions, and other organisms, including conspecifics (mates, competitors), interspecific competitors, predators, and coordinated group movements.

Author contributions: M.H., R.C., R.N., E.R., and O.S. designed research; M.H., R.C., R.N., and O.S. performed research; M.H., R.C., and R.N. analyzed data; and M.H., R.N., and O.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1]To whom correspondence should be addressed. E-mail: maholyoak@ucdavis.edu.

This article contains supporting information online at www.pnas.org/cgi/content/full/0800483105/DCSupplemental.

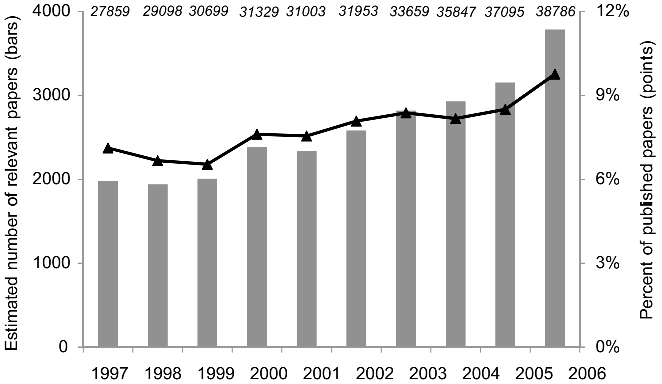

Fig. 1. An estimate of the number of papers published per year referring to movement, based on a literature survey by using the ISI Web of Knowledge and search terms in Table 2, and as a percentage of all papers published in 496 journals. Numbers in italics are the total numbers of articles in any subject published in the 496 journals per year.

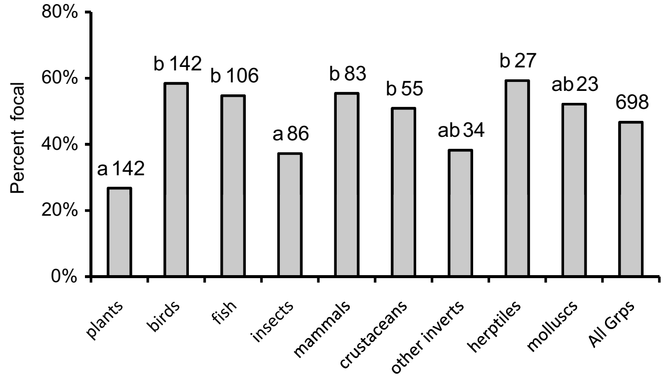

Fig. 2. The percentage of studies using movement terms that focused on movement for various taxa. For bars with different letters above them, means differed at $P < 0.05$ in a generalized linear model with a logit link function, binomial distribution of sampling error, and weighted for sample size. Numbers above bars are sample sizes. Only taxa with $n > 20$ are shown. Herptiles are amphibians and reptiles.

In practice, movement is studied by monitoring locations over time of individuals, entire populations, or both. Studies can explore movements within a generation, across multiple generations, or both. If populations are tracked it is often not clear how and why the individuals are moving. Our framework takes its mechanisms from individuals, because studying individuals promotes recognition of between-individual variation in movement patterns, be they random, sex- or age-specific, or organized in other ways. Revilla and Wiegand (6) illustrate how the movement ecology framework (5) can be applied to link movement behavior of individuals to population dynamics in spatially-structured landscapes. Yet, such studies are rare in the literature. At best, in studies at the population level, such differences are characterized by variance metrics. Multigenerational population studies risk confusing movement with other demographic processes (birth and death). We therefore investigated whether studies were conducted at the individual or population levels.

Results

Broad Patterns in the Study of Movement. The literature identified by searching keywords is enormous. Assuming that our keyword search was 73% successful in identifying relevant papers [see supporting information (SI) Text] and that the search words located 65% of relevant papers only (35% were missed by known search words) then we estimate that there were a minimum of 25,927 papers about organismal movement published during 1997–2006, or a mean of 2,593 papers per year. This estimate is minimal because it comes from only relatively reliable keywords and includes only journals likely to contain relevant articles. Fig. 1 shows that the number of papers increased by an average of 187 (or 7.2%) per year, which is about twice the rate of increase (3.5%) in total number of papers published by the 496 journals (Table S1). Thus, the proportion of papers referring to movement averaged 7.8% and increased 0.3% per year.

A complete review of this vast literature would have been prohibitive. Therefore, we randomly sampled 1,000 papers published between 1997 and 2006 to address four questions: (*i*) How many studies focused on movement by testing hypotheses about it or measuring it, and did this vary among taxa? (*ii*) Did studies address a single species, multiple species, a broad taxonomic group, or a specific ecosystem, or were they general in scope? (*iii*) How do studies of movement fit in with our conceptual framework? Specifically, which kinds of studies were most frequent and which were relatively infrequently studied, and did this vary among taxa? (*iv*) What terms were used to describe movement, both in general and in different taxa? We use this information, together with whether the terms are at the individual or population level, to help explain differences among subdisciplines of ecology and environmental sciences in how movement is studied.

The survey of 1,000 randomly-selected papers resulted in 768 articles (76.8%) that used movement terms in appropriate ways (movement being focal in Fig. 2). Relevant articles were on the following taxa: plants (19%), birds (19%), fishes (14%), insects (11%), mammals (12%, including humans 0.5%, marsupials 0.5%), crustaceans (7%, mainly marine forms, where zooplankton constituted 2.3%, larger forms constituted 4.8%), other invertebrates (4.4%, mostly marine taxa 2.6% and terrestrial arachnids 1.8), molluscs (3%), reptiles (2.1%), and amphibians (1.4%). Other taxa included fungi (1.3%), algae (1.0%), bacteria (0.8%), and protozoa (0.3%). An additional 39 studies (5%) were not taxon-specific.

Of the 768 articles, 339 (46.5%) focused on movement according to our definition, and the proportion of these studies did not vary with year of publication. However, movement was a focus significantly more frequently for vertebrates (55–59%) and crustaceans (51%) than for plants (27%) and insects (37%) (Fig. 2).

The vast majority (93%) of focal papers were purely empirical, 4% considered only theoretical models, and 3% considered both models and real organisms. Of focal articles, 77% were species-specific, 15% addressed multiple species, 5% addressed a broad taxonomic group at above the level of a genus, 1% were system specific (e.g., tropical coral reefs), and only 2% were general.

Placing Studies in the Movement Ecology Framework. For the 339 studies with movement as a focus, the breakdown with respect to different components of the movement ecology framework is shown in Fig. 3. Most frequently, studies linked the motion capacity to the measured movement or confirmed its occurrence in the life stage studied (link E in Fig. 3). Nearly two-thirds of studies looked at the effect of external factors on the occurrence or frequency of movement (link A in Fig. 3). Other parts of movement ecology were studied less frequently. Navigation and orientation mechanisms (link F in Fig. 3) were subjects of only 12% of studies, and effects of external factors (link B in Fig. 3) and internal state (link C in Fig. 3) on navigation were studied infrequently (9% and 2%, respectively; Fig. 3). Only 9% of studies addressed the effects of physiology, motivation, and other aspects of internal state on the ability to move (Fig. 3, link C).

We also found some notable differences between taxa. Studies of vertebrates were more likely to address the effect of external

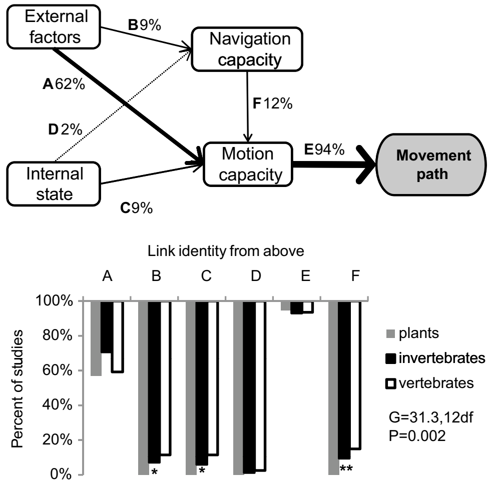

Fig. 3. The frequency of study of different components of the movement ecology framework. (*Upper*) Compared with the framework, published studies frequently omit feedbacks from movement path to internal state or external factors and links between internal and external factors. Arrow thickness represents the percent of focal studies in which each link was studied. Letters next to arrows label links and give percentages of cases. (*Lower*) The bar chart breaks the frequency of study into different taxa. *, the three taxa differed at $P < 0.05$; **, $P < 0.005$ in G tests. An overall G test for all links simultaneously (thereby protecting alpha) is given.

factors on navigation (Fig. 3, link B), of navigation on movement path (Fig. 3, link F), and of internal state on movement capacity (Fig. 3, link C) than studies of invertebrates. Links to navigation (Fig. 3, links B, D, and F) were completely absent from our sample of plant studies (see *Discussion*).

Terminology for Movement. The vast majority of relevant studies used three main terms: dispersal, migration, and movement (Table 1). Altogether these terms and the more specific word forms (e.g., long-distance dispersal) included in Table 1 appeared in >89% of the movement studies, and hence they are highly effective for identifying relevant papers. Surprisingly, the keyword "foraging," referring to foraging movements, appeared in only 2.2% of the studies about movement. An additional 8.2% of relevant papers used the term foraging to refer to feeding behavior in general (e.g., prey types taken, feeding preferences) rather than to foraging movements. Altogether 43 distinct terms were identified in our random sampling of terms (Table 1). Most of those terms other than dispersal, migration, and movement were used in <1% of papers.

There was marked variation in use of the terms dispersal, migration, and movement (in the strict sense) among well-represented taxonomic groups (Fig. 4). Most extreme was that dispersal was used in 89% of studies of plants (as opposed to migration in 9% and movement in 3%) and in 67% of insect studies and 71% of studies of other invertebrates (Fig. 4). By contrast 57% of studies of amphibians and reptiles used the term movement, and 54% of bird studies used migration (Fig. 4). Terminology used for mammals, fish, and crustaceans (including zooplankton) was somewhat evenly split between the terms movement, migration, and dispersal (Fig. 4). Crustaceans differed from other invertebrates in the frequent use of the term migration to describe the diel vertical movement of pelagic species (Fig. 4).

Organismal movement was measured quantitatively in 42% of relevant studies or 94% of the 339 studies with movement as a focus. Of these, movement was measured at the population level in 37% and at the individual level in 59%, and level was not distinguishable in 3%. There was also significant variation

Table 1. Frequency of usage of terms referring to movement

Taxa	Studies, *n*	Percentage, %
General terms for movement		
Dispersal	293	38.4
Migration	165	21.6
Movement	134	17.5
Gene flow	5	0.7
Other general terms*	15	2.0
Modes and patterns of movement		
Foraging	17	2.2
Diel vertical migration	11	1.4
Long-distance dispersal	11	1.4
Home range	9	1.2
Vertical migration	9	1.2
Homing	6	0.8
Nomadism	6	0.8
Other modes/patterns†	21	2.7
What is moving		
Seed dispersal	43	5.6
Larval dispersal	9	1.2
Other terms‡	5	0.7
Narrow movement terms		
Diel vertical migration	11	1.4
Vertical migration	9	1.2
Other narrow terms§	7	0.9

The analysis is based on a sampling of the first term encountered in 1,000 papers, resulting in 764 relevant term usages. A separate draw of 1,000 papers was made from Table 1.

*Additional terms: transport (3 studies), locomotor activity (2 studies), diffusion (2 studies), gene dispersal, passage, habitat use, distance traveled, site fidelity, population connectivity, interconnectivity, and traverse.

†Includes flight (4 studies), natal dispersal (3 studies), swimming (2 studies), zoochory (2 studies), hydrochory (2 studies), diel migration, diel movement, vertical dispersal, habitat shifts, flight performance, ballooning, walking activity, and orientation.

‡Includes pollen flow (2 studies), spore dispersal, pollen dispersal, and seed rain. Terms that are implicitly about a particular kind of organism (e.g., hydrochory for aquatic seed dispersal) and do not use the name of the item moving in the term were not included in this category.

§Includes zoochory (2 studies), hydrochory (2 studies), diel migration, diel movement, vertical dispersal.

among taxa in the frequency of measurement of movement at the individual vs. population levels (Fig. 5). In birds and mammals movement was usually measured at the individual level. By contrast, movement of crustaceans and plants was usually measured at the population level (Fig. 5). Other taxonomic groups did not differ from the mean rates of individual- and population-level measurement across all taxa (Fig. 5).

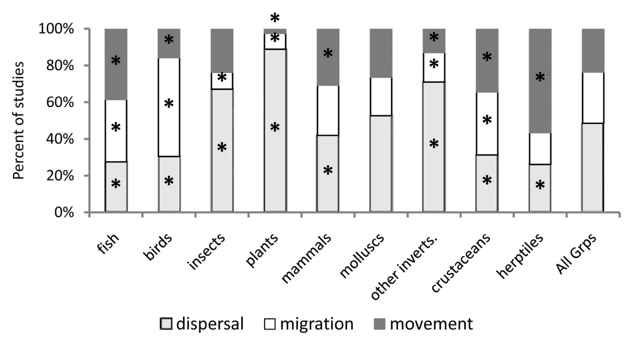

Fig. 4. The frequency of usage of movement, migration, and dispersal in major taxonomic groups. Asterisks indicate differences ($P < 0.05$) from the all taxon averages in G tests. Statistics and sample sizes are given in Table 3.

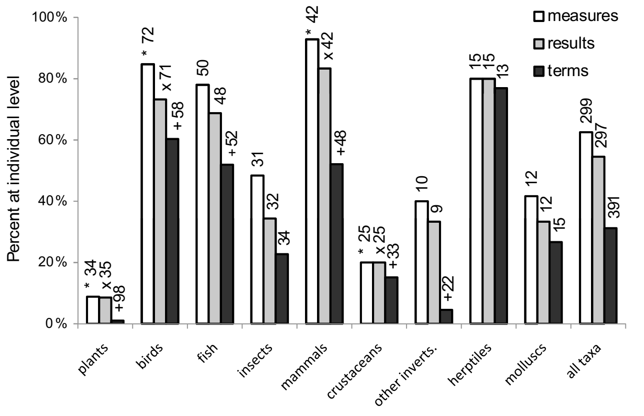

Fig. 5. The percentage of studies measuring movement, reporting results of measurement of movement, or using movement terminology at the individual level. The percentage considered only a binary classification of individual vs. population level. Unclear and ambiguous cases, which were 3% of papers, were excluded. Bars with symbols above them differed (at $P < 0.05$) from the overall all taxa average shown in χ^2 tests after Bonferroni correction for the overall number of comparisons. *, a difference for measurements; x, results; +, terminology. Numbers above bars are sample sizes.

Although movement may have been measured for individuals, it was sometimes reported by using terminology referring to populations or terms that were ambiguous in whether individuals or populations were studied (Fig. 5). Consequently, there is a loss of precision of reporting as we move from methods to results and then to general terminology for movement (Fig. 5).

Discussion

Organismal movement is represented by a vast literature. In our sample of 496 journals from ecology, evolution, behavioral science, and environmental science during 1997–2006, movement was referenced in nearly 8% of articles (or ≈2,600 per year; Fig. 1). Furthermore, both the absolute number of articles per year and the proportional representation of movement in these journals are growing (Fig. 1). These changes parallel an increase in the spatial scale of many ecological studies, with increased interest in topics like metapopulations (7), metacommunities (8), and macroecology (9). Changes have been facilitated by advances in technology in remote sensing, global positioning system, geographic information system, various biotelemetry techniques (5), molecular genetics (10), and stable isotopes tracers (11). However, studies of movement itself usually have stopped short of investigating movement's proximate and ultimate mechanisms. Below we highlight how features found in traditional studies of movement are hindering progress and should be avoided, and then we discuss key features that are missing from movement studies and offer exciting research opportunities.

There are three main problems with previous studies that should be avoided. First, previous taxonomies of movement (3, 4) have encouraged us to assume that we understand the patterns, mechanisms, and motivation for movement once movement has been named. Second, published studies frequently use indirect measures of movement motivated by explaining post-movement patterns in evolution or ecology, such as genetic diversity, or observed population dynamics. Yet, it is rare that studies include what is known about relevant behavior, physical transportation mechanisms, or navigation mechanisms. This omission has created a gap between the biology of movement and ecology and evolution, which hinders our ability to make predictions and understand mechanisms in these disciplines.

Third, there are broad disciplinary boundaries that make it difficult for authors to integrate perspectives of neurophysiology of navigation with those of ecology and evolution (see ref. 12). Similarly, ecophysiology and biomechanics are central to understanding movement, yet to be fully understood they need to be placed in an ecological and evolutionary context. For instance, plants have primarily been studied at the population level and rarely at the individual level (Fig. 5), which is exemplified by use of the population-level term dispersal (Fig. 4). The same is true of insects and other invertebrates (Figs. 4 and 5). By contrast, individual vertebrates were frequently studied (Fig. 5), and more links in the movement ecology framework were studied than for plants or invertebrates (Fig. 3). More generally, focus on individuals promotes recognition of important differences associated with age, sex, genetics, phenotype, or experience. Averaging out of such differences in populations can mask important differences in movement paths, navigation behaviors, orientation, and physiological and motivational states.

There are at least three important features that are missing from current studies and for which further study should be encouraged. First, the majority of studies simply measured movement, documented its occurrence (Fig. 3, link E), or described how it was influenced by the environment, conspecifics, or other species (Fig. 3, link A). Consequently, we rarely know why species follow particular movement paths and how their mode of movement relates to short-term and long-term costs and benefits. Bartumeus and Levin (13) propose that a focus on path intermittency could help identify the mechanism generating different movement patterns, although at this stage of inquiry, a long list of potential mechanisms can yield intermittent paths. One possible solution is to study model organisms, such as *Escherichia coli*, honey bees, cockroaches, salmon, and domestic pigeons, where more of the mechanisms are known and more sophisticated hypotheses can be tested. For example, the self-propelled movements of microorganisms occur over very limited spatial scale, enabling detailed measurements of individual movements, along with unparalleled detailed understanding of motion mechanisms at the molecular level, compared with macroorganisms. Larger and more integrative research projects are likely also valuable, where scientists studying navigation mechanisms come together with those interested in the physics of movement, physiologists, and theoreticians. Collaborations between ecologists and atmospheric scientists in this special feature illustrate the use of atmospheric models that are used to study the aerial movement of seeds (14) and vultures (15). A change in philosophy of studying movement is required for this integration to occur, so that the causes and consequences of movement are a focus of collaborative grant proposals.

A second challenge is how to overcome differences among taxa, such as those shown in Fig. 3. These differences result from variation among taxa in the spatial and temporal scales spanned, the timing and predictability of movement, and how difficult individuals are to mark and track (16). Hence, studies of vertebrates were much more likely to include links B, C, D, and F in Fig. 3 than were studies of plants or invertebrates. These differences reflect the difficulty of marking seeds and small larval invertebrates by current techniques. By comparison, satellite tagging and various other biotelemetry techniques have greatly aided the tracking of vertebrates at large scales (17). These differences make it difficult to generalize beyond closely related or otherwise similar species. The vast majority of studies (93%) were empirical, limiting the extent to which findings can be generalized beyond the study species. More than one species was considered in only 23% of studies. Further, only 3% of papers jointly considered both models and empirical measurements, which is surprising given that the use of nonsystem-specific models is an obvious way to generalize findings. This lack of generalization highlights the value of integrative cross-species analyses of movement, general models, and unifying frameworks (such as ref. 5).

Table 2. Search terms used

Term 1	Term 2	Hits	Successful hits	Success, %
Telemetry	None	27	21	77.8
Homing	None	6	4	66.7
Biotelemetry	None	2	2	100.0
Nomad*	None	2	2	100.0
Dispersal	None	76	57	75.0
Foraging	telemetry; migrat*; ecosystem	13	10	76.9
Orientation	telemetry; larva*; migrat*; coloni*	12	10	83.3
Movement*	climat*; forag*; gene flow; radio; telemetry; seed; pollen; larva*; migrat*; selection; communit*; ecosystem; coloni*; spread*; ecolog*; population; habitat; mortality	221	156	70.6
Gene?flow	behavi*; seed; pollen; migrat	13	11	84.6
Migration	ecolog*; population; patch; individual; larva*; mortality; habitat; telemetry; spread; radio	56	45	80.4

If a second term is given it was an AND search with the terms listed under term 2 in OR combinations (a semicolon indicates OR). Hits is the number of papers of 1,000 that used the term in this initial screening. Successful hits were the number of papers using the term to refer to relevant movement; this is expressed as a percentage of papers in success %. *, represents multiple wildcard characters; ?, represents a single wildcard character. Anemochory and zoochory were also included but had zero hits, and hydrochory produced 1 successful hit.

Third, there are some obvious understudied parts of the movement ecology framework that are specific to broad taxonomic groups, but that are general enough in their occurrence that they merit further study. For example, orientation and navigation in plants, fungi, and other organisms with passively-transported propagules (Fig. 3, links B–E) are understudied and little synthesis is available. Lacking neuromuscular systems, plants cannot navigate in the sense of selecting one direction over another and making decisions about how far to travel and where to cease movement. In an evolutionary sense, however, plants can affect the direction and distance of dispersed seeds, and even their specific deposition site (18, 19). For example, some wind-dispersed species release seeds during turbulent winds (14, 20, 21), when they are more likely to ride updrafts and reach distant sites (14). Some terrestrial plant seeds also have adaptations to facilitate movement along the ground and settlement in crevices (14). It has recently been suggested that navigation mechanisms can impact dispersal distance more effectively than motion mechanisms alone (22). Passively-transported life stages of nonplant taxa can also orient and navigate: for instance, fungi can have directional spore release (23), and some cyanobacteria adjust their buoyancy by a variety of means during diel vertical migration (24). Although there are elaborate terminologies for movement behaviors in motile cells (e.g., refs. 25 and 26) and a large literature about interactions between self-propelled movement and the environment (27), the movement of dormant and encysted stages is much less understood (e.g., refs. 25 and 28). Inadvertent movement by humans may also be an important source of dispersal in microorganisms (25), making it important to integrate studies of human movement patterns into ecology, as they have been in disease studies (29). Molecular genetic tools are also likely to be particularly valuable for investigating the movement patterns of microorganisms.

Consequently, the vast and sprawling movement literature badly needs a simple, integrative organizational scheme such as the movement ecology framework (5). The framework has several important properties. It transcends taxonomic boundaries and can be applied to any organism. It can consider both ecological and evolutionary processes. In fact, to apply the framework to transported propagules we need to consider evolved features such as propagule size, morphology, and release mechanisms (14, 20). It places the ecophysiology, neurophysiology, biomechanics, and ecology of movement into a framework that encourages integration of ideas, hypothesis generation, and connection of movement patterns (paths) with processes. Fig. 3 shows that it is rare for studies to consider all parts of this framework (but see refs. 30 and 31). For instance, only 11% of studies focusing on movement included the effect of internal factors, such as physiology and motivation (Fig. 3, links C and D). We are not suggesting that all studies should consider all parts of the framework. However, it is alarming that <1% of studies of movement integrate all of the relevant components. There is also need for comparative empirical and general theoretical work, particularly for studies that combine the two.

Finally, there is a broad need to expand thinking and improve integrative frameworks (5), so as to address a wide range of questions in ecology and evolution, including topics such as invasive species biology, epidemiology, and movements of individuals and populations in response to climate change and landscape fragmentation (32). We strongly encourage people to be more ambitious when working with movement in ecology and to recognize and study multiple integrated components.

Methods

Initially, a search was conducted to identify appropriate journals for inclusion in the survey. Then, by screening a list of 1,000 randomly selected papers from those journals and scoring their relevance, we tested the success rate of different search word combinations. Finally, a new set of 1,000 papers was randomly selected from the search results using this most appropriate list. Those papers were used in the detailed evaluation and analysis.

The ISI Web of Science Database (http://apps.isiknowledge.com) was used to conduct a search for terms in titles, abstracts, keywords, or keywords plus that indicated movement of whole organisms. An initial list of search terms (see *SI Text*) was used to randomly select 1,000 articles published during 1997–2006. In some specific cases, we avoided using terms that produced relevant articles but also produced large amounts of irrelevant literature. This effect was most pronounced for studies of microorganism movement, such as taxis or kinesis and related word forms (mostly chemotaxis), which primarily produced studies about molecular-level mechanisms of motion machineries. We therefore excluded these terms, keeping in mind that this exclusion biased against microorganism movement somewhat in our review.

We define a paper as relevant if it referred to the movement of whole organisms or gametes. Terms (either singularly or combination) with <60% of articles that were relevant were excluded, resulting in inclusion of terms in Table 2. From these methods, based on an initial screening sample of 1,000 articles, we estimated that 73% of retrieved articles were relevant. (Note this number comes from the initial screening survey, and not the final survey used,

Table 3. Frequencies of usage of dispersal, migration, and movement for different taxa

	Frequencies			G tests		
Taxa	Dispersal	Migration	Movement	Dispersal	Migration	Movement
Fish	25	31	35	**−26.83**	*14.28*	*36.44*
Birds	35	62	18	**−30.39**	*85.49*	**−13.62**
Insects	51	7	18	*36.36*	**−15.09**	1.29
Plants	72	7	2	*91.81*	**−15.98**	**−8.90**
Mammals	26	17	19	**−5.91**	0.45	*11.15*
Molluscs	10	4	5	2.27	−2.01	1.41
Other invertebrates	22	5	4	*18.15*	**−5.17**	**−4.57**
Crustaceans	10	11	11	**−8.16**	*5.27*	*8.98*
Herptiles	6	4	13	**−7.06**	−3.54	*23.55*
All groups	257	148	125	70.2	63.7	55.7

Overall G tests for differences in usage frequency between different taxonomic groups are reported in the all-taxa row with 8 df ($P < 0.001$ in all cases). The term usage frequency was significantly below (bold) or above (italics) the all-taxa mean in a G test with 1 df. Critical values are $P = 0.05$, $G = 3.85$; $P = 0.01$, $G = 6.63$; and $P = 0.001$ $G = 10.83$.

which resulted in 76.9% of articles being relevant; these are two random draws of 1,000 articles, which explains the difference in frequencies (see *SI Text* for further information and an accuracy assessment.) The exclusion of low relevance search terms led to an estimate that we retrieved 65% of relevant articles; this process represents a necessary compromise between precision (our 60% minimum relevance criterion for search terms) and inclusiveness. We did not attempt to estimate the proportion of articles for which we had no search terms. Therefore the estimate of 65% completeness is likely an overestimate, implying we probably underestimate the number of relevant articles published during the last decade.

Next, articles were selected for detailed analysis. Search terms in Table 2 were used to randomly locate an additional 1,000 articles published during 1997–2006. Papers scored as relevant or not. For relevant articles we recorded all of the following: the major taxonomic group studied (vector taxa were infrequently encountered and were not recorded); whether the study was specific to a particular species, a group of unrelated species, a study system, a broad taxonomic group (e.g., songbirds, freshwater fish), or was general; whether the paper was empirical, about a model, or a combination of the two; and whether terms used to refer to movement were used to refer to individuals or an entire population, or were ambiguous in this based on the term itself and its context. Additionally, relevant articles were scored for whether movement was focal. We defined movement as focal as including confirmation of the occurrence of movement, and measuring rates, seasonal or life-cycle timing of movement, and distances of movement. For papers in which movement was focal we recorded which of the links in the framework (figure 2 in ref. 5) were studied and whether measurements of movement were made and results given at the individual or population levels, or both, or were ambiguous in the level represented. In cases where information from abstracts was unclear we checked full papers.

ACKNOWLEDGMENTS. We thank the Institute for Advanced Studies in Jerusalem for hosting and sponsoring the Movement Ecology Working Group and other group members, particularly Ronen Kadmon, David Saltz, Peter Smouse, and Wayne Getz, for help in development of the methodologies and questions addressed and James Brown and an anonymous referee for helpful comments. M.H. was supported by National Science Foundation Grant DEB 0414465. R.N. was supported by National Science Foundation Grant DEB-0453665, Israel Science Foundation Grant ISF-FIRST 1316/05, U.S.-Israel Binational Science Foundation Grant 124/2004, and the Friedrich Wilhelm Bessel Award, Humboldt Foundation.

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