environment and the genome. Testosterone, for example, is induced by social interactions[18], but in turn regulates gene transcription. To the extent that genetic variation in life histories – the strategic decisions of organisms during their lifetime – reflect gene-by-environment interactions, further knowledge about the translation of genetic information into physiology and subsequent life history is urgently needed.

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Martin Wikelski*
Dept of Ecology and Evolutionary Biology, Princeton University, 303 Guyot Hall, Princeton, NJ 08544, USA.
*e-mail: Wikelski@princeton.edu

Robert E. Ricklefs
Dept of Biology, University of Missouri–St Louis, 8001 Natural Bridge Rd, St Louis, MO 63121, USA.

The challenges of studying dispersal

Ran Nathan

The 2001 Annual Symposium of the British Ecological Society on Dispersal was held at the University of Reading, UK, from 3–5 April 2001.

Dispersal – the movement of organisms away from their parent source – is a fundamental biological process that operates at multiple temporal and spatial scales. The process therefore has overwhelmingly important implications at multiple scales of organization: for the survival, growth and reproduction of individuals; for the composition, structure and dynamics of populations and communities; and for the persistence, evolution and geographical distribution of species[1]. Although the importance of dispersal was emphasized by Charles Darwin, Alfred Russel Wallace, Philip Darlington, Robert MacArthur, among others, dispersal has been condemned as immeasurable and unimportant (see Ref. 2 for review).

However, those days are over, now that the study of dispersal has evolved to be a major theme in biology, unifying and incorporating fields of research as diverse as ecology, evolutionary biology, microbiology, molecular biology, mathematics, physics, epidemiology, agricultural and atmospheric sciences, engineering and geography. The current bloom in dispersal research was illustrated by this recent British Ecological Society Dispersal symposium, which included discussions of multiple facets of dispersal for a wide range of organisms in diverse ecosystems across multiple spatial scales.

Describing dispersal patterns
The most fundamental task in studying the process of dispersal is describing the patterns that it generates. The immense difficulty of measuring dispersal, especially long-distance dispersal (LDD), was mentioned by nearly all speakers. Fortunately, many of them also suggested and exemplified potential solutions, reflecting major technological advances that enable one to measure dispersal systems that were previously impossible to measure. Three major methodological groups were emphasized: (1) movement–redistribution methods and direct tracking of individuals in particular; (2) genetic analyses; and (3) mathematical models.

Using movement–redistribution methods
The direct measurement of movements of an individual depends on appropriate methods being used relative to the body size of the organism being studied, especially for species dispersing over large distances. Tracking larger organisms is easier and can be more comprehensive than tracking small organisms (tracking is simply impracticable for the smallest organisms), but technology is advancing rapidly.

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At one extreme, Ian Boyd (British Antarctic Survey, Cambridge, UK) showed a picture of a ~400 kg southern elephant seal *Mirounga leonina* equipped with satellite tag, radio tag and four other different marks, enabling its movements to be tracked at very large spatial scales. At the other extreme of measurement possibility, Juliet Osborne *et al.* (Institute of Arable Crops Research, Rothamsted, UK) showed that ~250 mg bumblebees *Bombus terrestris* tagged with diode transponders of just a few milligrams can be detected from hundreds of meters by harmonic radar. Recently, this technology revealed an exceptional power and precision in insect flight: bumblebees can maintain direct routes of flight, even in strong cross winds[3].

Robert Kenward's (NERC Centre for Ecology and Hydrology, Dorchester, UK) review of marking techniques in terrestrial vertebrates illustrated applications of a wide array of redistribution methods (e.g. mark–recapture) and other techniques. Although there are many practical problems that need to be resolved (e.g. low accuracy of spatial position, disproportionate mortality of marked individuals and high costs), the emergence of many ingenious marking techniques promises even better future descriptions of dispersal patterns. However, Chris Thomas and Robert Wilson (University of Leeds, UK) suggested that, rather than pursuing 'perfect' descriptions of dispersal, the focus should be on the identification of, and correction for, biases, and the resulting interpretation of dispersal data.

Using genetic methods

Several speakers illustrated the use of genetic methods for quantifying dispersal patterns through analyses of the variation in genetic markers such as microsatellites and rDNA. According to James Brown *et al.* (John Innes Centre, Norwich, UK), spores of one particular virulent clone of wheat yellow rust fungus *Puccinia striiformis* have been dispersed by winds between UK and Denmark several times during the past two decades, causing severe epidemics in both countries.

Another study using genetic markers, by Beth Okamura and Joanna Freeland (University of Reading, UK), demonstrated the problems that are associated with genetic analysis. Their findings of low levels of gene flow in European and North American populations of *Cristattella mucedo*, an aquatic invertebrate, conflicted with ecological evidence of significantly higher rates of dispersal (e.g. by waterfowl). This discrepancy could emerge from one of several causes, including effects of the sampling design, the existence of storage effects by dormant propagules retained in sediments over prolonged periods, or violations of the basic assumptions of F_{ST}-type estimators. The use of F_{ST}-type estimators – which measure the among-population difference in allele frequency – to infer dispersal patterns has been widely criticized recently (e.g. Refs 4,5 for review). However, Alan Raybould (NERC Centre for Ecology and Hydrology) argued that F_{ST}-based approaches could still provide insights into dispersal patterns. In particular, calculating correlations between all pairs of subpopulations in a sample, coupled with partial regression and randomization tests, can help distinguish between alternative dispersal models.

Using mathematical models

The key description of dispersal patterns is the 'dispersal curve', which gives either the frequency distribution of dispersal distances, or the number of propagules per unit area as a function of the distance from the source. When the latter is given as a probability density function, it is called the 'dispersal kernel' (see Ref. 6 for definitions and examples of dispersal curves and dispersal kernels).

Dispersal curves were presented by almost all speakers, and were thoroughly discussed by David Greene (Concordia University, Montreal, Canada) and Nanako Shigesada and Kohkichi Kawasaki (Nara's Women University, Nara, Japan). Although estimated for different organisms and with different methods, these curves universally described an abundance of relatively short dispersal distances and a rarity of LDD. A general consensus emerged from the symposium about the disproportionate importance of rare LDD events. Such events determine the rate of invasions, epidemics and range expansions, maintain metapopulation structures, enable gene flow between distant locations, and are likely to be crucially important in the face of climate changes. This explains the willingness of many researchers to pursue ways of quantifying LDD and unravelling its mechanisms. Along with many beneficial effects, LDD can also have detrimental effects on species survival; for example, using spatially explicit models, Andy South *et al.* (University of Oxford, UK) showed that LDD promotes Allee effects, such as difficulties in finding a mate.

Dispersal curves can be fitted by several mathematical functions. James Bullock (NERC Centre for Ecology and Hydrology) and Greene showed that seed dispersal data frequently fit fat-tailed dispersal kernels, indicating relatively high LDD. Bullock applied a theoretical framework[7] that incorporates the effects of variation in demography and dispersal on spatial spread to two dwarf shrub species *Calluna vulgaris* and *Erica cinerea* in Britain. He found that the frequency and magnitude (spatial extent) of extreme LDD events are of enormous importance in determining the rate of spread. Steve Compton (University of Leeds) illustrated staggering indirect evidence of LDD of fig wasps *Ceratosolen arabicus* that pollinated an isolated fig tree *Ficus sycomorus* >68 km from the nearest conspecific in the Namibian desert. The challenge now is to understand the mechanisms allowing such weak flyers, which are also short-lived (two–three days) and highly host specific, to retain such a remarkable long-distance colonization ability.

Understanding the causes and consequences of dispersal

In addition to their role as tools for describing dispersal, models can also provide the means for examining and generating hypotheses about the causes and consequences of dispersal. Several speakers integrated models and empirical data to highlight the importance of considering behavioral aspects of animal dispersal and the scale, context and conditions within which it occurs. Nils Stenseth and Harry Andreassen (Oslo University, Norway) incorporated behavioral aspects of dispersal and population dynamics into their model of small mammal dispersal in patchy habitats. They emphasized that dispersal rates are likely to be density dependent, because they are conditioned to population density – both at the source and in the recipient habitat patch[8].

Positive versus negative density-dependent dispersal

Whereas Stenseth and Andreassen assumed negative density-dependent dispersal (based on empirical evidence[9] from the root vole *Microtus oeconomus*), Bill Sutherland (University of East Anglia, Norwich, UK) argued that, in many terrestrial vertebrates, such density dependence is actually positive. This debate is important, because theoretical studies have shown that the presence and sign of density-dependent dispersal can strongly affect the spatial and genetic structure of populations. The controversy over the sign of density-dependent dispersal might result from variation in the spatial dimension of population synchrony relative to the spatial scale of dispersal[10].

Dispersal and predator–prey dynamics

In a related talk, Xavier Lambin *et al.* (University of Aberdeen, UK) discussed the role of dispersal in inducing spatial synchrony in predator–prey systems. They argued that low rates of dispersal are sufficient to explain the observed periodic travelling waves in oscillatory predator–prey systems. By contrast, Ims and Andreassen[9] concluded that such waves emerge primarily from predation, and that dispersal is only linked indirectly because 'risky' dispersal away from a patch increases the rate of predation.

Dispersal and invasions

Two important consequences of dispersal involve species invasions and response to global climate change. Andy Cohen (San Francisco Estuary Institute, Richmond, CA, USA) discussed the factors that determine the success of human-mediated invasions. He argued that previous generalizations, such as those linking invasion success to highly fecund species and to highly disturbed habitats, are not supported by quantitative analyses. The apparent lack of generality makes management decisions difficult. However, general explanations of invasion success might be exposed by exploring unconventional possibilities, such as the possible link between invasion success and factors affecting growth of small isolated populations.

Dispersal and climate changes

Range shift through dispersal, along with adaptation and extinction, is a possible response to climate changes. Pollen and genetic analyses show that different species behaved differently in response to past climate changes[11]. Andrew Watkinson (University of East Anglia) observed differential behavior that is currently occurring in British birds, where changes in the distribution of only 12 out of 204 species were significantly associated with climate. The differential response can be explained given that dispersal is not the sole process affecting species distribution[2]. In addition, dispersal varies considerably between species, partly because adaptations to dispersal involve tradeoffs with other fitness components. Thus, predictions of species responses to climate change are likely to be species specific, rather than general across species; such predictions also take into account the role of processes other than dispersal.

Dispersal tradeoffs

Tradeoffs between dispersal ability and other life-history characteristics are also important in plants. Using phylogenetically independent contrasts, Ken Thompson (University of Sheffield) re-examined three adaptive tradeoffs, between seed dispersal and: (1) chemical composition of seeds; (2) seed persistence in the soil; and (3) the competitive ability of the emerging seedlings. Surprisingly (at least for the third tradeoff, which many view as well established), he found no evidence for any of them. However, Thompson's use of the terminal velocity of seeds in still air as a surrogate for dispersal ability is questionable, because this trait only explains a small fraction of the variation in dispersal distances[12]. Other traits, such as those associated with differential release of seeds in relatively strong winds, might be more important determinants of dispersal ability in wind-dispersed plants.

Future challenges

The symposium highlighted the major challenges for dispersal studies in the near future. The challenge of quantifying and understanding the mechanisms of dispersal – and LDD in particular – is now widely acknowledged and is being actively pursued. Towards this end, the integration of technological advances, mathematical models and comprehensive empirical studies promises new insights into the patterns, causes and consequences of dispersal. The process of establishment, especially following LDD events, is poorly understood, and it is important to recognize the process of establishment as being separate from, but complementary to, the process of dispersal (movement) itself.

Advances in the study of dispersal and establishment set the stage for resolving this great challenge, which would advance our understanding of the consequences of dispersal for populations, metapopulations and communities at multiple spatial scales. The current state of dispersal research – as reflected by this symposium – is characterized by exciting progress with many questions still unresolved, thus providing fertile ground for colonization by researchers who are able to develop genuinely interdisciplinary research.

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Ran Nathan
Dept of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003, USA.
e-mail: rann@eno.princeton.edu