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Population ecology

Meeting report

Spatial ecology across scales

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The international conference 'Models in population dynamics and ecology 2010: animal movement, dispersal and spatial ecology' took place at the University of Leicester, UK, on 1–3 September 2010, focusing on mathematical approaches to spatial population dynamics and emphasizing cross-scale issues. Exciting new developments in scaling up from individual level movement to descriptions of this movement at the macroscopic level highlighted the importance of mechanistic approaches, with different descriptions at the microscopic level leading to different ecological outcomes. At higher levels of organization, different macroscopic descriptions of movement also led to different properties at the ecosystem and larger scales. New developments from Levy flight descriptions to the incorporation of new methods from physics and elsewhere are revitalizing research in spatial ecology, which will both increase understanding of fundamental ecological processes and lead to tools for better management.

Keywords: dispersal; individual movement; fat tails; biological invasion; pattern formation; synchronization

1. INTRODUCTION

Spatial ecology remains an exciting and important area of study with the goal of determining the causes and consequences of the distribution of species over time and space [1]. We note several particular areas that were emphasized in the meeting: scaling, the interplay between ecological and evolutionary aspects and the determination of group behaviour by the behaviour of individuals. There is also great potential for cross-fertilization with other biological disciplines, such as models of tumour growth and cellular processes and neuroscience.

Descriptions of spatial processes in ecology have long focused on the reaction–diffusion framework, which can be thought of as one of the simplest ways of relating dynamics at the level of an individual (random walk) to dynamics at the population level. Among the classic results in ecology emerging from the diffusion description is the rate of spread of an invading species. Other results that arise include ones on spatial pattern [2].

Yet, ecologists have increasingly recognized problems with using reaction–diffusion frameworks as the primary description of spatial processes. These models make assumptions about movement at the individual level, that the distribution of individual movement steps is Gaussian (i.e. Brownian), that may not always be appropriate. Different descriptions of microscopic movement may be needed. Levy flights, in contrast to Brownian motion, allow more general distributions of jump sizes that still scale so that the sum of N jumps has the same distribution as a single jump. The original hypothesis that animal movement may show scale invariance and fractal properties was made by Mandelbrot [3]. The difficulty in determining appropriate descriptions of movement is exacerbated by insufficient amount of data for rare events like long steps.

Thus, a central issue is the understanding of how the patterns of movement and dispersal on the individual (microscopic) level would affect the dynamics on higher (population, ecosystem and community) levels. This would explain, for instance, the observed persistence of populations in harsh environments, effective mechanisms of grazing control, the success or failure of biological invasions, etc. Another important issue is how to incorporate efficiently observed complex patterns of animal movement (or/and dispersal) into ecological models. In this sense, some new modelling approaches and techniques borrowed from other sciences (e.g. statistical physics) provide exciting opportunities. Thirdly, the recent progress has emphasized the importance of collective motion in populations or animal groups which is crucial for modelling of social animals [4]. Finally, there are still large gaps in our understanding of patterns of movement of individuals in their natural environment, which seriously undermines the predictive power of models.

2. NEW APPROACHES AND RESULTS IN SPATIAL ECOLOGY

The main aim of the conference 'Models in population dynamics and ecology 2010: animal movement, dispersal and spatial ecology' was to bring together researchers with different backgrounds (ecology, tumour modelling, theoretical physics, mathematics, statistics, etc.) to demonstrate and discuss recent progress in the above issues, as well as to develop interdisciplinary approaches and emphasize the common nature of the underlying mechanisms and processes of individual movement and dispersal across space and time scales. The conference was organized by S.P. and sponsored by the London Mathematical Society and the University of Leicester, UK.

(a) *Appropriate microscopic descriptions of movement matter*

The theme of the appropriate microscopic description of movement was central and here the spatial scale becomes crucial. Karl Hadeler showed that on small spatial and time scales, movement of some organisms can be described by transport equations, rather than diffusion equations. Frederic Bartumeus argued, on theoretical grounds, that a Levy walk should arise as a result of an optimal food search strategy. Alex James showed the difficulties of identifying the

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underlying movement processes based on the observed patterns, especially when the data are taken at discrete time. Andy Reynolds emphasized the importance of the time scale of observation for revealing the nature of animal movement. On a small time scale, Levy walks become undistinguishable from correlated random walks (i.e. Brownian-type motion). Another important issue, when one is searching for an empirical evidence for a Levy flight, is interspecific variation between individuals within population. Alla Mashanova demonstrated that a random work in statistically structured populations can result in Levy-type patterns of animal movement. Similar mechanisms of fat-tail dispersal patterns were described earlier [5], but new insights arise from consideration of more detailed data on individual animal tracks.

Traditional reaction–diffusion models are additive with respect to the contribution from dispersal and from population growth, but will it remain the same in the case when the underlying individual movement is not Brownian? Sergei Fedotov demonstrated that, if movement is not Brownian, the spatial dynamics and local growth cannot be separated. The diffusion–reaction-type model arising as a result of a rigorous theoretical approach possesses properties significantly different from those of the heuristic models [6].

Given different descriptions of movement, how can the appropriate one be chosen? Field data can be misleading if they are collected on an inappropriate spatial/temporal scale, affected by irregularities of the ecological protocol or pooled together from non-identical subsystems such as different individuals or different subpopulations. It is well known that the Levy flight of albatrosses changes to something looking much more like a diffusive movement when the intermittency of the flight is taken into account [7,8]. Rod Blackshaw emphasized the importance of the details of trap experiments in the natural environment aimed at discriminating between different patterns of individual movement of insects. The results of conventional trap experiments (e.g. differentiation between Levy and correlated Brownian motion) become very sensitive to details of the experimental design.

(b) *Consequences at larger scales*

The application of movement models to questions of ecological interest was the other primary focus of the conference, with conclusions depending on the underlying movement model. Scaling from individual movement to a statistical description at the population level involves assumptions, as in the derivation of the Fokker–Planck equation [9]. Nitant Kenkre showed, using the Fokker–Planck formalism, how the macroscopic property of animal territoriality can be related to the peculiarities of individual movement, and used this analysis to describe the spread of Hantavirus epidemics in animal populations. Nick Britton showed that the patterns of movement of organisms on the individual level can be drastically affected by collective decision (where to go) made by the whole population (the dynamics of social insects was a case study). Edward Codling revisited the 'many wrongs principle' by introducing a leader in each group of animals and emphasizing the importance of such a leader in enhancing the total group performance. An important idea, which came from the talk by Jamie Wood, was to demonstrate the importance of heterogeneity of life-trait characteristics within a group (population) on the collective motion of this group.

Other applications were more focused on scaling up to still higher levels of organization, while taking into account heterogeneities and other complications required for understanding natural systems. Biological invasions make one of the major threats to biodiversity and agriculture around the globe; yet species spread in heterogeneous settings remains poorly understood (but see [10]). Nanako Shigesada addressed this problem for a few different cases of environment structure (strip-like, island-like and corridor-like) where favourable and unfavourable patches alternate, and arrived at an unexpected conclusion that the rate of spread can drop down to zero abruptly when the proportion of the area occupied by a favourable habitat is still rather high (of the order of 50%). Advection (e.g. wind for airborne species) helps the species to persist and spread over unfavourable habitats where it would go extinct without advection, but it changes the system response to the scale of the fragmentation. Horst Malchow showed how competition among other species can stop the spread of an invader, so that introducing a specialized weed consumer would have the strongest effect on slowing down spread and may lead to eradication. This result is in a good agreement with earlier studies (cf. [11]).

The speed and mode of movement becomes crucial for shaping and understanding the behaviour of an ecosystem. Richard Law emphasized that, for persistence and spread of populations of plants, the dispersal range of seeds should be optimal (neither too small, nor too large), where this optimality is determined by the landscape properties in conjunction with evolution within the species. A.M. showed that fast-moving predators in an extended ecosystem can guarantee a successful grazing control even in the case of an unlimited stock of resource of the prey. An important ecological application includes plankton communities in eutrophic waters where the zooplankton is capable of quick adjustment of its vertical position throughout the whole vertical column [12]. Mauro Mobilia showed that, in the case of a supercritical mobility of individuals, the persistence of populations can be threatened. Interestingly, the existence of threshold for mobility of bacteria, which becomes necessary for their survival, has been reported experimentally as well (see references in Reichenbach [13]).

On still larger spatial scales (e.g. from the metapopulation to the ecosystem scales), animal movement and dispersal can be modelled in a conventional way (using reaction–diffusion, integro-differential or coupled-map lattice frameworks, which are, respectively, continuous in time and space, discrete in time and continuous in space, or discrete in both). Large-scale synchronization in population dynamics has been another long-standing mystery. A.H. gave an account of the recent progress in understanding of this phenomenon and its implications [14] using a system of weakly coupled oscillators as a paradigm. Finally, mathematical descriptions of dispersal on the largest spatial scales (cross-continental and planetary scales) can be obtained using a network framework, as discussed by Michael Gastner, with applications to biological invasions caused by cargo ships [15].

3. CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

There is a need to determine what the patterns of animal movement are on a microscale under varying conditions. This would imply refining observational and experimental techniques and frameworks as well as revisiting existing empirical data. Secondly, a crucial issue is an adequate macroscopic description of animal movement at both population and ecosystem levels. This would require implementation of techniques of reduction of variables (e.g. from the individually based modelling to mean-field approximation). Some new modelling techniques borrowed from other sciences (e.g. theoretical/statistical physics) have great potential (cf. [16]). Thirdly, complex patterns of animal movement and dispersal should be considered together with evolutionary aspects. Indeed, patterns of animal movements and dispersals observed in nature are likely to be evolutionarily stable. Finally, developing interdisciplinary collaborations among mathematicians, biologists, statisticians and physicists is becoming still more important for future progress in modelling of animal movement and dispersal in spatial ecology.

The key questions remain the determination of what are the most useful descriptions of movement and their consequences, recognizing that any model is an approximation. For example, since infinitely large step lengths are biologically unrealistic, Levy flights in the exact mathematical sense can hardly exist in nature at all; instead, one should rather talk about a scale range where Levy statistics may be applicable, cf. 'truncated power laws'. The themes of tightening the interplay between models and data, with a more rigorous approach both to data and theory, and the need for developing multi-scale approaches to dispersal are clearly the keys to future progress.

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