Mathematical Medicine and Biology (2011) **28**, 85–88
doi:10.1093/imammb/dqr003
Advance Access publication on May 5, 2011

Collective dynamics: when one plus one does not make two

ALEXANDER GORBAN AND SERGEI PETROVSKII*
Department of Mathematics, University of Leicester LE1 7RH, Leicester, UK
*Corresponding author: sp237@le.ac.uk

[Received on 30 November 2010; revised on 10 January 2011;
accepted on 16 February 2011]

A brief introduction into the interdisciplinary field of collective dynamics is given, followed by an overview of 'Mathematical Models of Collective Dynamics in Biology and Evolution' (University of Leicester, 11–13 May 2009).

Keywords: population dynamics; biological evolution; pattern formation; nonlinear dynamics.

Indeed, when? Solution to this apparent paradox is amazingly simple, provided we do not interpret the problem straightforwardly. Take one female and one male individual of any animal species, keep them together for a sufficiently long time, feed them properly and then after a while you will normally get more than two of them. Otherwise, keep them far away from each other or do not feed them well enough and you will obtain zero at the end.

The above example may look somewhat like an anecdote but it is, in fact, quite serious. As a matter of fact, it grasps the essence of the population dynamics and very much that of collective dynamics in general: once the interaction between subsystems becomes strong enough, a new entity may emerge. It emphasizes the importance of different temporal and spatial scales and also stresses the principal difference between the dynamics of closed and open systems. Once the system is open to influxes of mass, energy and information, one plus one is not necessarily two any more.

Collective dynamics—understood as the dynamics arising from the interplay between the constituting elementary argents or parts of a more complex system—has been one of the main paradigms of the natural sciences over the last several decades. Interactions between the argents are often non-linear and therefore it also greatly fertilized mathematical development, in particular, in the areas such as non-linear ordinary differential equations, partial differential equations and dynamical systems in general. The importance of collective and non-linear effects was perhaps best appreciated in physics, resulting in new fields of non-equilibrium thermodynamics and synergetics (Glansdorff & Prigogine, 1971; Nicolis & Prigogine, 1977; Haken, 1978), but eventually spreading across different disciplines. Especially over the last three decades, its most fruitful applications were arguably in the life sciences. Dynamics of interacting populations in ecology, natural selection and the theory of evolution, and tumour growth in medicine give a few examples where application of concepts and tools of collective dynamics have been especially fruitful.

Collective dynamics had reached the stage of maturity in the works by I. Prigogine and H. Haken (see the references above), culminating in Prigogine winning 1977 Nobel Prize, but it has a much longer history. *Ecological dynamics* was created by Lotka (1925) and Volterra (1926). They modified the mass action law proposed for chemical dynamics by Guldberg & Waage (1879) and applied this approach to population dynamics. Simple as it may seem nowadays, these works created the cornerstone of the whole discipline of mathematical ecology, with the idea of self-organized population cycles being one of its central points.

The mathematical approach to *biological evolution* was intensively developed in the 1930s. The notion of 'Darwinian fitness' was reconstructed mathematically. Fisher (1930) proposed to construct fitness as a combination of independent individual contribution of various traits. Haldane (1932) criticized the approach based on independent actions of traits. Gause (1934) modelled the concurrent exclusion on the base of ecological dynamics. Modern synthetic definitions of the fitness function are based on adaptation dynamics. For the structured populations, the fitness should be defined through the dominant Lyapunov exponents (Metz *et al.*, 1992). Recent developments have seen an interplay and convergence between different approaches. In particular, Fisher's and Haldane's approaches were combined (Waxman & Welch, 2005): Haldane's concern is incorporated into Fisher's model by allowing the intensity of selection to vary between traits.

Is this synthesis now complete? Not yet. This is an endless story. *Animal behavior* introduces a new dimensions in the problem. Emerging phenomena in space and time (Malchow *et al.*, 2008) make the whole game mysterious and complicated. Elementary processes seem to be known and well understood but how do they combine in the complete dynamics? This may be a difficult question. Efforts to understand complexity creates new challenges and lead to new synthesis. We have to combine ecology, evolution, behaviour and emerging phenomena in space and time dynamics. Sometimes, we also have to revisit the formal mathematical background of the main phenomena like natural selection (Gorban, 2007) or reaction–diffusion waves in biology (Volpert & Petrovskii, 2009) and then resume our struggle with complexity.

It is impossible to perform such a synthesis in one paper or even in one life. This should be a collective work with regular intensive communication between participants. The challenges that have risen from the recent development in life sciences, especially in mathematical medicine, population dynamics, ecology and evolution have been the focus of 'Mathematical Models of Collective Dynamics in Biology and Evolution' (University of Leicester, 11–13 May 2009), an international conference and London Mathematical Society workshop organized by S. Petrovskii. Presentations by 38 participants, including eight keynote speakers (F. Berezovskaya, D. Grunbaum, A. Hastings, G. Karev, J. King, A. Neishtadt, D. Rand, and E. Venturino) covered a broad range of topics. The following specific issues were examined and discussed in detail:

- interplay between deterministic and stochastic approaches to modelling biological systems, with emphasis on scenarios of pattern formation and spatial spread;
- hybrid models of the collective dynamics arising as a result of the interplay between agents of different origin, with emphasis on eco-epidemiological systems;
- complexity of biological dynamics and models reduction;
- progress in the mathematical theory of evolution and interplay between the population dynamics on the evolutionary and ecological time scales.

The honorary lecture 'Invasion using microcorrelations in spatial and network games' was given by D. Rand (University of Warwick). He presented some new results on the influence of microcorrelations on spatial and network game dynamics and developed new techniques that allow one to deduce analytical results about such games. In particular, he applied the analytical theory to the case where the number of neighbours (the so-called coordination number) is not constant and varies from site to site. A general result was obtained that allows application of these ideas to a very broad range of models including those involving imitation and learning in addition to birth–death ecological processes. Also, a new analytical approach to invasion was presented which sees it as a two-stage process in which firstly the invaders create a local micro-correlated population and then the microcorrelations determine whether or not this local population can invade the resident population. Effectiveness of these methods was demonstrated by applying them to the Prisoner's Dilemma game where an exact criteria for the case of cooperative strategies invasion were obtained.

We also mention here a few other keynote talks.

A. Hastings (University of California at Davis) addressed the issue of multiple scales in ecological dynamics. He considered ways that time (and necessarily space) scales enter into ecological understanding, and how ecological dynamics plays out over intermediate time and space scales. The concepts were illustrated with examples drawn from variety of ecological systems ranging from diseases to marine systems (including coral reefs) and many others.

J. King (University of Nottingham) revisited recent progress in cancer modelling with emphasis on multi-scale properties of tumour growth.

The issue of collective dynamics in its most literal sense was the focus of the talk by D. Grunbaum (University of Washington) who considered the dynamics of social groups such as schools, swarms, flocks and herds, which are a common feature of many animal species. Grouping strongly affects the ecological and evolutionary dynamics of these species. However, a theoretical understanding of the mechanics of social groups sufficient to describe and predict their evolutionary causes and ecological consequences is lacking. The talk revisited recent efforts to quantitatively link individual social behaviours, group-level characteristics and population dynamics.

G. Karev (National Institute of Health USA) considered mathematical models of several seemingly different phenomena such as global demography, early biological evolution, tree stand self-thinning, and some others, and showed that their properties can be described in a unified manner by relating them to replicator equations minimizing the production of information (Karev *et al.*, 2011).

This volume includes seven carefully selected papers from the total of about 40 presented at the workshop. Ecology was one of the major themes at the workshop and hence it is not surprising that most of these papers are concerned with ecological problems. A broad range of topics is covered. Banerjee (2011) considered an old problem of ecological pattern formation and addressed it using a novel mathematical technique based on higher order stability analysis. Berezovskaya *et al.* (2011) considered the dynamics of interacting population on a fragmented habitat under the presence of the strong Allee effect and presented a careful and exhaustive mathematical analysis of the problem. Full bifurcation structure has been restored and the rich variety of dynamical regimes has been revealed. Malchow *et al.* (2011) considered biological invasions in an unstable environment stochastically perturbed and applied their findings to weeds invasion in New Zealand. Sazonov *et al.* (2011) accomplished a detailed mathematical study of epidemics spread on a fragmented habitat focusing on a particular but important one-dimensional case. The results make an important contribution to understanding peculiarities of epidemics spread on a network. Morozov et al. (2011) considered a generic mechanism of self-regulation of plankton dynamics in eutrophic ecosystems based on the interplay between the vertical gradient of the phytoplankton growth rate due to the light attenuation with depth and the grazing by fast-moving zooplankton. Finally, Zemskov *et al.* (2011) studied a reaction–diffusion system of FitzHugh–Nagumo type with linear cross-diffusion terms. Based on the analytical description using piecewise linear approximations of the reaction functions, they accomplished a complete analytical study of travelling pulses for two generic reaction–diffusion systems of high relevance for many applications in physical and biological sciences.

REFERENCES

BANERJEE, M. (2011) Spatial pattern formation in ratio-dependent model: higher order stability analysis. *Math. Med. Biol.*, **28**, 111–128.

BEREZOVSKAYA, F., WIRKUS, S., SONG, B. & CASTILLO-CHAVEZ, C. (2011) Dynamics of population communities with prey migrations and strong Allee effects: a bifurcation approach. *Math. Med. Biol.*, **28**, 129–152.

FISHER, R. A. (1930) *The Genetical Theory of Natural Selection*. Oxford: Oxford University Press.

GAUSE, G. F. (1934) *The Struggle for Existence*. Baltimore, MD: Williams & Wilkins.

GLANSDORFF, P. & PRIGOGINE, I. (1971) *Thermodynamics of Structure, Stability, and Fluctuations*. New York: Wiley-Interscience.

GORBAN, A. N. (2007) Selection theorem for systems with inheritance. *Math. Model. Nat. Phenom.*, **2**, 1–45. E-print: arXiv:cond-mat/0405451 [cond-mat.stat-mech].

GULDBERG, C. M. & WAAGE, P. (1879) Concerning chemical affinity. *Erdmann's J. Practische Chemie*, **127**, 69–114.

HAKEN, H. (1978) *Synergetics*. Berlin: Springer.

HAKEN, H. (1983) *Advanced Synergetics*. Berlin: Springer.

HALDANE, J. B. S. (1932) *The Causes of Evolution*. London: Longmans Green.

KAREV, G. P., NOVOZHILOV, A. S. & BEREZOVSKAYA, F. S. (2011) On the asymptotic behavior of the solutions to the replicator equation. *Math. Med. Biol.*, **28**, 89–110.

LOTKA, A. J. (1925) *Elements of Physical Biology*. Baltimore, MD: Williams and Wilkins.

MALCHOW, H., JAMES, A. & BROWN, R. (2011) Competition and diffusive invasion in a noisy environment. *Math. Med. Biol.*, **28**, 153–163.

MALCHOW, H., PETROVSKII, S. V. & VENTURINO, E. (2008) *Spatiotemporal Patterns in Ecology and Epidemiology: Theory, Models, and Simulations*. London: Chapman & Hall/CRC Press.

METZ, J. A. J., NISBET, R. M. & GERITZ, S. A. H. (1992) How should wedefine fitness for general ecological scenarios. *Trends Ecol. Evol.*, **7**, 198–202.

NICOLIS, G. & PRIGOGINE, I. (1977) *Self-organization in Nonequilibrium Systems*. New York: Wiley-Interscience.

MOROZOV, A. Y., ARASHKEVICH, E., NIKISHINA, A. & SOLOVYEV, K. (2011) Nutrient-rich plankton communities stabilized via predator-prey interactions: revisiting the role of vertical heterogeneity. *Math. Med. Biol.*, **28**, 185–215.

SAZONOV, I., KELBERT, M. & GRAVENOR, M. B. (2011) Travelling waves in a network of SIR epidemic nodes with an approximation of weak coupling. *Math. Med. Biol.*, **28**, 165–183.

VOLPERT, V. & PETROVSKII, S. V. (2009) Reaction-diffusion waves in biology. *Phys. Life Rev.*, **6**, 267–310.

VOLTERRA, V. (1926) Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Mem. R. Accad. Naz. dei Lincei*, **2**, 31–113.

WAXMAN, D. & WELCH, J. J. (2005) Fisher's microscope and Haldane's ellipse. *Am. Nat.*, **166**, 447–457.

ZEMSKOV, E. P., EPSTEIN, I. R. & MUNTEAN, A. (2011) Oscillatory pulses in the FitzHugh-Nagumo type systems with cross-diffusion. *Math. Med. Biol.*, **28**, 217–226.