

a pluralistic activity. The recent advent of genomic sequences of pathogens (e.g. *Mycobacterium tuberculosis* and *M. leprae* [8,9]) and the increasing availability of micro-arrays now provide a novel set of tools in a post-genomic era for understanding the functional diversity of parasite and their genes. Coupling this with individual-level responses, population dynamic analyses and evolutionary insights, the stage is set for addressing fundamental problems at the interface of host–parasite interactions. Although challenging, the rewards make understanding how parasites impact on physiology,

behaviour, populations and assemblages a contemporary research theme in evolutionary ecology.

References

- 1 Kermack, W.O. and McKendrick, A.G. (1927) A contribution to the mathematical theory of epidemics. *Proc. R. Soc. Lond. Ser. A* 115, 700–721
- 2 Bartlett, M.S. (1960) *Stochastic Population Models in Ecology and Epidemiology*. Methuen & Co.
- 3 Anderson, R.M. and May, R.M. (1991) *Infectious Diseases of Humans. Dynamics and Control*. Oxford Science Publications
- 4 Omacini, M. *et al.* (2001) Symbiotic fungal endophytes control insect host–parasite interaction webs. *Nature* 409, 78–81
- 5 Kraaijeveld, A.R. and Godfray, H.C.J. (1997) Trade-off between parasitoid resistance and

larval competitive ability in *Drosophila melanogaster*. *Nature* 389, 278–280

- 6 Gandon, S. *et al.* (2001) Imperfect vaccines and the evolution of pathogen virulence. *Nature* 414, 751–756
- 7 Earn, D.J.D. *et al.* (2000) A simple model for complex dynamical transitions in epidemics. *Science* 287, 667–670
- 8 Cole, S.T. *et al.* (1998) Deciphering the biology of *Mycobacterium tuberculosis* from the complete genome sequence. *Nature* 393, 537–544
- 9 Cole, S.T. *et al.* (2001) Massive gene decay in the leprosy bacillus. *Nature* 409, 1007–1011

Mike Bonsall

Imperial College at Silwood Park, Ascot, Berkshire, UK SL5 7PY.
e-mail: m.bonsall@ic.ac.uk

Modeling insect societies: from genes to colony behavior

Zachary Y. Huang and Jennifer H. Fewell

The workshop, Modeling Complexity Across Levels: Social Insect Societies as Multilevel Integrated Systems, was held in Santa Fe, NM, USA, from 23 to 26 May 2002.

Published online: 11 July 2002

Social insects have intrigued naturalists and historians since Aristotle [1] and have been widely studied because of their complexity [2]. Social insects are unique in that they have one more level of complexity compared to nonsocial organisms [3]. Each individual (worker) is more or less autonomous in its movement and activities. Yet, a colony of 40 000 honeybees or millions of ants exhibits such cohesion and coordination that it exhibits colony behavior that is not a simple summation of individual behavioral repertoire. How do these individuals produce complex behaviors, such as trail forming in ants, or allocating the correct proportion of foragers and nurses in honeybees? A recent workshop organized by Robert Page (University of California, Davis, CA, USA) and Sandra Mitchell (University of Pittsburgh, PA, USA) not only tried to provide answers, but also explored tools useful for this endeavor. This was the third in a series of workshops on this topic held by the SFI Social Insect Working Group (<http://sfi.cyberbee.net>) at the Santa Fe Institute, and its main purpose was to educate researchers about multilevel approaches to behavioral science,

and to strengthen the connection between empirical studies and abstract modeling.

In spite of their empirical advantages, the use of animal societies generally, and social insects specifically, for exploring self-organization has been limited by the ability of researchers to place their work in a formal mathematical framework. In other words, there are many good social insect biologists, but few of us can model. One of the primary objectives of the workshop was to determine whether different modeling techniques might be applicable to different problems, and whether we can agree on a common platform (regardless of whether it is a commercial product) to allow better exchange and collaboration. MATLAB, in conjunction with SimuLink (The Mathworks Inc, MA, USA) seems, to empirical biologists, to be user-friendly, and also has the necessary robustness to scale across different levels of analyses. Its ease of use, as well as power, were tested (and verified) by the participants, who had opportunities to practice with real life examples in modeling tutorials. Tor Johansen (Norwegian University of Science and Technology, Norway) gave an overview of MATLAB from an engineering cybernetics view, showed the applicability of the platform for population-level modeling, using Lotka–Volterra differential equations of predator–prey population oscillations.

Stig Omholt (Agricultural University of Norway, Norway) integrated

within individual mechanisms (hormones and genes) with worker–worker interactions [4] to show that a colony can make ‘intelligent decisions’ for regulating the nurse–forager transition. Extending the approach of vertical integration from the genetic to the colony level, Robert Page and Joachim Erber (Berlin Technical University, Germany) presented a working MATLAB/SimuLink model using genetic variation in octopamine levels to produce variation in sucrose response thresholds in worker honey bees. The model provided an output in which colonies responded flexibly to changes in stimuli for pollen collection, and in which workers showed a division of labor for foraging for nectar or pollen. This model also provided a good example of how the use of a common platform can enable empiricists working at different organizational levels to talk with one another. The input parameters and their relationships were generated from empirical data gathered at multiple levels of organization, from quantitative trait loci assessments of genetic effects, to neurophysiological studies of hormonal effects, to colony-level assays of foraging regulation.

Another modeling approach was demonstrated by Claire Detrain and Jean-Louis Deneubourg (University of Brussels, Belgium). Using a combination of simple analytical modeling and elegant observations of collective behaviors in ants, they showed how manipulations of

specific behaviors, such as trail laying and aggregation, can be used to dissect the interaction effects that generate emergent behaviors. As an example, ants were offered choices between two routes to a single source. Random initial differences in trail laying generated cascading effects resulting in one trail becoming the dominant route. The accumulation of ants along this route allows calculation of how trail laying imposes an amplification of the stimulus for choosing a given route, which can be calculated formally. Both this 'fine-scale' approach and the coarser but multi-level approach shown by the Page–Erber model produced valuable information about the emergence of collective patterns. Questions that need to be addressed to decide which modeling technique is the most fruitful are whether we can integrate successfully across the scales of these two approaches, and what complementary information they can provide.

Good models are built upon known mechanisms (causes and effects), but is it possible to sort out causation and correlation, when controlled experiments to manipulate many variables are not

possible? Bill Shipley (Universite de Sherbrooke, Canada) says yes [5]. The hands-on use of the programs that he has developed helped delegates to understand the use of path analysis in ecological research and modeling.

One of the most encouraging components of this workshop was the number (11, or 50%) of graduate students and postdocs in attendance, and the small cross-disciplinary group discussions between students and faculty. Closing the gap between empirical and theoretical approaches is vital to the goal of understanding social groups (or any biological system) as emergent systems. The development of tools and tutorials moves us closer to that goal. However, although established empirical scientists need to understand these models, they are probably not the best bet for generating them. Perhaps the most promising way is to train new scientists in the interface between theory and data.

Acknowledgements

We thank Robert Page and Sandra Mitchell for constructive comments on this article. The workshop

was jointly funded by the National Science Foundation and the Santa Fe Institute.

References

- 1 Page, R.E., Jr and Erber, J. (2001) The evolutionary dynamics of social organization in insect societies: from behavior to genes and back. *SFI Bull.* 16, 1–7 (center section)
- 2 Page, R.E., Jr and Erber, J. (2002) Levels of behavioral organization and the evolution of division of labor. *Naturwissenschaften* 89, 91–106
- 3 Mitchell, S. (1995) The superorganism metaphor: then and now. In *Biology as Society, Society as Biology: Metaphors* (Maasen, S. et al. eds), pp. 231–248, Kluwer Academic Publishers
- 4 Huang, Z.-Y. and Robinson, G.E. (1992) Honey bee colony integration: worker–worker interactions mediate plasticity in endocrine and behavioral development. *Proc. Natl. Acad. Sci. U. S. A.* 89, 11726–11729
- 5 Shipley, B. (2000) *Cause and Correlation in Biology: A User's Guide to Path Analysis, Structural Equations and Causal Inference*, Cambridge University Press

Zachary Huang

Dept of Entomology, Michigan State University, East Lansing, MI 48824, USA.
*e-mail: bees@msu.edu

Jennifer Fewell

Dept of Biology, Arizona State University, Tempe, AZ 85287, USA.

Announcement from the Society for Conservation Biology, July 2002 Declaration to the 3rd United Nations World Summit on Sustainable Development Johannesburg, South Africa

We, the largest group of conservation scientists ever assembled in Europe, believe that humanity faces a biodiversity crisis. We are nearly 1,200 experts from over 50 disciplines and more than 60 countries, gathered for the 16th Annual Society for Conservation Biology Meeting, co-hosted by the British Ecological Society and the Durrell Institute of Conservation and Ecology at the University of Kent at Canterbury. Our collective research and experience confirm that conservation of the diversity of life on earth, the lands and waters it needs to survive, and the natural processes that sustain it, are essential to long-term human survival and prosperity. A future for all humankind that nurtures the full potential and dignity of each individual is inseparably linked to robust, functioning ecological systems.

With this knowledge, we, on behalf of our colleagues around the globe, urge the delegates to the 3rd United Nations World Summit on Sustainable Development to support the Secretary General and embrace and include conservation of biodiversity as a keystone element of the agenda emerging from your historic Summit. Alleviation of poverty and pursuit of a sustainable human future depend on a diverse, vibrant, and healthy planet. This can only be achieved by fully integrating the maintenance of biodiversity with sustainable development.

Malcolm L. Hunter, Jr
President
Society for Conservation Biology

John Grace
President
British Ecological Society

Nigel Leader-Williams
Director
Durrell Institute of Conservation and Ecology, University of Kent at Canterbury

17th July 2002