Social interactions, nonlinear dynamics and task allocation in groups

One of the great intellectual revolutions of the past 20 years – led in part by ecologists like Robert May and former ecologists like George Oster – has been the development of nonlinear dynamics and deterministic chaos[1]. A main message of this work is that relatively simple but nonlinear mathematical relationships between different state variables may lead to incredibly complex dynamical relations, and that predicting the behavior of nonlinear systems is fraught with difficulty. These messages are somewhat depressing for those who want to understand biology using mathematics as a tool (versus those who want to use biology to motivate mathematical studies).

A new paper by Stephen Pacala, Deborah Gordon and Charles Godfray[2] in *Evolutionary Ecology* is a refreshing alternative. In this work, they show that social interactions, which are inherently nonlinear, may lead to order and division of labor within groups. Although the motivations for their work are the social insects, the conceptual foundations of this paper are very broad.

The approach of Pacala *et al.* is based on models that use relative standard mathematical methods of ordinary different equations (reminiscent, in fact, of the Lorenz equations that generate deterministic chaos) and elementary stochastic processes. This means that the results should be accessible to a wide readership, even though it may be tough going at some points to understand fully what they have done. Although I might quibble with the choice of assumptions, some of the results are quite new and extremely interesting. The models involve individuals that can perform one of a number of tasks (e.g. foraging at different kinds of sites) for the group. The behavior of a target individual is determined by social interactions and by environmental stimuli. Rather than assuming that individuals are fixed in the task that they perform, Pacala *et al.* allow switching, which is commonly observed in social insects in response to changes in food supply, predation rates or nest structure.

It is also known that social insects regulate the rate of interactions with conspecifics. Interactions lead to the exchange of information and this can affect both individual fitness and colony fitness. Whether an individual switches or not depends on the success of the current task, an assessment of the environment, and interactions with other individuals. The last criterion is especially important: changes in the rate of social interaction with population density and changes of density with group size (so that group size may influence the rate at which individuals switch tasks) underlie their work. The mathematical models then focus on the dynamics of the fraction of the total population involved in different tasks. The models involve the local population density and a simple individual assessment rule that determines whether or not the current task is profitable.

Pacala *et al.* begin with evolutionary (ultimate) arguments concerning maximization of individual or colony fitness. They show that the evolutionary optimum for individuals is a form of the ideal free distribution in which all tasks that are performed provide the same fitness pay-off to individuals. On the other hand, the evolutionary optimum for the colony is one in which tasks that are performed yield equal marginal benefits. One limitation of evolutionary arguments is that proximate mechanisms for attaining them are usually not described[3]. However, one focus of the paper by Pacala *et al.* is exactly that question. They show, in fact, that different mechanisms for regulating group interactions and for determining the success of the current task can lead to either the individual optimum or to the colony optimum, or very close to these.

Another of their results, that larger groups are likely to be more efficient in tracking a changing environment than smaller ones, is well known[4]. A less-appreciated corollary that they also show is that large groups may experience a disadvantage when information from social interactions overwhelms that from the environment, and individuals consequently continue in unprofitable tasks when they should switch.

Their other main results are extremely exciting. First, simple interactions among individuals with limited abilility to process information often leads to group behavior that is close to the behavior predicted by evolutionary optimization models. This result helps fortify the conclusion that simple proximate mechanisms can achieve nearly optimal fitnesses[5,6]. Second, Pacala *et al.* predict that organisms will regulate per capita rates of social interaction as a function of group size. Third, the effects that they observe can occur in stochastic models with groups even as small as ten individuals.

This new work also sheds light on the outstanding conceptual problem in the study of groups. At the present time, we know much about the evolutionary or functional advantages of group living[7]. However, as Niko Tinbergen[8] noted years ago, it is valuable to understand not only the ultimate cause of a behavior but its proximate mechanism. Currently, we know much less about the proximate mechanisms for group formation and fission. The work of Pacala *et al.*, especially if it is extended from the context of social insects, has the potential to provide a conceptual foundation for the study of the proximate mechanisms of group formation. These insights are complemented by recent work of Gene Robinson and his colleagues[9,10], which provides an understanding of the actual (versus mathematical) mechanisms by which social regulations of behavioral development occurs in honeybee colonies. These biological mechanisms involve worker–worker interactions that mediate hormonally regulated plasticity in the division of labor[9] within an overarching genetic component to behavioral development[10].

In summary, then, Pacala *et al.* show that by regulating the rate of interaction with conspecifics, individuals can solve the problem of balancing environmental stimuli and information transfer. This is a welcome result.

Marc Mangel

Section of Evolution and Ecology, University of California, Davis, CA 95616, USA

References

1 Lasota, A. and Mackey, M.C. (1994) *Chaos, Fractals and Noise: Stochastic Aspects of Dynamics* (2nd edn), Springer-Verlag
2 Pacala, S.W., Gordon, D.M. and Godfray, H.C.J. *Evol. Ecol.* (in press)
3 Szathmáry, E. and Maynard Smith, J. (1995) *Nature* 374, 227–232
4 Clark, C.W. and Mangel, M. (1984) *Am. Nat.* 123, 626–647
5 Putters, F. and Vonk, M. (1990) *Behaviour* 114, 148–159
6 Mangel, M. (1990) *J. Math. Biol.* 28, 237–256
7 Pulliam, H.R. and Caraco, T. (1984) in *Behavioural Ecology: An Evolutionary Approach* (Krebs, J.R. and Davies, N.B., eds), pp. 122–147, Blackwell
8 Tinbergen, N. (1963) *Z. Tierpsychol.* 20, 410–433
9 Huang, Z-Y. and Robinson, G.E. (1992) *Proc. Natl Acad. Sci. USA* 89, 11726–11729
10 Giray, T. and Robinson, G.E. (1994) *Behav. Ecol. Sociobiol.* 35, 13–20

