## Social interactions, information use, and the evolution of collective migration V Guttal and I D Couzin; PNAS 107 (2010) 16172-16177 Recommended and with a commentary by Sriram Ramaswamy, IISc, Bangalore

Collective migration is widely observed in organisms as small as cells and as large as gnus. The motion of migrating groups owes its high coherence to the fact that each individual orients itself not only in response to external fields but by comparison to the orientation of its neighbours. It is therefore natural to understand the phenomenon through models in which individuals try to align with their immediate neighbours, with a small random error, and move in the direction in which they are pointing. The models display a nonequilibrium phase transition to an ordered state, known as a flock, as density is increased and/or noise is lowered [see T Vicsek and A Zafiris, arXiv:1010.5017v1 ; Chaté et al., Phys. Rev. E **77** (2008) 046113].

In the literature on flocking models the parameter values of such models are generally treated as given, and the resulting ranges of behaviours compared to observations. Guttal and Couzin point out that the tendency to follow gradients, and the inclination to align with one's neighbours, should be regarded as heritable, evolvable traits. They therefore consider models in which the *i*th individual is endowed with an initial value for gradient-climbing ability  $\omega_{ai}$  and a value  $\omega_{si}$  (sociality) for the attraction towards, and tendency to align direction of movement with, its neighbours. The model is allowed to run for a specified duration defined as the reproductive cycle time, at which point each individual produces in its vicinity a number of new individuals that inherit these values of  $\omega_{qi}$  and  $\omega_{si}$  with a slight variation, corresponding to a mutation. The number of such offspring produced is specified to be proportional to the present value of the individual's fitness. This fitness in turn is defined to be the difference between the benefit that it has gained by gradient-climbing, minus the cost of possessing this attribute. The benefit is simply how far the creature has moved in a specified direction. The idea is that it is moving in the direction of increasing resources, so has fed and grown well. The cost calculation assumes that possessing more of a given attribute, in this case gradient-following ability, is a draw on internal resources because it involves a computation of some kind, or diversion of attention from other vital activities such as predator-avoidance. The authors assume the cost is a simple increasing function of  $\omega_{qi}$ , the same for all individuals *i*. The authors ask what Evolutionarily Stable Strategies (ESS) emerge from this dynamics, i.e., around what points in the  $(\omega_{qi}, \omega_{si})$  strategy space the population is peaked at long times.

For a wide parameter range, the authors find that evolution leads to a steady state with coexistence of two distinct strategies with the same fitness. These are: "leaders" with relatively high ability to detect gradients but weak sociality, and "social individuals" with poor gradient-detection but strong sociality. The spatial structure consists of mixed groups with both populations. The social individuals in these groups look like they're climbing gradients well, but they're just playing follow-the-leader. The studies reveal, on evolutionary time scales, a striking splitting of an initially homogeneous population into these two subpopulations. The area where leaders and social individuals coexist is a large fraction of the space spanned by density and cost of gradient detection.

An important perturbation is to make the benefit accrued a strongly nonlinear function of distance walked, with a positive curvature. This is known as habitat fragmentation, and means the creatures have to walk an inordinately long way to find food. Once imposed, the authors find the system evolves to a non-migrating state. Moreover, the reappearance of migration once a homogeneous habitat is restored shows a large hysteresis. Thus means restoring migratory behaviour is much harder than losing it.

I consider this work important for several reasons: It is an important first step in introducing evolutionary realism into flocking models; it offers simple mechanisms for the emergence of distinct behavioural types from undifferentiated initial conditions. It brings out a role for social interactions even at very low densities; and, lastly, it is an elegant demonstration of evolutionary principles in models with a natural appeal to the physicist.