

Experimental evidence for cooperation, an important process in evolution of complex systems

Mallikarjun Shakarad

Received: 31 July 2009 / Accepted: 3 August 2009

© Association of Microbiologists of India 2009

Understanding the possible evolutionary steps that may have led to the formation of complex (animal) societies is an important exercise in biology. Cooperation–association for common benefit has been suggested to be the driving force behind major evolutionary transitions from associations of replicator molecules to single-celled organism to complex multicelled organisms to animal societies. The theory per se is hard to validate empirically and hence has been confined to the domain of mathematical theorists. Hamilton advanced ‘kin selection’ theory that said cooperation will be favored in a population provided it is directed towards genetic relatives [1]. Further, he suggested that the genetic relatedness between interacting individuals can increase by two mechanisms: (1) kin recognition between interacting entities and (2) limited dispersal of genetically close individuals. The role of kin recognition has been tested and validated by the social insect community. The role of limited dispersal of interacting entities in favoring cooperation is paramount as it does not require kin recognition [1], and hence has seen a flurry of theoretical activity [2]. Since kin recognition is not a prerequisite for cooperation to evolve under limited dispersal, it can potentially occur even in simplest living system. Interestingly some of the theoretical studies have suggested that limited dispersal will not favor evolution of cooperation [3, 4] as limited dispersal per se can result in intense competition among interacting individuals for valuable resources. Unfortunately, empirical work to test the predictions that have been forwarded

by various groups indulging in theoretical work is lacking. Kümmerli et al. have attempted to provide the empirical proof and have shown what form of dispersal would indeed favor evolution of cooperation [5].

Kümmerli et al. tested the effects of dispersal on the relative fitness of two strains of a gram-negative bacteria, *Pseudomonas aeruginosa* with the larger aim of understanding how population structure influences the evolution of cooperation [5]. The two bacterial strains were pyoverdinin producer- ATC 15692 (cooperators) and pvd-negative- PA06609 (cheats), and the three dispersal types employed were: (1) *limited dispersal* in which three randomly chosen bacterial colonies were allowed to disperse within subpopulations, (2) *high dispersal* in which 36 randomly chosen bacterial colonies were mixed and redistributed among 12 subpopulations (3 per subpopulation) and (3) *budding dispersal* in which bacteria were allowed to disperse as groups between subpopulations. The initial seeding population consisted of a mix of cooperators and cheats in 1:1 overall population ratio.

Among the three dispersal types studied, it was found that after 12 dispersal events the proportion of cooperators were significantly higher in budding dispersal type than that in limited or high dispersal type, suggesting that budding dispersal favored the evolution of cooperation. For the making of a multicellular organism as well as the evolution of sociality, two conditions have to be satisfied, viz., high relatedness among constituent individuals (cells in the former and individual organisms in the latter) and maintenance of homeostasis. If the relatedness is high, then it is possible to maintain biochemical and physiological harmony among interacting entities as such semblance is in the larger interest of every participating individual. The relief and joy to the evolutionary biologist comes from the finding that the average within subpopulation relatedness in populations subjected to budding dispersal reached an equilibrium value of 1 (meaning all individuals are of identical genotype at

M. Shakarad (✉)
Department of Zoology,
University of Delhi,
Delhi - 110 007, India

E-mail: beelab.ms@gmail.com

least with respect to the locus under study, in this case pyoverdinin just after five events of dispersal in 8 of the 12 subpopulations, while in the remaining 4 subpopulations it wavered between a little over $r = 0.5$ and 0.8. Even the slight increase in the relatedness among the constituent individuals within a subpopulation can predispose them to cooperate with each other, eventually resulting in integrity of the complex multicellular as well as multi-individual system.

Kümmerli et al. provide the much needed experimental proof for the evolution of cooperation among interacting individual (bacterial) cells, which could explain the evolution of complex multicellular organism as well as animal societies from single-celled ancestors [5].

References

1. Hamilton WD (1964) The genetical evolution of social behavior. *J Theor Biol* 7:1–52
2. Shaw CM and Gardner A (2008) Nice natives and mean migrants: the evolution of dispersal-dependent social behaviour in viscous populations. *J Evol Biol* 21:1480–1491
3. Taylor PD (1992a) Altruism in viscous population—an inclusive fitness model. *Evol Ecol* 6:352–356
4. Taylor PD (1992b) Inclusive fitness in a homogeneous environment. *Proc R Soc Lond B* 249: 299–302
5. Kümmerli R, Gardner A, West SA and Griffin AS (2009) Limited dispersal, budding dispersal, and cooperation: an experimental study. *Evolution* 63: 939–949