Raghavendra Gadagkar

Principles of Social Evolution[1]

Many animal species live in societies of varying degrees of complexity. Among insects such as ants, bees, wasps, and termites we see the whole range of social complexity, starting from relatively loose associations of a few individuals living together and cooperating occasionally all the way to the extremely well-organized honeybee and ant societies with one or a small number of morphologically specialized queens and tens of thousands or even millions of sterile workers. The evolution by natural selection of extreme forms of cooperation and altruism as well as the evolution of social organization, communication, and division of labor are among the most vigorously investigated problems in modern evolutionary biology. Empirical and theoretical research is progressing rapidly, often overturning previously held concepts and ideas. The aim of this workshop, therefore, was to review the current status of the field in a manner that would be challenging to the specialists and accessible to the non-specialists.

Themes Presented and Discussed During the Symposium

The workshop began with an overview of the application of game theory in understanding the evolution of cooperation. One of the better-studied mechanisms promoting the evolution of cooperation is the theory of inclusive fitness, which often requires close genetic relatedness among the cooperators. Another is the theory of reciprocal altruism, which is applicable even to cooperation among unrelated individuals. Game theory is a useful tool to investigate the dynamics of reciprocal altruism. When an act of altruism is reciprocated at a later time by the recipient of the altruism, this is called direct reciprocity. When an altruistic act is rewarded by someone other than the recipient of that altruism, this is termed indirect reciprocity. Direct reciprocity requires that those interacting individually recognize each other and remember previous acts of altruism. Indirect reciprocity does not require this and may serve to increase the prestige or social standing of altruistic individuals. The relative roles of

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direct and indirect reciprocity are currently being investigated through a number of experiments involving animals as well as human subjects and through a number of theoretical models. These topics were discussed by Peter Hammerstein, who provided an overview of the field; Jeff Fletcher, who presented an n-player prisoner's dilemma model; and Arun D'Souza, who discussed his work on market effects in cleaner fish mutualism.

How can cooperation evolve among organisms without common descent or sophisticated cognition, such as in microbial symbioses? It can be shown that cooperation evolves readily under positive assortment, where individuals are segregated into groups on the basis of their cooperativeness. Whether positive assortment can arise without common descent or sophisticated cognition has been debated, but no generally accepted mechanisms have been proposed. John Pepper described a mechanism for positive assortment, termed "environmental feedback", which requires only that the cooperative trait in question affects the quality of the local environment in some way and that individuals are more likely to leave low- than high-quality environments. This dynamic was illustrated using both agent-based ecological models and a very simple minimal model. The mechanism appears to be a general one that could play a role in the evolution of many kinds of cooperation in nature. If so, then William Hamilton was correct in his claim that kin selection is a special case of inclusive fitness, which constitutes a more general mechanism for the evolution of cooperation.

As mentioned above, one of the better-understood mechanisms of social evolution involves cooperation among close genetic relatives. While considerable evidence has accumulated that animals behave as if they direct their altruism to close genetic relatedness, the mechanism by which they recognize their close genetic relatives remains unclear. In many cases, animals simply use "rules of thumb"; for example, neighbors or individuals growing up in the same nest are likely to be close genetic relatives. Theoreticians, however, have postulated that sometimes genes that make individuals altruistic may also be able to program such individuals to directly recognize other bearers of similar genes. Richard Dawkins (The author of *The Selfish Gene*) dubbed such hypothetical genes "green beard genes" and made them famous with the words, "It is theoretically possible that a gene could arise which conferred an externally visible 'label' say a pale skin, or a green beard or anything conspicuous, and also a tendency to be specially nice to bearers of that conspicuous label." Green beard genes have been discussed frequently in the literature, but have generally been dismissed as unlikely for two kinds of reasons. One, to expect a single gene to confer a conspicuous label, make the bearers of this label recognize a similar label on other individuals, and also make them behave differently toward such individuals, seems unlikely. Second, even if a green beard gene did arise, it would soon go to fixation, meaning that everyone in the population would possess a green beard and we would then no longer recognize this as something special. Notwithstanding these theoretical difficulties, at least one green beard gene seems to have been discovered in the imported fire ant, *Solenopsis invicta* in North America. This discovery and many other facets of social organizations in fire ants were presented by Laurent Keller.

The association between fig trees and fig wasps is one of the best studied examples of the evolution of mutualism. Typically, male wasps emerge earlier from a fig and mate with their sisters. It was therefore expected that these males (who are brothers) would not fight with each other. However, recent studies have revealed considerable fighting among the males. Jaco Greef showed that fighting between brothers has evolved at least four and possibly six times in the evolution of pollinating fig wasps. This finding faults the hypothesis that high relatedness between rival fig wasps will impede the evolution of fighting and supports the idea that local competition between relatives can cancel the ameliorating effects of relatedness. The presence and absence of fighting are explained by variation in the physical conditions within figs and the operational sex ratios.

Using the theory and methods of non-linear dynamics, Leticia Avilés explored the consequences of cooperation on the size and dynamics of social groups. She presented a model that incorporates into a discrete growth equation a positive density-dependent factor to represent the synergistic effects of cooperation. Analysis of this model shows that, by increasing the net reproductive output of group-living organisms, cooperation could either stabilize or destabilize the dynamics of a social group. At one end of this spectrum, group living and cooperation could make persistence possible under harsh demographic or ecological conditions. At the other end of the spectrum, in populations already organized in social groups, cooperation could lead to more highly integrated social groups that are subject to a boom-and-bust pattern of growth. When groups last for multiple generations, such a pattern could take the form of periodic or chaotic dynamics. It was suggested that dynamic instability could result in rates of group turnover large enough for selection among the highly integrated social groups to take over as the primary evolutionary force. Consideration of the dynamic effects of cooperation, therefore, may shed light both on the ecological and demographic conditions leading to the origin and maintenance of group living as well as on the forces responsible for shaping the diversity of animal societies.

Michal Woyciechowski explored the hypothesis that division of labor is a consequence of division of risk among honeybee workers with different expected life spans. In workers with different expected life spans, age at onset of foraging (the moment when the safe nest tasks are completed and the much more risky foraging is begun) was observed. In both experiments, workers originated from one queen, inseminated with the semen of one drone, and were divided into five groups. One group of workers was anaesthetized with CO_2 on the first day of their life. Workers from the other three groups were individually inoculated with a constant number of *Nosema apis* spores on the first, sixth, and eleventh days of their lives. Workers from the control group were not treated in any way. A laboratory experiment with caged workers showed that anaesthetized and infected workers had a shorter expected life span than control bees. Among infected workers, those inoculated earlier in life lived for significantly less time than those infected later in life. In agreement with the expectation from the above mentioned hypothesis, field experiments showed that anaesthetized and infected workers with shorter expected life span started foraging earlier than control workers. Among the infected workers, age at inoculation correlated with age when they started foraging. Although a "division of labor by division of risk" hypothesis is not the only possible explanation, these results are the first experimental ones supporting this idea.

Raghavendra Gadagkar gave an overview of his studies on the primitively eusocial wasp *Ropalidia marginata*. In this primitive insect society, new nests may be founded by a single wasp or by a group of female wasps. In single-foundress nests, the lone female lays eggs and also performs all the tasks associated with nest building and brood care. In a multiple-foundress nest, one individual specializes in egg laying while the remaining function as sterile workers, performing all the tasks associated with nest building and brood caring. This system therefore provides a unique opportunity to compare and contrast the costs and benefits of solitary and social life in the same species and in the same environment.

Adapting Hamilton's rule to compare the inclusive fitness of solitary nest-foundresses and workers, inclusive fitness was computed as the product of an intrinsic productivity factor, the coefficient of genetic relatedness, and a demographic correction factor. For the convenience of empirical investigations, inequalities between workers and solitary foundresses in adult-brood genetic relatedness (genetic predisposition), in intrinsic productivity levels (ecological and physiological predisposition), and in the demographic correction factors (demographic predisposition) were explored. This study found little evidence for genetic predisposition, but considerable evidence for the role of ecological, physiological, and demographic predisposition in the evolution of sociality.

Although many factors that might tilt the inclusive fitness balance in favor of workers are yet to be considered, a unified model combining such genetic, ecological, physiological, and demographic factors as can now be quantified predicts that about 5% of the wasps should opt for the solitary nesting strategy, while the remaining 95% should opt for the worker strategy. This is remarkably close to the empirically observed proportions of solitary nest-foundresses and workers in nature. Perhaps the single most important message from this study is that ecological, physiological, and demographic factors can be more important in promoting the evolution of eusociality than the genetic relatedness asymmetries potentially created by haplodiploidy. Put in another way, the benefit and cost terms in Hamilton's rule deserve more attention than the relatedness term.

The workshop concluded with a general discussion, led by Amitabh Joshi, which took stock of the state of the subject and highlighted many new and controversial topics. Perhaps the most important conclusion to emerge from this general discussion was that the so-called multilevel selection models that are fashionable today are mathematically equivalent to the more classical inclusive-fitness models. Thus, these two classes of models provide a rich diversity of ways of studying the evolution of social behavior.

Participants and Contributions

Leticia Avilés, University of Arizona, Tucson, USA and Fellow, Wissenschaftskolleg zu Berlin, Germany: "On Social Spiders, Nonlinear Dynamics, and Sociality or Why Cooperate?" and "Nonlinear Dynamics and the Evolution of Sociality"

Arun D'Souza, University of Würzburg, Germany: "Market Effects in the Cleaner Fish Mutualism"

Raghavendra Gadagkar, Indian Institute of Science and Fellow, Wissenschaftskolleg zu Berlin, Germany: "Social Biology of

Ropalidia marginata: Toward Understanding the Evolution of Eusociality" and "Cooperation and Conflict in Animal Aocieties"

Jaco Greef, University of Pretoria, South Africa: "Arms Procurement for Sibling Rivalry in Pollinating Fig Wasps"

Jeffrey A. Flechter, Portland State University, USA: "A Game Theoretic Model of Multilevel Selection: Implications for the Evolution of Altruistic Behavior"

Peter Hammerstein, Humboldt University, Berlin, Germany: "Basic Concepts in Game Theory and the Evolution of Cooperation"

Laurent Keller, University of Lausanne, Switzerland: "Selfish Genes and Social Organization in Fire Ants"

John Pepper, Santa Fe Institute, USA: "A New Mechanism for the Evolution of Cooperation: Positive Assortment Through Environmental Feedback"

Michal Woyciechowski, Agricultural University, Krakow, Poland: "Life Expectancy and Division of Labor in the Honeybee"