The evolving field of cooperation **Joel Sachs***

Genetic and Cultural Evolution of Cooperation
Peter Hammerstein, Ed.
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In the last forty years the field of cooperation has experienced a revolution. Naïve ideals about benefit for the good of species have been supplanted with a selfish-gene world view which instructs that cooperation can only evolve under restrictive conditions. However, our understanding of such conditions for the widespread forms of cooperation in nature remains fragmentary. Can a simple set of evolutionary models explain cooperation not just within and between species, but at the inter-cellular and genomic levels? The book *Genetic and Cultural Evolution of Cooperation* offers an expansive review on this topic, and makes progress towards such a synthesis. This book emerges from the June 2003 Dahlem Workshop which proposed to "elucidate the mechanisms and processes beyond kin selection that promote the emergence of cooperation in systems that range from molecules to societies." (pg. 1) In light of an ambitious goal, this volume skillfully surveys this complex and often idiosyncratic subject and will be useful to beginning and accomplished researchers alike. The book is organized into four blocks of papers, each ending with a group report summarizing findings and highlighting controversial topics. These reports offer the reader a most up to date view of key questions being studied in fields ranging from cognition and human alliances to cooperation at the levels of genomes, cells and species.

An worthy example is the group report by Bergstrom et al. addressing interspecific mutualism. This report describes many key puzzles begging empirical attention and reviews the history of this dynamic field. The theory of this field began with Trivers' reciprocal altruism model, which explained that altruistic acts can be selectively advantageous as long as benefits are later returned to the donating individual. A subsequent paper by Axelrod and Hamilton dominated virtually all thinking in the field, concluding that 'tit-for-tat' interactions could stabilize cooperation between individuals with repeated interactions. However, contemporary work - some aptly described in this chapter - recognizes multiple mechanisms underlying the evolution of reciprocal

altruism. These include partner choice (or biological market) models, where individuals preferentially benefit cooperative partners, byproduct models, where individuals benefit others as an automatic consequence of selfish actions, and finally models in which repeated interactions alone stabilize cooperation (partner fidelity). While biological markets and byproducts are reviewed in detail, partner fidelity models are not covered.

Once this history is reviewed Bergstrom et al. make some (admittedly) bold forecasts for the field. They predict that (i) reciprocal altruism will never be observed in interspecific mutualism, that (ii) partner sanctions (punishment of non-cooperators) will be found to be a rare compared to partner choice (reward of cooperators), and finally that (iii) mutualism invariably has commensal origins. While such bold theoretical predictions may spur empirical testing, the first two predictions seem predicated on artificially narrow model definitions. For example, under another view reciprocal altruism extends (beyond strict assumptions of tit-for-tat cooperation) to any interaction where costly benefits are exchanged between non-relatives (including all the models above). Similarly, the above distinctions between partner choice and sanctions are perplexing: whenever an individual preferentially benefits a cooperative partner over an uncooperative one (partner choice) the latter is punished merely by exclusion, and under the sanctions models cooperative partners similarly benefit more than those which are punished. Finally, and in contrast their conclusion, sanctions appears to be a widespread mechanism stabilizing cooperation. Organisms as diverse as legumes and squid can punish uncooperative bacterial symbionts, and yucca plants are known to punish greedy yucca-moth pollinators. It seems clear that the lack of universally agreed/accepted terminology remains an unfortunate impediment to synthesis in this field.

The block of papers on genomic and inter-cellular cooperation explains mechanisms supporting cooperation at these fundamental levels and offers examples of within-organism conflict that may be startling to the uninitiated reader. Hoekstra tidily reviews a menagerie of genomic parasites and the proposed mechanisms of their suppression, ranging from the general (recombination) to the specific (RNA interference). Blackstone and Kirkwood describe the potential roles of selfish mitochondria in programmed cell death and offer a novel perspective on the evolutionary history of this

organelle. While common themes are evident between these chapters and those on interspecific cooperation, integration of theory between subjects is not emphasized.

The goal of synthesis seems especially challenging in light of the chapters highlighting human cooperation. Several papers as well as the group report on human societies actively separate theory of human cooperation from the models commonly applied to other organisms. Group selection and culture-gene coevolution are invoked, with the justification that cooperation is more important for human evolution than for other life and thus requires different models. To make matters more complex, the field of human evolution is inundated by models based on past evolutionary scenarios, and such data are both speculative yet difficult to refute. While Smith attempts to counter the separatist approach in his chapter, it is clear that the debate is far from closed.

Genetic and Cultural Evolution of Cooperation offers an excellent and timely assessment of a dynamic field. The book brings the reader up to date on studies and theory of cooperation at a diversity of levels (i.e. genomes, species, societies). However, what is missing is an attempt to synthesize the theory of this field. Such a synthesis remains a major challenge to biologists studying the evolution of cooperation.

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