DESIGN BY NATURE

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Back to the Drawing Board

Genetic and Cultural Evolution of Cooperation. Peter Hammerstein, ed. MIT Press, Cambridge, MA, 2003. 450 pp., illus. $45.00 (ISBN 0262083264 cloth).

The question of how cooperation evolves is fundamentally a question of mathematical biology or sociology. Recent theory about cooperation has been overwhelmingly mathematical, and virtually all of the 40 contributors to the 90th Dahlem Workshop report, *Genetic and Cultural Evolution of Cooperation,* are in some sense mathematicians. Yet arguably the most striking feature of this four-part book is a virtual absence of mathematics. What could be the reason for that? Could it simply reflect that publishers like to sell books, and equations reduce sales dramatically? Could it just mean that brainstorming at a workshop is more conducive to talking than to doing? Or is it perhaps a sober reflection of how little we truly understand about the evolution of cooperation, despite decades of concerted effort?

In a timely article, Michael Reed (2004) has reminded us that evolution makes mathematical biology hard for many reasons, including that a priori reasoning is frequently misleading, and that different species may accomplish the same task by different mechanisms, astounding in their variety. For example, that reciprocity can sustain cooperation has been demonstrated ad nauseam in theory; but there is surprisingly little evidence of such "reciprocal altruism" in nature, as editor Peter Hammerstein—lamenting the amount of energy invested "in the publishing of toy models with limited applicability"—protests in his personal contribution to part 1 of the volume. Indeed, as Joan Silk stresses, keeping score—and how can there be reciprocity without scorekeeping?—is a proven detriment to friendships.

To be sure, reciprocity is not the only mechanism for cooperation that theoreticians have considered. There is first of all relatedness, but this book addresses only cooperation among unrelated individuals. Can such cooperation be sustained in humans, if not by reciprocal altruism, then by "costly signaling," "indirect reciprocity,"' or "genetic group selection"? The usual suspects are trotted out by Ernst Fehr and Joseph Henrich, but soon dismissed as unlikely perpetrators of "strong reciprocity"—defined to arise when one is willing to incur long-term net costs from helping another in response to a kindness. Of the known suspects, only "cultural group selection" survives pretrial scrutiny, to be revisited in part 4 by Peter Richerson, Robert Boyd, and Henrich.

The evidence for such strong reciprocity, now seemingly overwhelming, is effectively evidence that animals—especially humans—are much more cooperative than game theory has predicted. So what have the models been neglecting? One good answer is psychological mechanisms. Daniel Fessler and Kevin Haley argue that "our emotions, long disparaged as both a reflection of our animality and the source of our irrationality, are… exactly the opposite, namely, the keys to our complexity, efficacy, and remarkable ability to cooperate," and they discuss the "thirteen emotions that seem to have the greatest impact": anger, contempt, envy, guilt, gratitude, righteousness, romantic love, pride, shame, moral approbation or outrage, admiration, elevation, and mirth. Their view is echoed by Edward Hagen, who argues that depression, far from being a mental illness, may be an adaptive emotional strategy. These and other themes (e.g., reputation) coalesce in the final chapter of part 1, a group report by Richard McElreath and 10 others on cognitive and emotional mechanisms that may sustain cooperation.

The flavor of part 2, on markets and exploitation in mutualism and symbiosis, is markedly different from that of part 1. The emphasis switches from humans to other organisms, and from intraspecific to interspecific cooperation. Samuel Bowles and Hammerstein discuss market theory in relation to biology; Redouan Bshary, Ronald Noë, and Judith Bronstein highlight the importance of model systems; Olof Leimar and Richard Connor discuss "pseudo-reciprocity"; and Carl Bergstrom and Michael Lachmann argue that slowly evolving species are likely to gain a disproportionate fraction of the surplus generated through mutualism. A group report by Bergstrom and 10 others concludes part 2.

In part 3, the focus switches all the way from the interspecific to the intercellular. Rolf Hoekstra discusses mechanisms that prevent or promote genomic parasitism; Eörs Szathmáry and Lewis Wolpert discuss the transition from single cells to multicellular organisms; conflict mediation during this transition is Richard Michod's topic; Neil Blackstone and Thomas Kirkwood discuss the capacity of programmed death to restrain the selfish replicatory potential of individual cells in multicellular groups; and Lachmann and seven others intertwine these strands in a group report on cooperation and conflict in the evolution of genomes, cells, and multicellular organisms. Part 3 is arguably somewhat detached from the rest of the book. However, even if its mechanisms operate only at the level of the cell, it may yet offer lessons at the level of whole organisms. Certainly, there is nothing in the group report to suggest that the level of cooperation within organisms is any more perfect than the minimum level of cooperation among humans that our planet's future well-being now clearly and urgently requires.

Part 4 of the book, on cooperation in human societies, picks up a thread left dangling at the end of part 1. Richerson, Boyd, and Henrich propose that group selection on cultural variation is at the heart of human cooperation (though they acknowledge a role for other mechanisms); Peyton Young describes how social norms can coalesce from the decentralized, uncoordinated choices of many interacting individuals; Eric Smith emphasizes the importance of language's role in human cooperation; Bowles and Herbert Gintis discuss a special mechanism for human cooperation that stresses the role of gene–culture coevolution in group dynamics; and Henrich and eight others conclude with a group report.

Although this book identifies numerous gaps in both empirical and theoretical knowledge—indeed, that is precisely its strength—it is arguable that the most critical lacunae concern the modeling of psychological factors. In this regard, the book is the tip of an iceberg, because its emphasis on the role of emotions in cooperation reflects a rapidly growing consensus that "psychological traits must be incorporated into our model, however difficult that may be" (Nesse 2001, p. 162): Emotions are capable of sustaining commitments that may otherwise seem irrational, and commitments are often crucial to cooperation, as discussed more fully elsewhere (see, for example, Frank 2001). Furthermore, the need to incorporate psychological factors transcends cooperation and commitment. For example, that the most egalitarian developed nations—as opposed to the richest—enjoy the best health has now been firmly established by Wilkinson (1996), who wrote that "although economics is far from exclusively asocial... rational choice theory has grossly underestimated human social needs and [that] their satisfaction should often take precendence [over] demands to maximise individual consumption. There is a missing social economy of well-being" (Wilkinson 1996, p. 109). Some have attempted to address this issue within the confines of top-down, neoclassical economic analysis by adding a social-capital term to the standard utility function (see, e.g., Becker and Murphy 2000); but if the linkages between health and social status, or between cooperation and commitment, are primarily psychosocial—as Wilkinson or Fessler and Haley (and others) have so convincingly argued—then the standard economic approach will soon yield diminishing returns. A much more radical, bottom-up approach is needed.

Hammerstein and his collaborators are among the pioneers of the requisite "behavioral game theory" (Camerer 2003). Aware not only of the many discrepancies between game theory's predictions and the kind of cooperation observed in nature but also of the tremendous variety of mechanisms that could in principle sustain cooperation in different contexts, they are effectively going back to the drawing board. And I for one would like to think that *that* is why this monograph contains so little mathematics: The precise structure of models that failed yesterday need no longer be relevant to models that may succeed tomorrow.

The book is a refreshingly candid portrait of what we know and—more important—don't yet know about the evolution of cooperation. Honest disagreements abound (e.g., between Smith and Boyd and Richerson over the importance of group selection in the evolution of human cooperation), yet there is at least a universal consensus that, as Silk puts it, "As always, more data and better models are needed." The group reports are splendid state-of-the-art summaries emphasizing open questions, unsolved problems, and directions for future research; and all agree that the challenges are considerable.

Which brings us full circle to Reed, who has warned against doing mathematical biology to satisfy a desire to find universal structural relationships, because "you'll be disappointed" (Reed 2004, p. 339). Is it therefore a strategic error even to seek a general theory of cooperation? That remains an open question, but if you want insightful perspectives on most of the relevant issues, I heartily recommend that you read this book. And even if now is not the time for a general theory, we mustn't forget that now is not forever. After all, when all is said and done, who will disagree with W. G. Runciman's categorical assertion that "our social behaviour is as reliably patterned as our individual behaviour is unmanageably diverse" (Runciman 2000, p. 88)?

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LIONS, MICE, AND PANDAS: SLEUTHING THE MAMMALIAN GENOME

Tears of the Cheetah and Other Tales from the Genetic Frontier. Stephen J. O'Brien. St. Martin's Press, Thomas Dunne Books, New York, 2003. 304 pp. $25.95 (ISBN 0312272863 cloth).

Since the emergence of molecular biology, researchers have quickly confirmed and expanded scientific knowledge of how living things are related and how natural selection works. Unfortunately, many people, including students entering college today, are generally unaware of the significance of these findings, or of the role that molecular biology plays in scientific inquiry. Undergraduate education about genetics and the biology of the genome too often stops at the structure of the nucleotides, leaving students puzzled and often uninterested in the significance of these structures they cannot see. *Tears of the Cheetah and Other Tales from the Genetic Frontier* is a collection of stories that tackle this problem head-on. Each chapter unfolds unexpected and sometimes shocking lessons about beloved animals—cheetahs, pandas, humpback whales, and others—that serve as "parables of hope and lessons of survival," in the words of the book's author, Stephen J. O'Brien.

For nearly 30 years, O'Brien, head of the Laboratory of Genomic Diversity at the National Institutes of Health, and his research group have used comparative genetics to study the evolution of the immune system, retroviruses, and cancer onset in mammalian species dispersed over the planet. This comparative approach has led to interesting discoveries about natural selection and evolutionary processes in the face of such trying conditions as disease and inbreeding. The stories that emerge in *Tears of the Cheetah* are an intimate look into the contributions this laboratory has made to comparative genomics, conservation biology, human forensics, and medicine.

In the years that I have known Steve O'Brien, he has always had real-life adventure stories to tell, which invariably prompt questions and keep his listeners on the edge of their seats. These stories fascinate not because they explain the complexity of genetic structure and inheritance but because they portray the significance of the hidden secrets of the mammalian genome. Molecular biology just happens to be one of the tools O'Brien and his students and colleagues use to investigate these mysteries.

In *Tears of the Cheetah,* O'Brien unveils the process of scientific inquiry—in other words, the interesting stuff for those who do not understand the intricate details of molecular biology. For instance, after revealing that cheetahs have strikingly little variation in their genome—90 to 99 percent less diversity than other cat species—he poses these important questions: What are the implications for disease and reproduction in a highly inbred species? How quickly can a species recover from near extinction? What can we learn from the natural history of this species that will assist in efforts to conserve it and other endangered mammals? This is not the stuff of a molecular biology textbook; *Tears of the Cheetah* is designed to convey a different scientific story, one of inquiry, not technique.

Each chapter is an independent tale that introduces an interesting problem and shows how the molecular sleuths take on the challenge. In the process, O'Brien introduces and explains terminology and techniques in molecular biology, providing just enough information about these concepts and techniques to give the reader "aha!" moments. For example, the first chapter relates a story dating back to the Ming Dynasty about a lethal cancer epidemic in mice. A retrovirus in the genome is the culprit, and the mystery to be solved is how descendant populations of mice evolved resistance and survive today. And what about humans, with 1 percent of our DNA retrovirus related—what secrets of our evolutionary past and future are hidden within our genome? It is an intriguing teaser for stories to come.

Subsequent chapters present a diverse array of legal, cultural, and political twists and turns. Among O'Brien's topics are the threat to the endangered species status of Florida panthers (the answer to which involves the genes of some Costa Rican cousins); whale poaching in Japan; and a mysterious, devastating plague in African lions. Orangutans from Borneo and pandas from China make their appearance. AIDS and the Black Death make more somber reading. Near the end is a murder mystery set on Prince Edward Island, involving a cat named Snowball. In every case, O'Brien showcases a brilliant story of genetic sleuthing and offers examples of carefully designed, inquiry-based science.

The book's strongest contribution is a revelation of what molecular biology is on the threshold of contributing to society.

O'Brien refers to countless experiments nature has "composed and performed" and implies that through comparative genomics, people will gain a greater understanding of how living organisms evolve and how they are connected. The implications for humanity are emphasized in the opening and closing chapters of the book. The Human Genome Project and human gene therapy are presented to reveal their potential, still in its infancy, for curing disease. It is impossible to read one of the stories and put the book down without wondering how lessons learned from the evolution of other species might be relevant to us. The potential to point the way for a cure to some human diseases, including AIDS, seems inevitable.

Each of the stories in *Tears of the Cheetah* contributes to an understanding of how science works in the real world, at least in part by showing how graduate students, researchers, and technicians work to solve problems. These are familiar stories to O'Brien, who was directly involved in each one. In fact, they are largely a chronology of his career, starting as a self-proclaimed "naïve" fruitfly geneticist and developing into an internationally renowned conservation biologist. O'Brien also touches on the difficulties involved in translating scientific knowledge into political action, portraying international scandal and courtroom intrigue as he systematically introduces familiar concepts reported in the news—polymerase chain reaction, DNA fingerprinting, and microsatellite markers, to name a few. A brief glossary explains the less familiar terminology.

Tears of the Cheetah is an excellent introduction to its subject, accessible to people without a background in genetics. It quickly reveals the potential of molecular biology for understanding mammalian evolution, assisting conservation efforts, aiding forensic science, and curing human disease. *Tears of the Cheetah* is also an enormously inspiring and entertaining read. As I mused on the book, I was struck by the relevance of the stories to many current issues involving conservation, disease, and forensics—issues that are relevant to the lives of undergraduates at the university where I teach, and doubtless at other campuses as well. *Tears of the Cheetah* will provoke discussion among nonmajor students and other readers who are searching for a way to connect science to their lives. It is a unique contribution to the literature and a superb introduction to the vast potential of molecular biology as a tool to help us understand how the natural world works. Finally, it is a reminder of human mortality and of our place among the other mammals that are so much like us.

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DESIGN BY NATURE

Organisms and Artifacts: Design in Nature and Elsewhere. Tim Lewens. MIT Press, Cambridge, MA, 2004. 183 pp., illus. $32.00 (ISBN 0262122618 cloth).

Biologists routinely deploy the language of intentional design in describing and explaining the characteristics of the entities they study. For example: The eyespots on the wings of some moths function to misdirect the pecks of avian predators, increasing the moths' chances of escape. Upon emerging from their long subterreanean sojourn, male 17-year cicadas have just one purpose: to find a mate and pass on their genes, thereby completing the bizarre life cycle that defines their existence. The exquisitely sensitive infrared heat sensors of pit vipers are superbly designed for detecting warm-blooded prey, even in total darkness.

The characteristics of organisms have functions, have purposes, are well or poorly designed, are *for* something. This is in striking contrast to the physical sciences. Physicists are not concerned with explaining the function of electrons; chemists do not struggle to identify the purpose of benzene molecules; geologists do not marvel at how well designed geodes are. Teleological language dropped out of the physical sciences in the 17th century when, for example, talk of the "purpose" of the celestial bodies signaled to the leading natural philosophers of the day a sterile and retrograde understanding of the natural world. By contrast, teleological language has been going strong in biology for the last two and a half millennia. Odd.

A popular philosophical pastime is to try to show that teleological language is not really essential to biology, that all talk of functions, purposes, design, and related concepts can be translated into nonteleological language of the sort that characterizes the physical sciences. Perhaps it can. But biologists continue to use teleological language nonetheless. They continue to think of living things as akin to human artifacts, that is, to objects intentionally created in order to serve some function, to have a purpose, and about which it makes sense to ask whether, or to what extent, they are well designed. None of this would be in the least bit puzzling if it could be assumed that living things reflect in their structure and behavior the will of a designer whose intentions they embody. But most biologists assume nothing of the sort, and when pressed on the issue will patiently explain that all of these teleological terms can be replaced by nonteleological terms through a suitable (albeit tedious) process of translation. Still, the language of "design" persists. How are we to make sense of such intentional language without positing an "intender" doing the intending?

In *Organisms and Artifacts: Design in Nature and Elsewhere,* Tim Lewens tackles this and related questions. Although Lewens is University Lecturer in History and Philosophy of Science at Cambridge University, historical analysis plays no significant role in his treatment. The book focuses instead on philosophical issues connected with what he calls "the artifact model" in biology: the approach that treats the organic world as though it were designed. Throughout the book it is evident that Lewens's concern is to acknowledge what is right about artifact thinking in biology, to point out its limitations, and to find the *via media* (middle way) between wholesale adoption and wholesale rejection of this approach. Such balance makes Lewens's insightful book rewarding to read but difficult to summarize in a short review.

Begin with the fact that despite its pervasiveness in biology, the artifact model—which includes talk of species facing "problems" that they "solve" using various "strategies"—is also controversial. For example, Richard Lewontin has argued that the very concept of an adaptive problem, upon which so much of the artifact model (and adaptationism more generally) is built, is bankrupt because in fixed environments, species do not encounter preexisting adaptive problems that they then solve. Rather, organisms actively construct their environments according to their needs. Lewens concedes that organisms frequently manipulate, rather than merely conform to, their environments, yet notes that organisms do face specific selective pressures; evolving in response to them is a way in which species solve adaptive problems. Thus a concept of an environmental problem can be constructed that preserves the problem-solving element of the artifact model.

This does not, however, mean that the artifact model is in the clear. Lewens points out a number of additional shortcomings, among them that the model tends to lead its devotees to ignore drift, it exaggerates the independence of organismic traits while encouraging biologists to ignore developmental relations between traits, and it overlooks the fact that selection is—necessarily—a population-level process rather than a force that acts on individual entities. But these are merely qualifications, not vanquishers, of the artifact model. His conclusion, restated throughout the book, is that artifact thinking in biology is often useful but "needs to proceed with caution."

This much will, I suspect, seem familar to most biologists. On the other hand, the heart of the book is an in-depth analysis of "function talk" in biology, which is likely to test the resolve of even the most interested reader. Puzzles about the meaning and proper ascription of functions have generated a large technical literature in the philosophy of biology, along with a number of competing accounts of how functions are to be understood. Lewens carefully sorts through these accounts, pointing out the strengths and weaknesses of each, finally noting somewhat anticlimatically that the results of their applications to real-world examples rarely diverge. Still, readers stand to learn something worthwhile along the way from Lewens's penetrating discussions of fundamental issues in evolutionary biology, including the sense in which selection explains (and fails to explain) adaptations, the differing meanings of *adaptationism,* the promise and pitfalls of evolutionary reverse engineering, and the role of development in evolution.

Readers expecting a wide-ranging discussion of "design in nature and elsewhere," however, of the sort one might get from a work in popular science, are likely to be disappointed. The book is not so much about design in nature in some inclusive sense as it is about design talk in biology. Moreover, the discussion of design elsewhere is for the most part confined to the last chapter, which addresses similarities and differences between biological evolution and technological change. There Lewens applies the results of the previous chapters to the question of technological change and to the claims of "intelligent design creationism," showing first that enthusiasts for evolutionary models of technological change need to be cautious in using concepts from biological evolution to explain the intentional creation of artifacts and, second, that, viewed in light of the foregoing discussions, the central claims of intelligent design creationism are quite simply eviscerated. This important take-home message is perhaps the chief value of the book for the general reader. While creationists are busy trying to convince anyone who will listen that we live in a world of nature by design, Lewens shows how biologists (and philosophers) are engaged in the much more interesting enterprise of describing, explaining, pondering, and debating the myriad forms of design by nature. What could be more inspiring than that?

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NEW TITLES

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