EVOLUTIONARY GENETICS

Broken Cogs or Strategic Agents?

Peter Hammerstein and Edward H. Hagen

Thirty years ago, Richard Dawkins shook the scientific community with provocative reflections on the role of genes in evolution (*1*). He drew our attention to the fact that "selfish genes" boosting their own transmission at the expense of the organism in which they act may spread in a population despite their harmful effects. Evolutionary biologists have subsequently debated how frequently such genes actually occur and how they have shaped animals, plants, and fungi.

Genes in Conflict
The Biology of Selfish Genetic Elements

by Austin Burt and Robert Trivers

Harvard University Press, Cambridge, MA, 2006. 620 pp. $35, £21.95. ISBN 0-674-01713-7.

Genes in Conflict, by evolutionary geneticist Austin Burt (Imperial College London) and biologist Robert Trivers (Rutgers University), is the first book to review the vast empirical literature on selfish genetic elements. It reveals how widespread these elements are in nature, what evolutionary effects they have had on fundamental aspects of the genetic system itself (such as its size, organization, and degree of recombination), and how they influence reproduction, development, and behavior. While enthusiastically addressing the ever-accelerating advance of genetic conflict studies, the authors also take care to identify many open questions. Their fascinating and comprehensive book provides a gold mine for anyone entering the field.

Selfish genetic elements are more than just genes; they also include stretches of noncoding DNA, fragments of chromosomes, etc. It is helpful to view these elements as agents "acting in their own interest" and "being in conflict" with other parts of the genome, as the book's title suggests. Using this heuristic, it is "in the interest" of some genes, for example, to protect chromosomes from damage, whereas it is in the interest of others to break chromosomes to get themselves replicated by the repair process or to jump across the DNA replication complex and thus get replicated more than once as the complex travels along a chromosome. The book beautifully demonstrates the power of the genes-as-agents perspective, which has opened our eyes to arms races within the genome and to limits imposed on the unity of the organism.

Theoretical biologists, however, would add a word of caution. Insights gained from this approach must be carefully checked using equations that describe how genetic elements invade a population and compete with one another. The dynamics of selfish elements in host populations is more complex than a simple heuristic can capture, as the following example shows. In the wasp *Nasonia vitripennis*, a selfish supernumerary chromosome, called PSR (for paternal sex ratio), disables the transmission of all regular chromosomes from father to offspring. Infected males thus contribute genetically no more than the selfish element to an offspring. This is in the interest of PSR because—skipping a little biology here—it also changes the offspring's sex from female to male, and males are better than females at passing PSR to offspring. Is this effect sufficient to understand the spread of PSR?

It is evidence of the high quality of *Genes in Conflict* that the book pays attention to mathematical results, as in its short verbal account of an analysis done by Jack Werren and Leo Beukeboom (*2*). That analysis revealed a surprise: PSR's trick only leads to invasion when there is a female-biased sex ratio. This insight comes from population biology rather than from anything resembling decision theory or game theory—the mathematical formalizations of strategic agents. Nevertheless, without the genes-as-agents heuristic, much of the material covered in the book would never have been understood, because mathematics is often better for scrutinizing ideas than for developing them.

Many readers will appreciate that in addition to presenting the state of the art, the book also includes a concise history of the long struggle to understand selfish elements. Exactly 100 years ago, for example, Carl Correns discovered the phenomenon of cytoplasmic male sterility (the suppression of male function by cytoplasmic genes) in plants (*3*). Thirty-five years passed before Dan Lewis realized that this effect of cytoplasmic genes conflicts with the interests of genes in the cell's nucleus (*4*). Another 40 years elapsed before conflict between the nucleus and cell organelles received more general attention from Leda Cosmides and John Tooby (*5*). Today, a quarter-century later, several examples of intracellular symbionts that kill males or prevent mothers from producing them have either been discovered or better understood as selfish genetic elements. The current rapid rate of progress in genetic conflict studies probably stems from the development of molecular and cytogenetic techniques plus the much closer links between empirical and conceptual advances than for most of the 20th century.

Given its primary goal, *Genes in Conflict* must present a rich variety of phenomena, but doing so risks drowning the reader in facts. To prevent this, the authors have written each chapter so that it stands alone (at the cost of some redundancy). They have also relied on a commendable conceptual clarity to guide readers through the jungle of details. In particular, Burt and Trivers acknowledge at the outset that most genes are cooperative, restricting the notion of selfish genes to those few genes that increase their own reproduction at the expense of the organism as a whole.

Are genes best conceptualized as agents? Or as cogs in a complex machine that cause problems when broken? Although molecular and population biology typically emphasize the latter view, Burt and Trivers convince us that we would be missing something important if the strategic gene were ignored. Nonetheless, we believe at least two criteria must be satisfied for a strategic framework to be productively applied to selfish genetic elements. First, such elements should show evidence of complex design that reflects multiple independent strategically advantageous modifications. (If the only examples were elements that hijack existing complex machinery via a single modification, the strategic framework would be overkill.) Second, there should be evidence of evolutionary moves and countermoves between selfish elements and other parts of the genome. The book's plethora of facts includes support for both criteria. Many selfish elements, for example, show directional movement, tissue specificity, or time-dependent effects—prima facie evidence for complex design. And the widespread occurrence of suppressors clearly indicates countermoves.

As much as we appreciate the strategic viewpoint, it presents some obvious pitfalls. To name one, just as our visual system readily interprets three dots as a face, our hypersocial brains might be seeing strategies where none exist. As the authors admit, the molecular mechanisms employed by selfish elements are in many cases unknown, which makes it difficult to interpret important aspects of their evolution. In providing such a superb review, Burt and Trivers have laid the foundation for further exploration of these important conceptual issues.

References

1. R. Dawkins, *The Selfish Gene* (Oxford Univ. Press, Oxford, 1976).
2. J. H. Werren, L. W. Beukeboom, *Am. Nat.* **142**, 224 1993).
3. C. Correns, *Ber. Dtsch. Bot. Ges.* **24**, 459 (1906).
4. D. Lewis, *New Phytol.* **40**, 56 (1941).
5. L. M. Cosmides, J. Tooby, *J. Theor. Biol.* **89**, 83 (1981).

10.1126/science.1125754

The reviewers are at the Institute for Theoretical Biology, Humboldt University, Invalidenstrasse 43, 10115 Berlin, Germany. E-mail: p.hammerstein@biologie.hu-berlin.de; e.hagen@biologie.hu-berlin.de