

EVOLUTION

Laws of Cooperation

David Krakauer

The greatest challenge to science is to explain the prevalence of improbable, stable structure in the universe. Entropy mercilessly ensures that through time disorder is bound to increase. Discovering general mechanisms that favor local order is in some sense the most important game that all theorists in the natural sciences have been playing since the mid-19th century. In biology, theorists have focused on the battle between the dissipative tendencies of selfishness and the structuring capabilities of cooperation. Theoretical biologists—like theoretical physicists working in the abiotic domain before them—have sought natural laws that explain when and where cooperative order, and consequently adaptive complexity of various kinds, might come into existence.

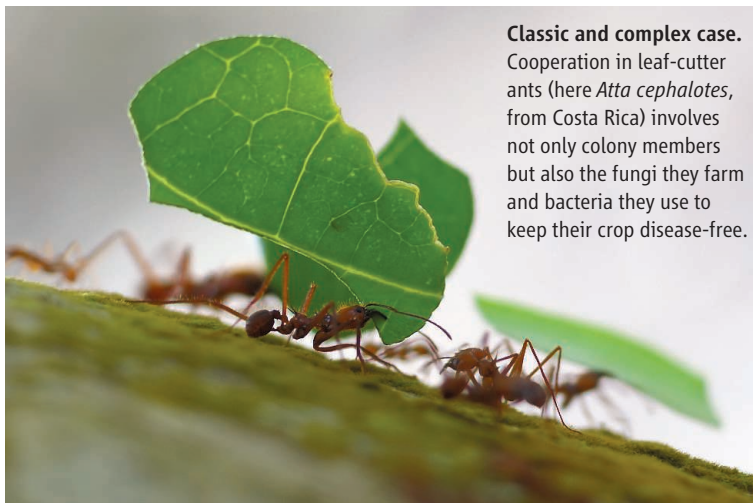
In *SuperCooperators*, mathematical biologist Martin Nowak and *New Scientist* editor Roger Highfield present for nonspecialists recent progress in understanding how cooperation evolves from the competitive interactions inherent in Darwinian dynamics. They argue that we now know enough about the mathematics of adaptation to conceive of cooperation as a fundamental evolutionary principle and not merely as a surprising feature of biology in some way at odds with evolutionary processes.

We currently think of mutation, competition, and selection as fundamental properties of all evolutionary processes at different levels of explanation. Nowak and Highfield suggest that cooperation should be elevated to a similar status. They devote much of the book to building their case, presenting five candidate mechanisms (repetition, reputation, space, multilevel selection, and kin selection) that, when key inequalities are satisfied, allow cooperative configurations to outnumber selfish ones.

Many readers will turn to the book for further insights into the ongoing argument that pits Nowak and his colleagues against pro-

ponents of Hamiltonian kin selection. I have been rather perplexed about the source of so much uproar (beyond the obvious sociology of science and the desire that precedence be acknowledged), and the book should go some way toward clarifying the nature of the debate for outsiders (albeit with a participant's perspective). Two chapters, "Kin selection—nepotism" and "The lord of the ants," most explicitly address the dispute.

Nowak's essential (and rather simple) claim is that all forms of cooperation can be understood in terms of individual-level selection operating in hierarchically structured populations. The source of structure can be kinship, spatial constraints on mobility, or

**Classic and complex case.**

Cooperation in leaf-cutter ants (here *Atta cephalotes*, from Costa Rica) involves not only colony members but also the fungi they farm and bacteria they use to keep their crop disease-free.

mechanisms of individual recognition and attraction. Historically, kin selection has suffered from a few ambiguities. As originally conceived by Bill Hamilton, kinship implied genetic relatedness. It was soon recognized that this was too restrictive, and the approach was expanded to include multiple forms of assortativity. Hamilton also introduced the concept of inclusive fitness, which is where the substantive argument arises. Inclusive fitness calculations are often articulated in terms of coefficients of relatedness (not assortativity in general), which moreover only make sense under rather limited conditions of weak

selection. Nowak and colleagues, along with several population geneticists before them, suggest that we model individual selection and hierarchical population structure explicitly and do away with the

phenomenological ambiguities of inclusive fitness arithmetic. I suspect that this is what will eventually happen, because theoretical science ultimately favors mathematical clarity and efficiency.

The book includes ideas that might reconcile the ground-breaking work of Hamilton and subsequent developments with the structured population dynamics offered by Nowak, Corina Tarnita, and Edward Wilson (1). Since the 1960s, when

Hamilton wrote down his famous rule for the fixation of cooperates in terms of the ratio of benefits to costs and the coefficient of relatedness ($rb > c$), there has been a proliferation of analogous inequalities. Nowak describes several, including a graph theoretic version, $b/c > k$ (where k is the average number of nodes to

which a focal node is connected in a network), and a group selection form, $b/c > 1 + n/g$ (where g is the number of groups and n the number of individuals per group). All of these recent inequalities explain the fixation of cooperation in terms of two classes of separable mechanisms: reproductive or growth terms (functions of time) and population structure terms (functions of space). Hamilton was the first to intuit the form of these evolutionary laws, and Nowak and col-

leagues have been pinning down their fundamental origins and meaning.

In the penultimate chapter, Nowak suggests unification in the form of one parameter, his sigma—the structure coefficient. Sigma measures the rate of like interactions in an evolutionary game (e.g., cooperators encountering cooperators or defectors encountering defectors). When sigma exceeds unity, cooperation invades; when below, selfishness. Sigma captures in one scalar value essential features of assortative interactions, and hence it points toward the essential processes underlying the origin of cooperation.

SuperCooperators

Altruism, Evolution, and Why We Need Each Other to Succeed/Evolution, Altruism and Human Behaviour or Why We Need Each Other to Succeed

by Martin A. Nowak, with Roger Highfield

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I have little doubt that *SuperCooperators* will generate great interest and debate and meet with its fair share of dissension. Nowak, a very successful and plainspoken scientist, has a disinclination to compromise. His style has always been to forge ahead with alacrity, and at times this has led to an absence of historical considerations that offends those working on related problems. But he and Highfield should be commended for communicating in an accessible language many fascinating insights into the nature of cooperation. Their readers will find an informative survey of the rich mathematical models and theories that define a lawlike realm of biological and cultural phenomena.

References

1. M. A. Nowak, C. E. Tarnita, E. O. Wilson, *Nature* **466**, 1057 (2010).

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POLITICAL SCIENCE

Dodging Responsibility

John Brehm

In *The Blame Game*, Christopher Hood identifies one of the most common gripes that citizens have about bureaucracy and government, namely, that no one in either accepts responsibility for making mistakes of omission or commission. In this brief and often illuminating book, Hood (a political scientist at Oxford University) explores the diverse and insidious ways in which ducking blame manifests in public life.

Hood's book follows in a spirit similar to other powerful approaches to politics by posing a single maximand (here, dodging blame) and inferring propositions that extend from this by-necessity unrealistic assumption. David Mayhew famously postulated that members of Congress must be single-minded seekers of reelection, for any other goal must be subordinate to seeking and retaining office (1). They may seek power, or have policy goals, or have aspirations for higher office, but all of these goals are for naught without election to office in the first place. With relevance to bureaucracy, Hood's blame dodging is akin to William Niskanen's budget-maximizing

bureaucrat, James March's slack-maximizing organization member, or Herbert Simon's satisficer (2–4). The weaknesses of such single-minded approaches are palpable: they require grotesquely simplified characterizations of the behavior of the actors (legislators, bureaucrats, organization members) they study.

Of course, all of these actors have other goals, some of which may provide better explanations of particular aspects of the actors' behavior. Yet the strength of single-minded approaches is that by providing clear assumptions about the maximands, authors can deduce specific, falsifiable propositions about behavior. Their methods of deduction might be formal (as with Niskanen), discursive (as with Mayhew), or a hybrid (as with Simon and March), but from each readers would learn to expect something: that the acquisition of a greater budget smotheres programmatic goals; that taking a position on controversial matters of politics matters less than claiming credit, which is in turn less frequent than simple advancement of name recognition; or that bureaucrats become less efficient in the long term by seeking resources that permit rapid response in the medium term.

What are the specific propositions that dodging blame implies? In his discussions, Hood identifies four main classes of actors: top leaders, street-level bureaucrats, intermediaries, and "all the different individuals with whom governments and public service providers deal." (Hood has the habit of colloquializing many of the names of the actors: Top leaders are variously "generals" or "bananas," and those directly serving the public are the "poor bloody infantry" or "frontline troops," but none of these, often military, terms are really apt.) All these actors have a repertoire of ways to accomplish the same essential task: Leaders deflect blame toward subordinates, other agencies, or entities entirely outside of government; the front line shoves blame toward their leaders, other agencies, or outside entities; middle management might pass responsibility up, down, sideways, or out; "civil society" (the least coherent of the groups of actors) pushes sideways or outward. In short, all directions of blame shifting are possible—hardly the precision desired from a one-motivation model. Some of these directions are rather dysfunctional. Top leaders who blame subordinates may find themselves bereft of essential support in subsequent crises, and subordinates

who blame their chiefs may find themselves called on the carpet before too long.

Actors may avoid blame by ignoring present problems until public attention shifts elsewhere, persuading the public that the problem is not as bad as it seems (or could be), diverting attention to another problem, or even apologizing for the problem in the first place. One wonders what is left over, especially if apologies count as blame ducking—perhaps the degree to which the actor dodges blame has to do with the very subjective notion of how sincere the apology is? Hood approvingly mentions President Obama's apology and acceptance of blame after the failed attempt to appoint former senator Tom Daschle to the post of Secretary of Health and Human Services ("I screwed up"). Yet it is far from obvious that Obama had any particular role to play in the failed appointment other than being in charge of an administration making its first appointment mistake.

The book contains multiple figures that resemble extensive form games and graphs displaying situations that suggest indifference curves, but Hood uses these graphical devices to illustrate rather than to press an argument. Nor does he provide much in the way of direct quantitative evidence for his

principal claims despite occasionally wishing for more useful indices. Instead, he supports his argument with qualitative evidence culled from stories of government or bureaucratic malfeasance. The anecdotes make for great story telling, but are they convincing data?

By the end of this short book, the reader may reach the rather unsatisfying conclusion that what we experience sporadically actually occurs regularly, for reasons that apply only occasionally. Bureaucracies may or may not be functional places where routine processing happens in a fair and appropriate way, but *The Blame Game* provides little guidance as to why politicians and government officials accept blame or how a polity might more effectively encourage appropriate responsibility.

References

1. D. R. Mayhew, *Congress: The Electoral Connection* (Yale Univ. Press, New Haven, CT, 1974).
2. W. A. Niskanen, *Bureaucracy and Representative Government* (Aldine, Atherton, Chicago, 1971).
3. J. G. March, H. A. Simon, *Organizations* (Wiley, New York, 1958).
4. H. A. Simon, *Administrative Behavior* (Macmillan, New York, 1947).

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