Title

In the Light of Evolution, Volume V: Cooperation and Conflict (an Introduction)

Journal

PNAS, 108

Authors

Avise, JC
Strassmann, JE
Queller, DC
et al.

Publication Date

2011

In the light of evolution V: Cooperation and conflict

Joan E. Strassmann[a], David C. Queller[a], John C. Avise[b], and Francisco J. Ayala[b,1]

[a]*Department of Ecology and Evolutionary Biology, Rice University, Houston, TX 77004; and* [b]*Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697*

This paper serves as an introduction to the fifth in a series of Colloquia under the general title "In the Light of Evolution" (ILE; see Box 1). Papers from the first four colloquia in the "In the Light of Evolution" series, titled "Adaptation and Complex Design," "Biodiversity and Extinction," "Two Centuries of Darwin," and "The Human Condition," are refs. 1–4, respectively. The current volume explores recent developments in the study of cooperation and conflict, ranging from the level of the gene to societies and symbioses.

Any student of history knows that humans can be a vicious lot, but paradoxically, we are also among nature's great cooperators. Which of us, as an individual, can manufacture a cell phone or an airplane? Even our great conflicts—wars—are extremely cooperative endeavors on each side. Some of this cooperation is best understood culturally, but we are also products of evolution, with bodies, brains, and behaviors molded by natural selection. How cooperation evolves has been one of the big questions in evolutionary biology, and how it pays or does not pay is a great intellectual puzzle.

If nothing makes sense in biology except in the light of evolution (5), then for the first century after Darwin, cooperation and altruism did not make much sense. We could see that individual organisms sometimes helped others, even at a cost to their own fitness. It was clear that such behavior could benefit the group, population, species, or even other species and whole communities. However, it was not obvious how such effects would be heritable. All our mathematical models—the hard work of the modern synthesis—were about individuals with one allele out-reproducing those with an alternative. This process would favor individuals with higher reproduction but would not be expected to produce self-sacrifice. However, apparent cooperation was routinely attributed to the good of the group, species, or community. This situation changed in the first decade of Darwinism's second century. Hamilton (6, 7) argued that cooperation was important in nature and that social evolution could be understood in terms of direct gains to the actor's own fitness or indirect benefits to the fitness of others who share the cooperation allele. There followed an intense period of exploring the indirect effects of cooperation and altruism, reinterpreting sexual selection and many other phenomena in terms of individual advantage, and understanding frequency-dependent effects through game theory, efforts that continue to the present.

The puzzle of cooperation was the dominant theme of research in the early years, whereas recent work has emphasized its importance and ubiquity. Far from being a rare trait shown by social insects and a few others, cooperation is both widespread taxonomically and essential to life. Major transitions in the hierarchy of life have often involved cooperation among lower-level units to the point where they evolve into higher-level organisms (8, 9). Examples include the assembly of the eukaryotic cell with its symbiotic organelles, the evolution of multicellular organisms, and the organismal colonies of some social insects. Organisms are, at multiple levels, those units that have evolved to have, within their boundaries, extreme cooperation and minimal conflict (10, 11). The depth of research on cooperation and conflict has increased greatly, most notably in the direction of the small organisms. Microbes turn out to have highly developed cooperation (12), and they, along with other model organisms, have proven instrumental in beginning to understand sociality at the genetic and molecular levels, the study of real selfish genes (13). The social evolution approach has given us insights on diseases often caused by microbes (14). At the other end of the spectrum, we are getting a much better understanding of the cooperation and conflict that matters most to our species (15). Cooperation has been central to humanity's spectacular success and will be central to our short- and long-term fates.

Fundamentals of Evolutionary Cooperation

Although most of this volume is about the new topics that are being treated as part of social evolution, such as genes, microbes, and medicine, the old fundamental topics still matter and remain the subject of vigorous research. The first four papers in these proceedings revisit some of these standard arenas, including social insects, cooperatively breeding birds, mutualisms, and models of social evolution.

There are many ways to think about and model social evolution. Inclusive fitness is one of the most venerable and most useful, and it is the framework used by many works in this volume. Queller (16) revisits why inclusive fitness has been so useful and suggests ways to expand it to speak more directly to interactions besides kin selection. He delimits two other kinds of social selection that can be treated more explicitly in Hamilton's rule (6, 7). Kind selection, which involves synergisms between individuals expressing the same traits, groups together greenbeards (genes that, in effect, can identify the presence of copies of themselves in other individuals) and many cases of frequency-dependent games. They share the feature that individuals expressing the trait have different effects on other expressers compared with nonexpressers, and they also share many differences from pure kin selection. Kith selection requires neither kin nor kind, but instead involves actors affecting partners in ways that feed back to the actor's fitness. Mutualism and manipulation are included in this category. The expanded version of Hamilton's rule with kin, kith, and kind could bring the advantages of Hamilton's methods to a broader range of social interactions (6, 7).

Interactions between individuals of different species are a major type of kith selection, where individuals are selected to affect their partners in ways that ultimately benefit themselves (or their kin). Such interactions need not be cooperative, but when they are, they typically involve exchange of different services that one partner needs and the other can easily provide; therefore, partners can be very different. Accordingly, Sachs et al. (17) explore associations or symbiosis among partners that are very different indeed, one being eukaryotic and the other being prokaryotic. Such symbioses, by leading to mitochondria and chloroplasts, were

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This paper introduces the PNAS supplement that resulted from the Arthur M. Sackler Colloquium "In the Light of Evolution V: Cooperation and Conflict," which was sponsored by the National Academy of Sciences on January 7–8, 2011, at the Academy's Arnold and Mabel Beckman Center in Irvine, CA. The complete program and audio files of most presentations are available on the NAS Web site at www.nasonline.org/SACKLER_cooperation.

Author contributions: J.E.S., D.C.Q., J.C.A., and F.J.A. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1] To whom correspondence should be addressed. E-mail: fjayala@uci.edu.

www.pnas.org/cgi/doi/10.1073/pnas.1100289108

responsible for the evolution of the eukaryotic cell itself. However, additional symbioses are widespread and sometimes ancient. Sachs et al. (17) use a combination of broad-scale phylogenetic analyses and case histories of particular systems to explore several transitions. They find, for example, that there is little phylogenetic signal to indicate that some bacterial groups are preadapted for eukaryotic symbiosis (17). Instead, the genes required seem to be quite widely available through horizontal transmission. Mutualistic interactions seem to arise from both parasitic and free-living ancestors. Once acquired, these mutualistic interactions seem to be quite stable, with few reversions to nonmutualistic forms. Given the tendency of vertically transmitted symbionts to degrade and the propensity of horizontally transmitted ones to cheat, this stability is somewhat surprising.

The social insects have long been viewed as the pinnacle of cooperation. This view is most tenable if one ignores the cooperation that goes on in transitions that are already complete, such as multicellular animals or the eukaryotic cell. However, some social insect colonies are so cooperative and integrated that they are viewed as superorganisms (organisms made up of other organisms). The motive force behind the evolution of these societies, which consist of close relatives, is kin selection (6). Nonacs (18) points out that predictions from kin selection theory have been both successful and also disappointing. The difference, he suggests, is not because of chance. The successful predictions from sex ratio theory and worker-policing theory occur when the predicted behaviors can be achieved using simple environmental cues that correlate with kinship. It is easy to treat males differently from females or workers differently from queens. The less successful kin selection predictions, such as parts of skew theory, may fail because they require genetic kin recognition mechanisms sufficient to detect closer from more distant relatives within colonies. This may not explain everything, because genetic kin recognition systems do exist, at least for distinguishing colony members from noncolony members. The interaction between environmental and genetic recognition systems has scarcely been explored, and Nonacs (18) runs computer simulations showing how greenbeard loci can perturb the outcomes expected under pedigree relatedness alone.

After the social insects, cooperative birds and mammals have attracted the most attention. Many bird species have helpers at the nest, usually offspring from previous broods who have remained at their natal site (19). Kinship is important here as well. Helping systems usually evolve from monogamous ones, and discrimination evolves in systems that show variation in relatedness (20). However, the story is more complicated for two reasons. First, although some helpers gain kin-selected benefits through helping close kin, others may gain direct benefits. Compared with the social insects, more research on birds has addressed the particular benefits of remaining at home and the ecological constraints that may limit independent breeding. Variance in reproductive success has played a role in these discussions, but Rubenstein (21) moves it to a more central position. He suggests that cooperative breeders may be bet hedgers, gaining advantage from a more uniform reproductive output in cooperative groups. Rubenstein (21) draws on many years of his field data on starlings in Africa, where there is much variation in both time and space, and he finds support for several predictions of this hypothesis.

Box 1. In the Light of Evolution

In 1973, Dobzhansky (5) penned a short commentary titled "Nothing in Biology Makes Sense Except in the Light of Evolution." Most scientists agree that evolution provides the unifying framework for interpreting biological phenomena that otherwise can often seem unrelated and perhaps unintelligible. Given the central position of evolutionary thought in biology, it is sadly ironic that evolutionary perspectives outside the sciences have often been neglected, misunderstood, or purposefully misrepresented. Biodiversity—the genetic variety of life—is an exuberant product of the evolutionary past, a vast human-supportive resource (aesthetic, intellectual, and material) of the present, and a rich legacy to cherish and preserve for the future. Two challenges (as well as opportunities) for 21st century science are to gain deeper insights into the evolutionary processes that foster biotic diversity and to translate that understanding into workable solutions for the regional and global crises that biodiversity currently faces. A grasp of evolutionary principles and processes is important in other societal arenas as well, such as education, medicine, sociology, and other applied fields including agriculture, pharmacology, and biotechnology. The ramifications of evolutionary thought extend into learned realms traditionally reserved for philosophy and religion. The central goal of the "In the Light of Evolution" series is to promote the evolutionary sciences through state of the art colloquia and their published proceedings. Each installment will explore evolutionary perspectives on a particular biological topic that is scientifically intriguing but also has special relevance to contemporary societal issues or challenges. Individually and collectively, the "In the Light of Evolution" series will aim to interpret phenomena in various areas of biology through the lens of evolution, address some of the most intellectually engaging as well as pragmatically important societal issues of our times, and foster a greater appreciation of evolutionary biology as a consolidating foundation for the life sciences.

Cooperation Writ Small: Microbes

Perhaps no taxa are as promising for enhancing both our understanding of cooperation and our understanding of the mechanisms as microbes. Early work on microbes concentrated on purifying and isolating them for growth in pure culture. The postulates by Koch (22) required this and were important for determining exactly which microbes caused a particular disease. However, in nature, microbes live in complex multispecies structured environments. Social interactions are profound, because microbes perform many functions (like digestion) extracellularly that animals perform inside. One of the recent transformative elements of the study of microbes has been an appreciation of the importance of their social interactions. Many of the types of social interactions found in animals have their counterparts in microbes. Some cooperative interactions are much more easily studied in microbes, particularly if the goal is to illuminate the genetic basis of behavior or use the power of experimental evolution.

Perhaps the best-studied social bacterium is *Myxococcus xanthus*, a species of δ-proteobacteria that spends its entire life in social groups (23). It is a predatory bacterium that hunts other bacteria in social packs, dissolving its prey in pools of cooperatively produced enzymes before ingesting them. Movement usually is based on Type IV pili and is fundamentally social. When food is scarce, individual bacteria aggregate into a fruiting body. In this stalkless fruiting body, most or nearly all cells lyse, perhaps to the benefit of the remaining few, which form hardy spores. Experimental evolution has shown us much about the nature of sociality in *M. xanthus*. For example, when food was patchily distributed, the species evolved more efficient group hunting techniques (24). Under other circumstances, social cheaters can drive population crashes (23, 25). In one fascinating case, a new cooperator evolved from the social cheater.

However, this work does not tell us how natural these events are; for that explanation, we must turn to natural variation in wild fruiting bodies. Kraemer and Velicer (26) explore natural phenotypic variation in social traits of distinct clones within a fruiting body. They took 10 fruiting bodies from nature, and from them, they isolated 48 individual clones and examined their social phenotypes (26). These clones varied within fruiting bodies in swarming and spore production, genetic traits likely to have arisen recently, because the clones from the same fruiting body were nearly genetically identical. This fascinating work will shed light on the nature of sociality in the absence of a single cell bottleneck, where variations that benefit single clones within the group can spread, even at the cost of other group members.

One advantage to studying microbial social systems is that attributes that are strong but sometimes hard to measure in animals are easily examined in experimental systems. One such attribute can be called restraint. It may not be easy to determine whether a cow in a herd is eating all that it could or is holding back so that others may eat. If it were holding back, this would be a social trait that would benefit others and thus, would be expected to evolve under kin selection only if the genes for that trait are also present in others (and they benefit accordingly). In an experiment, Nahum et al. (27) look at the evolution of restraint in a nontransitive hierarchy often described by the rock–paper–scissors game in which no one type consistently dominates. They used *Escherichia coli* clones and the colicin system (28). Colicins are costly to produce and resist, but sensitive strains are killed when producers release them. The researchers engineered double colicin producers and resisters so that production and resistance would not be lost or gained in their system, and then, they asked how the three types of clone would fare under different migration schemes compared with how the resistor performed on its own. They found that the resistor strain exhibited the most restraint with restricted migration in the presence of all three strains, just the conditions where their models expect cooperation to evolve (28).

Cooperation among clone mates arises easily, because the genes underlying cooperation are present in both partners. In microbes, cooperation often takes the form of extracellular secretions, including those used for quorum sensing, iron scavenging, and fruiting body formation. Therefore, a key question involves what favors the formation of clonal patches such that cooperation can be favored. One answer involves the physical structure of the environment. For example, microorganisms growing on substrates are more likely to be in contact with clone mates than those living in a more fluid environment. Another possibility, and one investigated in the models presented by Mitri et al. (29), is that other species can generate structure that favors within-species clonality. This paper uses a modeling approach to understand how additional species can change interactions within species for the case of a growth-promoting secretion (29). This agent-based modeling approach uses one other species to stand in for all competing species. The models indicate that other species can insulate secretors from selfish nonsecretors, even when the other species can use the secretions themselves. Other factors such as the role of dispersal and nutrient levels are also addressed in these models, which represent a beginning to the important task of considering microbial sociality and ecology simultaneously, because these factors must influence how selection operate on these systems in nature.

Real Selfish (and Cooperative) Genes

It is remarkable that a field founded on the concept of selfish genes (30) got so far for so long without paying much attention to specifiable genes. This fact is probably because we learned how phenotypic strategies of cooperation and conflict could be understood as the results of genes maximizing inclusive fitness. However, studies at the genetic level are now becoming common and should shed light both on the mechanisms and the manner in which social selection operates.

Fischman et al. (31) review and extend what is known about the molecular genetic mechanisms of eusociality. Some of the information comes from studies of particular genes and pathways, but much is now coming from evolutionary analyses of genome-scale data. To the seven sequenced genomes of social insects, Fischman et al. (31) add their own transcriptome-based protein-coding sequences for 10 social and nonsocial bee species, representing three origins of sociality. Some of the patterns are idiosyncratic. For example, early results from the honey bee genome pointed to the importance of odorant receptors and immunity genes, but this importance does not hold up in the broader analyses. Findings include increased rates of evolution of brain-related genes in the primitively eusocial bees, conceivably because of the increased cognitive demands of their competitive social environment. Juvenile hormone and insulin are often important in caste. This is not surprising if caste is nutritionally based, although the effects of juvenile hormone are quite different from the effects in nonsocial insects. There is also a rapid evolutionary change in proteins involved in fundamental carbohydrate metabolism. Again, this fits with a nutritional basis for caste, but it seems surprising that changes are common in such basic pathways. These issues should be clarified with additional genome sequences and functional studies of individual species.

Strassmann and Queller (32) explore a microbial social system where it is possible to manipulate genes. In the social amoeba *Dictyostelium discoideum*, starved cells come together in large groups in which 20% of the cells sacrifice themselves to make a stalk that aids in dispersal of the others as spores (33). Besides this impressive altruism, this species has been shown to have cheating, kin recognition, and even primitive farming of their bacterial food. Numerous genes of many functional types can be mutated to cheaters. Some cheaters could destroy cooperation, but cooperation is maintained for a variety of reasons, one being the rather high genetic relatedness in the field, part of which is caused by kin recognition mediated by highly polymorphic adhesion genes. Other controls on cheating that have been shown include the evolution of resistor genes, power asymmetries, and lottery-like mechanisms. Studies of the *dimA* and *csaA* genes have shown that cheating can also be controlled by idiosyncratic pleiotropies of particular genes. The cheating allele would be favored by selection, but other deleterious effects of the same allele keep it from spreading, suggesting that cheat-proof cooperation often may be built using elements that are essential for other reasons. Consistent with ongoing social conflicts and arms races, social genes evolve rapidly.

Dawkins (30) argued that all genes are selfish, but the ones that show the trait most distinctively are selfish genetic elements. These are the renegades of the genome, chunks of DNA that replicate, in part at least, through different pathways than most genes and thus, can be selected to conflict with other loci. Transposons, for example, increase their representation by jumping from one place to another, often at some cost to the organism. Other examples include meiotic drive elements, various modification rescue systems, imprinted genes, B chromosomes, and organellar genes. Werren (34) tackles the issues of the function and adaptation of these elements. He surveys the evidence, sometimes strong and sometimes suggestive, that such elements have had important functional consequences for their genomes. For example, parts of transposons sometimes evolve into regulatory regions, and defenses against selfish elements may have led to the eukaryotic intron-splicing apparatus. However, contrary to some recent suggestions, Werren (34) argues that there is as yet little evidence that these are the adaptive reasons for the maintenance of these elements. Instead, selfish genetic elements are maintained by their selfish behavior, but the new chunks of DNA that they sprinkle throughout genomes sometimes get co-opted, domesticated, or otherwise modified to cause some beneficial effect to the organism.

Sociality and Medicine

Most biologists probably work in biomedical fields. If nothing in biology makes sense except in the light of evolution, then medicine should have much to learn from evolutionary reasoning. The rapidly growing field of Darwinian medicine (35) is based on this premise and seeks to provide insight on topics like the evolution of virulence and diseases of altered evolutionary environments. A subfield, recently called Hamiltonian medicine (14), investigates the impact of social evolution, cooperation, and conflict on disease.

Read et al. (36) treat the vital problem of how to minimize the evolution of pathogen resistance and thereby extend the useful lives of our arsenal of antibiotic drugs. This involves a complex set of interacting causes, some of which have a social element and others do not. Read et al. (36) challenge the dogma that we minimize the evolution of resistance by radical pathogen cure: using enough of a drug to try to eliminate the pathogen from the patient's body. The reasonable rationale behind this practice is to lower the pathogen population size and minimize the occurrence of novel resistance mutations. However, Read et al. (36) argue that this ignores the selective phase, which may be more important in determining the time to drug impotence, particularly when resistance mutations arise with relatively ease. In this selective phase, the radical pathogen cure provides the strongest possible selection for resistance. According to Read et al. (36), the social structure of the pathogen can powerfully augment this selection. When a host is infected by multiple strains of the pathogen (as is often true of malaria) and the total density of the pathogen is regulated, then wiping out susceptible strains with antibiotics can greatly increase the frequency of formerly rare resistant strains. This raises the possibility that the medical community is ignoring an important human social dilemma: that the best treatment for a patient may not be the best outcome for society as a whole.

Some human disorders can spring not from a failure of adaptation per se but from disagreement and conflict over what is the correct adaptation. This is particularly so in the realm of human interpersonal relations, starting with fundamental conflicts between parent and offspring. Haig (37) has argued that such conflicts can lead to pathologies in pregnancy when there is an upset in the precarious resolution of embryo–maternal conflict. Taking a radical step further, he has pointed out that the optimal strategy of an embryo's gene differs according to whether it came from the dam or the sire, with maternal loci being less selected to take resources from the mother. Remarkably, imprinted genes seem to behave in accord with this theory. Haig (38) extends this thinking in several directions. He notes that most of our kin belong to categories that have asymmetrical relatedness to our maternal and paternal genes, and therefore, most of our psychological adaptations for dealing with kin, and perhaps pathologies, may reflect these kinds of conflicts. In particular, he shows how this perspective may illuminate unsolved problems surrounding the evolution of adolescence and the timing of sexual maturation in humans (38).

Frank and Crespi (39) extend and generalize the same theme: that conflict can lead to pathologies when opposing interests that are precariously balanced become unbalanced. Frank and Crespi (39) suggest that the conflict between maternal and paternal genes in offspring, through its shown effects on the regulation and pathologies of growth, may be responsible for some cancers. They then discuss the exciting idea that this same balance is partly responsible for a wide spectrum of psychiatric disorders, such as autism, that may result from an overexpression of paternal interests in offspring selfishness. Similarly, other disorders such as schizophrenia might result from an overexpression of genes underlying the maternal goal of greater social integration. Finally, Frank and Crespi (39) present a theory of conflict between autosomal and X chromosomes. X chromosomes spend two-thirds of their time in females and therefore, should be selected to give greater weight to female than male adaptation. Autosomes should give equal weight. It will be fascinating to see if empirical tests support the authors' prediction that such conflict will underlie pathologies of expression along the male–female axis.

Are Humans Different?

Evolutionary principles for cooperation that have been developed from studies of diverse social organisms should apply to humans. The more immediate roots to human cooperation and conflict also may be seen in primates. However, there are challenges in studying humans and their close relatives. Objectivity is essential. There are many possibilities for study techniques (such as the questionnaire or survey) in humans, but these also offer many opportunities for confusion. One powerful approach to studying human cooperation is to look at what humans do and what the outcomes are, just as one might do for other social animals. This technique can be particularly informative when the human group lives in ways consistent with humans over most of their evolutionary past. The Dogon of Mali, reported on by Strassmann (40), are millet and onion farming agriculturalists who do not use contraception, adhere largely to indigenous religions, practice polygyny, and have high mortality rates. In a 25-y longitudinal study, Strassmann (40) addresses the hypothesis that the Dogon are cooperative breeders, where some individuals help rear nondescendent kin rather than their own progeny. She does not find that the data support this hypothesis. First, neither women nor men delay reproduction in order to raise siblings. Although parents force daughters to care for extra siblings, this is better viewed as parental manipulation. as the presence of siblings reduces survivorship. Similarly, grandmothers do not appear to be effective alloparents. Rather than increasing survivorship, the presence of paternal grandmothers does the opposite, doubling the hazard of death for a child. What matters most for survival is the presence of the mother, and other relatives are not adequate replacements. Task cooperation occurs within the groups that work and eat together, but conflict is always present in ways that are carefully explained by Strassmann (40).

In an overview of vertebrate interactions, Cheney (41) shows that animals ranging from chickadees to chimpanzees are aware of their own status and their companions, and they behave accordingly. Eavesdropping on how individuals interact with others can change behaviors. Relatednesses are often known and impact interactions. In vervet monkeys, for example, an individual who has been attacked may turn and subsequently attack a relative of her opponent. Dominance hierarchies also impact such interactions. However, some animal interactions are more subtle. Ravens are more likely to cache food in hidden sites when competitors are present, for example. However, the calculations of gain, cost, and punishment necessary for reciprocal altruism (here called contingent altruism) seem largely lacking outside of humans. Instead, there is a great deal of tolerance in interactions and a lack of direct payback among close relatives and long-time partners. However, it is in these relationships where cooperation overwhelmingly occurs. A common feature of cooperative acts is that they are not necessarily transitive. Some individuals consistently take on the risky jobs, be it male chimps patrolling their territorial edges or female lions leading the hunt. This is also true in organisms (such as wasps) with much simpler brains, where cooperation flows from workers to the queen.

Observations of humans and primates in natural situations can teach us much about behavior, but environmental complexity can make causation difficult to discern. An alternative is to examine choices made under highly regulated circumstances. To address social acts such as generosity, trust, fairness, and punishment, many purportedly relevant games have been applied to humans, one simple example being the Dictator Game that allows a subject to decide whether to share a quantifiable resource with an unseen other (this game typically yields donations of 20–30% of the resource). Although such games have weaknesses, they seem to indicate that humans are willing to donate but only at levels indicating that they consistently value themselves most highly. These and other experiments further indicate that humans favor relatives, long-term partners, and group members over outsiders, and they will suffer costs to punish cheaters. As described by Silk and House (42), versions of social games involving food or tools that likewise have been used with primates produce complex results. Cooperation clearly occurs and tracks levels of sociality in the groups, but some results are controversial and remain open to alternative interpretations.

In the modern world, most of a person's material possessions are items that no individual could possibly make by herself. Instead they were produced with the learned and specialized expertise of others. In the final paper of these proceedings, Boyd et al. (43) argue that learning from others (and not intelligence alone) is the key to human success, the characteristic that has made us so adaptable. Initially in human history, these adaptations involved direct protection from the climate, food acquisition, and food storage. Thus, it is a particular kind of intelligence that involves the sharing and acquiring of information from others. These cultural learners have an advantage, because they can grasp the best from the past even if they innovate personally only occasionally. Tools and customs certainly make life for humans easier or possible.

The study of cooperation and conflict has come a very long way from the time, 50 years ago, when Hamilton (6,7) first pondered how to explain the evolution of worker behavior in social insects with a strange genetic system. It has spread out taxonomically, extending even to microbes. It has deepened mechanistically as we probe its molecular and genetic basis. It is beginning to show practical applications, as in medicine. Additionally, it has proven essential for understanding the structure of life from cells to multicellular organisms to societies. Finally, its study helps us to understand the mix of cooperation and conflict that makes the human animal both ordinary and remarkable.

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