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Book review

The Caucus-Race of the Dodo

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> "What is a Caucus-race?" said Alice ...
>
> "Why," said the Dodo, "the best way to explain it is to do it ..."
>
> First it marked out a race-course, in a sort of circle, ... and then all the party were placed along the course, here and there. There was no "One, two, three, and away!" but they began running when they liked, and left off when they liked, so that it was not easy to know when the race was over. However, when they had been running half an hour ... the Dodo suddenly called out "The race is over!" and they all crowded round it, panting, and asking "But who has won?"
>
> This question the Dodo could not answer without a great deal of thought, and it stood for a long time with one finger pressed upon its forehead ... while the rest waited in silence. At last the Dodo said "*Everybody* has won, and *all* must have prizes."
>
> *Alice's Adventures in Wonderland*
> Lewis Carroll 1865

A review of Peter Hammerstein (ed.), *Genetic and Cultural Evolution of Cooperation*, MIT Press, Cambridge, MA, 2003, 450 pp., ISBN 0-262-08326-4, $45.00.

1. Introduction

What do a slime mold cell, a cleaner fish and a human being have in common? Under casual inspection, the differences seem to overwhelm any similarities. However, each of these organisms participates in some sort of cooperative group action. Slime mold cells aggregate to form delicate fruiting bodies, in which some cells constitute a somatic "stalk," while other cells retain reproductive rights in a "spore head." Cleaner fish remove parasites from the client fish they serve and, in the process, receive food. Human pro-social behavior (e.g., cooperative hunting, food sharing and group defense) was probably crucial to the development of human societal organization. In each case, the organism has the option to defect (a slime mold cell might differentially migrate into the spore head, a cleaner fish might steal tissue from its client, a human may refuse to share food) and yet these systems are characterized by substantial cooperation.

Why is such cooperation a puzzle? In a Darwinian world, different organisms are often depicted as engaged in constant competition with one another – the contestants in an evolutionary race. An expectation arising from this view is that selfish individuals win the race and nice guys finish last. If the winners of the race are individuals that seek to improve their lot at the expense of others, the outcome of the Dodo's Caucas-race seems unattainable. How can all of the members of a group simultaneously "win?" How can selection favor cooperative or altruistic strategies leading to such harmony? Why doesn't a defecting type outrun the rest?

These are some of the issues tackled in the recently published *Genetic and Cultural Evolution of Cooperation* (Hammerstein 2003). This edited volume is the fruit of a Dahlem workshop, the 90th of a series of meetings designed to promote communication and problem-solving among scientists from different disciplines. As the problem of cooperation arises in many scientific fields outside biology (e.g., the social dilemmas of psychology, the public goods games of economics, and the Prisoner's Dilemma of game theory) the Dahlem forum is particularly apposite. The diverse backgrounds of the participants echoed the basic Dahlem mission statement: the group consisted of behavioral economists, cellular biologists, cultural anthropologists, ecologists, evolutionary psychologists, mathematicians and primatologists. Consequently, the topics of the contributed chapters were richly diverse, exploring (i) the role of cognition and emotion in primate cooperation, (ii) mutualism and symbiosis from a market perspective, (iii) cooperation within cells and (iv) human cooperation (these four topics define the sections in the book).

Rather than dissecting each part of the text, in this review, I lay out what I take to be the major themes of this volume. These themes concern the way biological entities, from genes to interacting species, manage to run the Caucas-race of the Dodo. I then discuss how perspectives about groups (especially groups of humans) lead different authors in this book to different hypotheses about mechanisms for the evolution of cooperation and different views on the levels of selection controversy. I end with my thoughts on the role this volume will play in the study of cooperation.

2. Themes

Beyond kin selection and reciprocal altruism

In general, alleles are expected to increase in frequency by virtue of the positive effects they have on their owners (improving fecundity or viability). Hamilton's (1963, 1964) great insight was that a copy of an allele could improve its future representation through its positive effects on selfsame copies housed in *other* individuals. Even if a particular individual incurs a cost through helping others, an allele affecting the helping behavior can increase as long as the benefit to the other party is large enough, where this benefit is "weighted" by the probability that the other party contains copies of this allele.[1] Hamilton's development of inclusive fitness theory led researchers to look at the relatedness between cooperating entities. For instance, the fact that many organisms develop from a single cell means that, barring mutation, cells in a multicellular organism are clones. This high level of relatedness is invoked to explain the high degree of coordination (e.g., during development) and extreme altruism (e.g., the relinquishing of reproductive rights by somatic cells).

Kin selection has enjoyed theoretical prominence in explaining the evolution of cooperation and altruism. However, there are many cases of cooperation that occur between individuals with very low relatedness. For instance, the partners of mutualisms are often members of different species and thus mutualistic cooperation is outside the scope of classic inclusive fitness theory. Trivers (1972) introduced the concept of reciprocal altruism to explain cooperation in such contexts. Trivers argued that if individuals interact repeatedly with one another (such that each individual is in a position to give and receive altruistic acts from the other) and if the benefits to one's partner outweigh the personal costs of the altruistic act, then altruism can be selected, because the long-term net benefits to an individual are higher in a reciprocally cooperating pair than in one lacking cooperation. However, what prevents an individual from reneging on the deal? That is, why not receive the benefits from others and refuse to provide benefits later? Trivers argued that defection could be punished if an altruist responded to a non-altruistic partner by withholding future altruistic acts. Axelrod and Hamilton formalized these ideas using a game theoretic approach to analyze strategies within an iterated Prisoner's Dilemma (Axelrod and Hamilton 1981; Axelrod 1984).

So, we have two seemingly powerful theoretical tools to dissect cooperation: kin selection and reciprocal altruism. However, several chapters in *Genetic and Cultural Evolution of Cooperation* (GCEC hereafter) propose that many cases of cooperation can be explained neither by blood ties nor by reciprocation. In part, Trivers' ideas were motivated by cooperative *interspecific* interactions; however, the majority of species engaged in mutualisms do not seem to use a strict tit-for-tat mechanism (Bergstrom et al. [13]).[2] While there is evidence for short-term reciprocation in intraspecific interactions (e.g., in ungulates, monkeys, fish and lions), there is less evidence of long-term reciprocation in nonhuman social animals (Silk [3], Hammerstein [5], and McElreath et al. [7]). And it seems that coefficients of relatedness are insufficient for kin selection to carry the full explanatory burden of cooperative behavior within these species.

Human social behavior seems to pose the strongest challenge to kin selection and reciprocal altruism. Silk [3] suggests that communal friendships (between non-relatives) operate routinely without explicit tracking of exchange of benefits (indeed there are tendencies *not* to keep track of favors or reciprocate right away). Fehr and Heinrich [4] discuss the "strong reciprocity" of subjects in *one-shot* experimental games. These players are neither relatives, nor are they playing repeatedly. However, if allowed, these players will reward cooperation and punish defection even when costly to themselves. Such experimental findings are difficult to explain with either kin selection or reciprocation theory (Fehr and Heinrich [4], Bowles and Gintis [22], Heinrich et al. [23]).

So what replaces the classic theory? One possibility is indirect reciprocity (McElreath et al. [7], Bshary and Noë [9], Smith [21], Heinrich et al. [23]). That is, an individual behaves cooperatively in order to secure a better reputation, which could be cashed in for better reproductive options. A second possibility is that cooperative behavior is an honest signal of quality (Smith [21], Bowles and Gintis [22], Heinrich et al. [23]). Further, it is often assumed that the cooperative nature of the signal is what attracts the audience to receive it. A third possibility is that selection operates at the level of groups and properties that promote group viability or group fertility can increase under conditions where the variation of types within groups is low and the variation of types between groups is high (Fehr and Heinrich [4], Richerson et al. [19], Bowles and Gintis [22], Heinrich et al. [23]). A last possibility deals with cooperative interactions within a market framework.

Biological markets

The market view of cooperative interactions is to treat partnerships as exchanges of goods, where the rate of exchange can be attributed to the balance of supply and demand forces (Bowles and Hammerstein [8]). A recurring theme in GCEC is that these biological markets are characterized by the phenomenon of partner choice. In contrast with reciprocity theory, in which partnerships are often assumed to be fixed, termination of a relationship and choice among partners is common in many biological interactions (Hammerstein [5], Bowles and Hammerstein [8], Bergstrom et al. [13]). For instance, lazuli bunting and purple martin males will sometimes allow a younger male to co-occupy their territory in exchange for access to the younger male's mate (Bowles and Hammerstein [8], Bshary and Noë [9]). The territory-holding males will generally choose to admit dull-colored male birds and reject bright colored males. Some yearlings are dull-colored (whereas both adults and other yearlings are bright). A dull-colored yearling does not seem to pose a threat to a territory holder and is admitted in exchange for reproductive rights to the yearling's mate. Certainly the availability of empty versus occupied high quality territories will determine the rate of exchange, and partner choice influences the identity of the beneficiaries of the exchange (and, in this case, may actually influence the evolution of plumage maturation).

Bshary and Noë [9] discuss one of the most famous mutualisms, that between cleaner fish and their clients. *Labroides dimidiatus* (the cleaner wrasse) generally occupies a station, where it removes ectoparasites from several different visiting client fish species. There are two types of clients, resident species (which remain near a single cleaning station) and roving species (which cover large areas and thus can reach several cleaning stations). Partner choice is predicted to influence the nature of these cleaning interactions. Cleaners are able to choose between their resident clients and the available roving clients. Roving clients are able to choose among various stations. A market model of the mutualism predicts that cleaners should always prefer roving clients to resident clients (as the former has access to other cleaning options and the latter can always be cleaned later). Also, market theory predicts that roving clients should return to stations where they received better service (cleaning where the wrasse does not cheat by stealing fish tissue in addition to the parasites). It turns out that field results and experiments support these predictions (Bshary and Noë [9]). This is an example of where one partner (the roving client) can exert control over the other (the cleaner) to minimize exploitation within the partnership.

Exploitation, control and power

The Achilles' heel of cooperative interactions and mutualisms is the possibility of exploitation. This could take the form of defection within an interacting pair or opportunistic free-riding by a third party. How can such exploitation be avoided? In part, the answer depends on how much control each partner has over the other. When there are strong asymmetries in control, then one partner has power over the other. Such differences in power can have strong effects on the nature of biological interactions.

Hoekstra [14] considers exploitation in genetic systems and the various methods of control. For instance, segregation distorters are alleles in heterozygous diploid organisms that are overrepresented in the haploid products of meiosis. Even if such alleles have negative effects on the organism's fitness, they can increase in frequency due to their exploitation of meiosis. The well-studied segregation distorter systems have revealed that the distorter is actually made up of two linked genes: one that produces a "toxin" and one that produces the "antidote". All products of meiosis have accumulated the "toxin," but only those with an "antidote" allele are able to survive; thus, the tightly linked toxin/antidote pair can "drive" meiosis in its favor by killing the non-toxic/non-immune pair in the gametes of heterozygotes. It turns out that genetic recombination, which uncouples the toxin/antidote pair, could be an important way of controlling the rise of such distorters (note that when an antidote allele is matched with a non-toxin allele, a pair "resistant" to segregation distortion results).

There also may be "modifier" loci that control segregation distortion. This possibility has been explored theoretically (Eshel 1985) and evidence for such modifiers has been found in *Drosophila quinaria* (Jaenike 1998). A genetic outlaw, such as the segregation distorter, harms the whole organism (and thus the many other genes it houses) in exchange for a personal gain. Consequently, there should be pressure on the rest of the genome to suppress meiotic drive. Some authors have argued that because of the sheer number of genes (or, more specifically, the number of mutational options of these genes) there ought to be more ways to suppress the distortion than ways for the distorter to avoid suppression. That is, the outlaw should be outgunned. The idea that there is power in numbers lies behind the concept of the "parliament of the genes" (Hoekstra [14], Lachmann et al. [18]).

Exploitation also occurs at the cellular level. In multicellular organisms, some cells proliferate at the expense of the organism (e.g., cancer). How can such exploitation be controlled? Michod [16] takes a modifier approach to these problems. Specifically, he considers how modifiers creating a germ line, policing mutant cells, changing the propagule size, and changing how cells aggregate can invade and fix. Modifiers that reduce the propagule size will quench genetic variation and can be selected when selfish mutations in cells occur. Modifiers to sequester cells into the germ line earlier may invade when there are low costs to losing the would-be somatic cells (and such sequestering may prevent oxidative mutagenesis) (Michod [16], Lachmann et al. [18]).

Cancer-like exploitation is a problem at the subcellular level as well. Some mitochondria in fungal species possess plasmids that lead to rapid replication and displacement of normal mitochondria. As a consequence, the fungal cells age and die from this mitochondrial cancer (Hoekstra [14]). In sexual species, uniparental inheritance of organelles reduces the diversity of organelles and thus the opportunities for within-cell organelle competition. Interestingly, uniparental inheritance may control one type of organelle exploitation (organelle cancer), but simultaneously open the door for another type of exploitation (sex-ratio distortion). That is, there should be selection for organelle genes that skew the sex-ratio in favor of the one sex that carries the organelles into the next generation. Ironically, as one problem is solved, a new one is created.

Bronstein [10] presents evidence that several types of exploitation are common in mutualisms and discusses how partner choice may be a way to stem exploitation within the mutualism (see also Bergstrom et al. [13]). Bshary and Noë [9] illustrate this point in their discussion of the cleaner fish mutualism. It would seem that the roving client can control cheating (the stealing of fish tissue by the cleaner) by choosing which cleaning station to frequent. Indeed, roving clients tend not to return to stations where cheating occurred or even where they witnessed cheating by the cleaner on another fish! Cleaners were also less likely to cheat when a roving client was watching, but not a resident client.[3]

In a fascinating contribution to GCEC, Bergstrom and Lachmann [12] investigate a subtle aspect of control. These authors use an evolutionary game theory approach to explore the dynamics of two species whose members are engaged in an inter-specific mutualism. The fitness of each individual in its interaction with its partner depends both on its own strategy and that of its partner. The fitnesses are such that there are two evolutionarily stable equilibria, each corresponding to a different one of the two species benefiting disproportionately from the mutualism. They explore the dynamics of two species that evolve at different rates and uncover a surprising result: the slower evolving species ends up (more often than not) at its preferred equilibrium![4] It is as if a contestant in the Dodo's Caucas race can get a bigger prize by slowing down. They label this phenomenon the Red King Effect (after another of Alice's acquaintances) in contrast with the Red Queen Effect, where evolving faster allows a species to prosper in coevolutionary interactions.

Exaptation

Gould and Vrba (1982) proposed the term "exaptation" to apply to traits initially selected for one role (or even initially unselected) and later co-opted for a new role. For instance, if feathers in birds were originally selected for their role in thermoregulation and only later co-opted for flight, then feathers were originally an exaptation for flight. What do feathers have to do with cooperation? Although few authors in GCEC refer explicitly to the concept of exaptation, this theme surfaces in several chapters.

In the development of multicellular organisms, differentiated cells are engaged in a staggering feat of coordination. Szathmáry and Wolpert [15] discuss how the unicellular ancestors of multicellulars were most likely equipped with many of the prerequisites of multicellular development, including epigenetic inheritance, intercellular signaling, and motility. Thus, these features were available for use in the coordination of a group of cells, the proto-multicellular organism. As mentioned above, within a multicellular organism, there is always the threat of defection. Apoptosis (or programmed cell death) may be an effective policing mechanism (Michod [16]). Mitochondrial processes are implicated in programmed cell death within multicellular organisms. Blackstone and Kirkwood [17] suggest that mechanisms that originally led to host cell fusion and recombination in mitochondrial ancestral communities could have been co-opted for use in apoptosis in the multicellular context. According to Blackstone and Kirkwood [17], a process that could have originally benefited proto-mitochondria could have leaped levels in the biological hierarchy when co-opted to benefit the multicellular organism.

Leimar and Connor [11] discuss how the by-products of organisms may lead to the establishment of mutualism. For instance, aphids excrete products that ants eat and, in turn, ants will protect aphids from their natural enemies. In the evolutionary past of aphids, such products may not have fed ants (indeed, these products were most likely waste). Similarly, ant defense of a valuable resource probably evolved before ants and aphids became intimate. However, as ants and aphids started to interact, both of these behaviors could be tuned. Aphids could time the extrusion of the waste when ants were near and in turn ants would vigorously defend a reliable resource. This is an example of pseudoreciprocity, the evolution of traits in one species in order to receive by-product benefits from a second species. In this conception, the aphid-ant pseudoreciprocity is founded on exaptation: the production of waste products was co-opted to feed ants and thereby receive by-product defense. Leimar and Connor suggest that pseudoreciprocity may explain the evolution of many different mutualisms (see also Bergstrom et al. [13]).

In several of the chapters on human cooperation, the concept of exaptation again arises. Fessler and Haley [2] suggest the emotions of anger (gratitude) found in dyadic relationships when a partner defects (cooperates) may have been co-opted for the moral outrage (approbation) that operates in larger groups when an individual witnesses the violation (satisfaction) of a cultural norm by a third party. Silk [3] critically discusses a hypothesis that current human friendship evolved out of positive interactions between kin or out of tit-for-tat reciprocation in small groups. Richerson et al. [19] discuss how human tribal instincts may have been co-opted in the formation of larger-scale societies – termed "work-arounds." For instance, given strong conformist tendencies in small groups, the use of symbols (e.g., flags, clothing, language) could define an in-group at a much larger scale.

Human cooperation

Over half of GCEC deals explicitly with cooperation in human groups. In human groups, some of the classic explanations of cooperation (kin selection and reciprocation) seem to break down. How and why do humans engage in pro-social behavior?

Culture and norms

Richerson et al. [19] suggest that the human proclivity to learn socially was essential in establishing a second form of inheritance: *cultural inheritance*. In general, genes and cultural hand-me-downs will differ in their rules of transmission (see Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985). If individuals culturally emulate successful members of their group or the majority of their group, the result can be strong within-group conformity. Such a state of affairs may be more difficult to achieve genetically (migrants into a group can change their normative behavior, but cannot change their genes). Several authors in GCEC suggest that this diminution of cultural variance within groups (leaving most cultural variance between groups) can lead to cultural sorting at the group level; and that such group selection can lead to highly cooperative behavior (Fehr and Heinrich [4], Richerson et al. [19], Bowles and Gintis [22], Heinrich et al. [23]). I shall return to the topic of multi-level selection below.

Young [20] discusses how classic economic theory often does not explicitly incorporate the cultural norms of human groups. He then presents fascinating data of agricultural share contracts in the Midwestern United States where there is very little heterogeneity locally in the shares, but more at large regional scales. Traditional theory would predict heterogeneity locally when there is heterogeneity in the underlying land quality. However, if there are strong tendencies for landlords to offer their tenants the local "going" share, then homogeneity in shares can result even with underlying heterogeneity in land quality. It would seem that norms are so powerful that they can distort basic economic predictions.

Emotions

Emotions are sometimes described as irrational – a wrench in the cogs of adaptive decision-making. In contrast to this view, Fessler and Haley [2] claim that emotions are instruments guiding behavior in adaptive ways. Further, they claim that emotions may work as mechanisms that cement cooperative interaction in human groups. For example, anger over a transgression by a partner may cause punishment of that partner and such punishment may lead to attenuation of future transgression. Alternatively, anger may lead an individual to terminate the partnership and find a more cooperative individual. Shame or guilt over a violation of group norms may cause efforts to repair relationships without the need of external punishment (Fessler and Haley [2], Bowles and Gintis [22]).

Language

Several authors argue that symbolic representation in the form of language was a critical innovation on the road to human cooperation. Arguments that use indirect reciprocity to explain human cooperation depend on some sort of bookkeeping of reputation (McElreath et al. [7]). Fessler and Haley [2] claim that symbolic communication is necessary for monitoring reputation.[5] Smith [21] suggests that language was critical to the formation of norms. Also, gossip and third-party communication can disseminate the reputation of individuals through a social network. Norm violation (fulfillment) can then be punished (rewarded) by individuals that got the information second-hand.

3. The levels of selection controversy

Collections or collectives?

Over the past 40 years, the concept of group selection has seen its peaks and valleys (with the valleys outnumbering the peaks in the biological mainstream).[6] Group selection was effectively excommunicated by Williams' (1966) *Adaptation and Natural Selection*, in which he argued that group-level adaptations do not generally exist and that traits which seem to benefit the group at a cost to the individual can (and should) be explained in terms of individual-level selection. Indeed, kin selection and reciprocal altruism were framed explicitly as *alternatives* to group-level explanations of altruism and cooperation (Hamilton 1963; Trivers 1971).

However, from the smoldering ashes of this concept, a new school of group selection emerged. In the vanguard of this movement was D. S. Wilson (1975, 1977, 1980, 1983, 1990), but there were other authors seriously investigating group selection as well (e.g., Price 1972; Wade 1978; Uyenoyama and Feldman 1980; Sober 1984). Price applied his famous covariance equation (Price 1970) to selection in group-structured populations. The two statistical terms of his equation seemed to partition selection cleanly into within and between group forces. Indeed, Price's equation led Hamilton (1975) to reconsider group selection and form new connections between kin and group selection. In recent years, there has been a renewed interest by both philosophers of biology and evolutionary biologists in probing the relationships between individualism and multi-level selection theory (Dugatkin and Reeve 1994; Sterelny 1996; Sober and Wilson 1998; Kerr and Godfrey-Smith 2002; Okasha 2003).

While embraced by some, the concept of group selection (or, more generally, multi-level selection) is still stigmatized in many biological circles. This polarization is apparent in GCEC. In several chapters, authors explicitly appeal to a group selectionist account of the evolution of cooperation (e.g., Fehr and Heinrich [4], Richerson et al. [19], Bowles and Gintis [22], Heinrich et al. [23]). In other chapters, authors are more tentative about invoking group selection (e.g., McElreath et al. [7], Smith [21]). I would argue that some of the disagreement boils down to how groups of organisms are treated. If one sees groups as entities that compete and replace one another, a multi-level view including selection within and between groups is very natural. In this view, groups have fitnesses *themselves*.[7] A second perspective consigns groups a different role – the social context of individuals. Here, the focus is on the individuals within the groups and these are the *only* entities that are assigned fitness. The first perspective sees groups as *collectives*, the second perspective sees groups as *collections*.[8] Consider the following two quotes from GCEC:

> The adaptationist program ... proposes that natural selection has designed organisms to respond to environmental conditions in fitness-enhancing ways. ... Human behavioral ecologists generally attempt to explain complex patterns of behavioral variation as forms of phenotypic adaptation to varying social and ecological conditions.
>
> Smith [21]

> When the group is threatened with extinction or dispersal, say through war, pestilence, or famine, cooperation is most needed for survival. ... A small number of strong reciprocators, who punish defectors without regard for the probability of future repayment, can dramatically improve the survival chances of human groups.
>
> Bowles and Gintis [22]

In the first quote, groups *are* the "social conditions" relevant for evolution of individually adaptive behavior. In the second quote, groups are seen in a different light, as entities that live and die as organisms do. I believe this difference in perspective leads authors to consider different explanations for the evolution of human cooperation. If one is focused on individuals, there is often less consideration of an intergroup replacement process. This is most clear in the alternative accounts of one possible intergroup replacement process: warfare.

Smith [21] considers the following hypotheses: (i) those who engage in violent combat garner high reputations and have better reproductive options in the future, (ii) those who engage in violent combat are giving a costly signal to others in their band about their superior quality, and (iii) those who engage in violent combat may obtain reproduction through abduction of the females in other groups. Bowles and Gintis [22] interpret cooperative action in warfare as preserving the chance that the group will survive. Smith's hypotheses are focused on the reproductive success of an individual within a group. In Bowles and Gintis' account, an individual's fitness will depend on whether the group survives (i.e., a high reputation or a costly signal means very little if one's group has been decimated). Of course, these explanations are not mutually exclusive. Indeed, norms for rewarding cooperative behavior may change the cost-benefit structure of engaging in combat, which may simultaneously lift the within group incentive of the individual to cooperate *and* the probability of group survival. (However, we then need to discuss how the norms and norm enforcement evolved).

Those who think of the group selection account as antithetical to Darwinian selection might consider the following quote from *The Descent of Man*:

> When two tribes of primeval man, living in the same country, came into competition, if the one tribe included (other circumstances being equal) a greater number of courageous, sympathetic and faithful members, who were always ready to warn each other of danger, to aid and defend each other, this tribe would without doubt succeed best and conquer the other. . . . At all times throughout the world tribes have supplanted other tribes, and as morality is one important element in their success, the standard of morality and the number of well-endowed men will thus everywhere tend to rise and increase.
>
> Darwin (1871)

Darwin himself uses a group selection explanation for the evolution of morality (see Sober and Wilson (1998) for more discussion of this point).

Individual-centered explanations

In general, most of the explanations of cooperation in GCEC that focus on individuals invoke kin selection, reciprocal altruism, indirect reciprocity or costly signaling. Smith [21] discusses the phenomenon of food sharing in the Aché of Paraguay, where food obtained in hunts is spread evenly throughout the band. Individualistic explanations for food sharing claim that an individual capable of sharing is providing an honest signal of quality. The reason an individual might give away the food (as opposed to showing it and then hoarding it) is that this individual may be able to attract a larger audience by giving food away, and thereby obtain a higher status with a larger section of the group.

Fessler and Haley [2] frame human emotions as instruments to steer their owner in the right direction. Anger over a transgression leads the angry individual to punish another which may reduce future transgressions and thus stabilize cooperation for the emotional individual. A similar argument is laid out by Trivers (1971), who framed his ideas in an explicitly individualistic tone. Moral outrage and approbation are interpreted as advertisements to others in the group, improving one's reputation or probability of gaining access to future cooperative interactions (Fessler and Haley [2]).

Hagen [6] suggests that depression in humans is an adaptive bargaining strategy in which benefits are withheld in order to manipulate others to improve social relations. That is, depression is a signal that is costly to the signaler and the receiver, but induces the receiver to adjust behavior to improve the signaler's state.

Cultural group selection

Selection (at any level in the biological hierarchy) is dependent on variation between the units being selected. Thus, one of the early problems of group selection was to explain how variation could be large between groups, but small within groups.[9] Richerson et al. [19] argue that conformist transmission in human groups (e.g., copy the majority) tends to promote *cultural* variation between and reduce variation within human groups (see also Bowles and Gintis [22], Heinrich et al. [23]). These authors argue that group selection can then work on the cultural variants. Note that with conformist transmission of normative behavior, groups are not easily invaded by cultural migrants (because the immigrating individual can switch its behavior to reflect local norms). Once stable cultural variants between groups are established, the process of cultural group selection can operate. Heinrich et al. [23] argue that the group selection can work through demographic swamping (more successful groups produce more individuals) or intergroup competition (e.g., war). Note that cultural group selection need not operate through the death of group members – cultural conversion to the successful variant is sufficient.

The cultural group selectionists in GCEC have directly challenged some of the standard individualistic explanations for cooperation. For example, why would effective signals in groups be pro-social? Why might we not see some non-social or anti-social signals of quality? An individualistic response might be that the audience tends to be larger when the signal is pro-social and thus a pro-social signaler benefits more than an anti-social signaler. The cultural group selectionists claim that groups whose members are anti-social are simply out-competed by groups with pro-social members (Bowles and Gintis [22], Heinrich et al. [23]).[10]

Strong reciprocity

Imagine the following scenario. You walk into a laboratory and are offered two choices, either you can take \$10 or leave with nothing. This is really a no-brainer – most people would take the money and run. Now, consider a second scenario. You walk into a laboratory and are told that you are going to play a one-shot anonymous ultimatum game with another player. The other player has been randomly chosen to make an offer about how to split \$100. You then have the option to accept the offer and get your share or reject the offer and both players leave with nothing. Let's say the other player offers to give you \$10 and keep \$90 for himself/herself. In a sense, you are being asked to make the same decision as in the previous scenario – a selfish individual should certainly take the \$10. However, it turns out that low offers like this one are often rejected in such ultimatum games and this result holds across many cultures (Fehr and Heinrich [4]).

Strong reciprocity is defined as the propensity to reciprocate cooperation and punish defection even when costly. In one-shot anonymous experimental games where players are dealing with sizeable monetary incentives, there are still tendencies to strongly reciprocate. This result does not seem to make sense in a view that individuals are endowed with behavior that maximizes their fitness. The obvious solution from an individualistic perspective is to see strong reciprocity in these experiments as a maladaptation. The basic idea is that natural selection favored strong reciprocity in environments in which repeated interactions were common. There would have been reciprocation in these ancestral social environments or the interactions could have been with kin. Perhaps strong reciprocators earned a good reputation among their peers. It is the one-shot anonymous nature of the experimental games that is novel and the formerly adaptive behavior is not adaptive in this context.

However, Fehr and Heinrich [4] argue against all of these individualistic hypotheses. First, they claim there is good evidence that subjects can tell kin from non-kin (and that our ancestors could too). Second, subjects in experimental games play differently when the interactions are repeated (they generally cooperate more). Thus, subjects are sensitive to the number of interactions and are probably not confused about the one-shot nature of the game (surveys confirm this intuition). Third, when reputation is involved, subjects again tend to cooperate even more. This result suggests that subjects are probably not confused about the anonymity of these games (surveys confirm this intuition).

This flexibility in subject behavior suggests that there may be very real effects of reciprocation and reputation on the stabilization of cooperation, however, it also attests to the idea that human beings are equipped to react to many different social circumstances. If reciprocation theory or indirect reciprocity were the only theoretical explanations available and we believe that human ancestors did interact over short periods with strangers, then a strong reciprocator in an anonymous one-shot interaction is an enigma. Fehr and Heinrich [4] present anthropological data that suggests that such interactions were probable in our evolutionary past. For example, the hxaro trading partnerships of the !Kung would likely lead to interactions between strangers and one-shot partnerships may have been common.

If the individualistic machinery fails to explain strong reciprocity, another theoretical avenue is to invoke group selection. Bowles and Gintis [22] say that strong reciprocity can exist when there is a serious threat of group extinction. Indeed, models have shown that altruistic punishment can be maintained because the within group force against the costly punishment shrinks as the defection in the group decreases (see Boyd et al. 2003). Emotions favoring the internalization of norms may be the mechanistic underpinnings of such strong reciprocity[11] and these authors argue that mechanisms that make for effective, efficient groups could be selected (Heinrich et al. [23]).

The evolution of the organism

It is interesting that the levels of selection controversy is muted in the section on genomic and cellular cooperation in GCEC. However, the language is similar to that of the cultural group selectionists. Szathmáry and Wolpert [15] discuss how cheater types in *Dictyostelium dendricticum* benefit within groups, but groups of cheaters do worse. A big issue in the origin of multicellularity is: do separate cells come together or do the daughters of one cell stick together as they split? The reason this question is important is because the mode of multicellular formation may strongly influence the number of cellular variants inside the organism (Szathmary and Wolpert [15], Michod [16] and Lachmann et al. [18]). Michod [16] suggests modifiers of the various developmental stages of multicellular organisms play two basic roles: (1) they decrease variance within groups and (2) increase variance between groups. This is precisely what conformist transmission does for cultural variants in humans.

The organism is perched at an interesting place in the biological hierarchy. As organisms ourselves, we can see how tightly integrated individual organisms are. They brim with cooperation. It is easy for us to take a collective approach when we consider the trillions of cells that make up an African elephant. However, the same empathy makes it hard to see individuals as mere components of a "social group organism." Sometimes individuals are so interconnected that the idea of a superorganism seems appropriate (e.g., the eusocial insect colonies, see Emerson 1960). In other cases, such as human groups, the analogy may be more difficult. However, by treating human tribes as organism-like, a variety of new theoretical possibilities emerge.[12]

4. The volume as a whole

This volume has several major selling points. First, its authors have previously made profound empirical or theoretical contributions to the understanding of cooperation in their fields. Consequently, the authors are in a good position to explain the intricacies of cooperation and the remaining big questions. Second, the volume is packed with extremely relevant (and very interesting) data from experimental games, ethnographic studies, cellular/molecular analysis, animal behavior studies and theoretical models. Third, several chapters do much to contribute to conceptual organization of terms that are sometimes used ambiguously in the literature. (For example, classifications of mutualisms, types of exploiters and types of exploiter control are laid out nicely by Bronstein [10] and Bergstrom et al. [13], while Lachmann et al. [18] present a very useful break-down of the important elements in cooperative interactions). Fourth, this book is divided into four nearly self-contained sections, each of which ends with a well-written group report. The reader could easily read a group report first to gauge his/her interest in a particular section of the book.

Lastly, this volume gives the reader an ear for cross-talk between different scientific fields. I found the interdisciplinary character of the book to be extremely refreshing. Economists clearly have much to offer evolutionary biologists and *vice versa*. Anthropologists, psychologists and behavioral ecologists can provide one another with complementing approaches to overlapping interests in the evolution of social behavior. Theoreticians can make sincere connections to empirical evidence and the interpretation of empirical results can be informed by theory. Even the disagreement (e.g., invoking group selection versus individual selection) was tremendously stimulating.

In general, problems that cross disciplines are likely deep and important. There is something empowering and exciting about rediscovering an old problem in a new field. Besides the solidarity of finding other soldiers in the trenches, one has access to new perspectives, ideas and tools to approach the problem. The evolution of cooperation is a superb example of such a problem and this volume provides a service in allowing the reader access to the interdisciplinary crossroads.

5. Conclusions

Over the past decade, a number of books have been published that explore the evolution of cooperation and altruism (Bourke and Franks 1995; Maynard Smith and Szathmáry 1995; Frank 1998; Sober and Wilson 1998; Michod 1999; Keller 2001). However, you should make a little extra space on your bookshelf for one more. It is a rare volume that can cover programmed cell death, ant-lycaenid interactions, and cultural group selection in under 500 pages. However, there is a fascination, which cross-cuts disciplines, about how previously autonomous entities come to benefit when together. In a book about cooperation, it is only fitting that researchers from so many different fields have collaborated. What emerges is an interesting and informative account of how and why so many different entities (from genes to human beings) have run the Caucas-race of the Dodo.

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Notes

[1] Hamilton's rule, which formalizes these ideas, depends on several assumptions (including an additive fitness structure). The rule is $rb > c$, with c as the fitness cost of helping, b as the fitness benefit provided and r as the coefficient of relatedness between the helper and the receiver.

[2] When citing a chapter in GCEC, I will place the chapter in brackets following the author's name.

[3] As it turns out, cleaners cheat at about the same rates on resident and roving clients. Resident clients chase their cleaners after an instance of cheating which is costly enough to the cleaner that rates of defection fall. Bshary and Noë [9] claim that a resident gains control over cleaner exploitation through punishment, while a roving client achieves the same control by exercising choice.

[4] This result does depend on the form of the asymmetric game matrix (see Bergstrom and Lachmann [12] for details).

[5] Experimental games in which the reputation of each player is known lead to higher levels of cooperation than similarly structured games where the past histories of players are not known (Fehr and Heinrich [4] and Heinrich et al. [23]).

[6] Sober and Wilson (1998) offer a splendid treatment of the history of this debate.

[7] Often these group fitnesses are simply group productivities. Of course, within a complete multi-level view we must also monitor the change in individual types within the groups.

[8] There have been a number of attempts made to connect these two perspectives (see Dugatkin and Reeve 1994; Sterelny 1996; Kerr and Godfrey-Smith 2002).

[9] Note that the production of a kin group does this naturally. That is, if groups consist of kin, say, produced by two parents into a nest, then groups will have more (genetic) variance between nests and less (genetic) variance within nests than if these kin groups were randomly reshuffled among nests. Here we see a key connection between kin selection models and group selection models, they both work best by skewing the group frequency distribution so that like types end up interacting in the same groups.

[10] These authors do not deny that reputation or signaling may be important to cooperative behavior; rather they claim that these individualistic mechanisms cannot fully explain all cooperative behavior.

[11] One way to see this point is to ask yourself how you would *feel* if a partner in an ultimatum game offered you only 10% of a large prize.

[12] I would argue the innovation of the group selection models in the context of cultural variants is that they explicitly deal with inter-group cultural replacement processes. In some sense, this falls out of thinking of groups as entities that live or die.

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