The Adaptationist Theory of Cooperation in Groups: Evolutionary Predictions for Organizational Cooperation

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Abstract Managers could more effectively promote cooperation within their organizations if they had greater understanding of how evolution designed people to cooperate. Here we present a theory of group cooperation – the Adaptationist Theory of Cooperation in Groups (ATCG) – that is primarily an effort to pull together the scattered findings of a large number of evolution-minded researchers, and to integrate these findings into a single coherent theory. We present ATCG in three main sections: first, we discuss the basic premise that group cooperation evolved because it allowed individuals to acquire personal fitness benefits from acting in synergy with others; second, we examine the cooperative strategy that most often prevails in successful groups, "reciprocal altruism", and the free rider problem that constantly threatens it; and third, we explore how cooperative behavior is affected by differences (a) among individuals, (b) between the sexes, and (c) among different kinds of resources that a group may share. Throughout all of these sections, we suggest ways in which ATCG's predictions could be usefully applied in real organizations. We conclude that while ATCG is consistent in some regards with existing theories from organizational behaviour, its individual-level adaptationist perspective allows it to make a variety of novel predictions.

Keywords Cooperation · Groups · Teams · Reciprocal altruism · Free riders · Organizational behavior · Evolutionary psychology

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1 Introduction

Unlike the vast majority of other species, human individuals achieve remarkable levels of cooperation, even among large groups of non-relations or strangers. This ability is a vital characteristic of human nature; without it, human social life would be unrecognizably different: there would be no villages, cities, or nations; no organized religions, armies, or political parties; and no communities, collectives, or companies. Researchers in the biological and social sciences have long been preoccupied with understanding group cooperation, not only because of its importance, but also because achieving this understanding has proven surprisingly challenging. However, significant progress has been made in our understanding of the evolutionarily adaptations humans possess for cooperating in groups. If we are to understand how to improve cooperation today, we need to understand what these adaptations are, how they work, when they align or clash with modern social settings, and how to trigger them to increase efficiency. In this chapter we present a new evolutionary theory of group cooperation—the "Adaptationist Theory of Cooperation in Groups"—that is a product of this progress. We will abbreviate this theory as ATCG, both for the sake of efficiency, and because this acronym recalls the four bases of DNA (adenine, thymine, cytosine, and guanine) and thus conveniently highlights the theory's biological foundations.

We should be clear from the beginning that ATCG is not "our" theory of cooperation in groups. ATCG has been informed by our own research, but it is first and foremost an effort to integrate the scattered findings of a large number of researchers – most of whom have investigated cooperation from an explicitly evolutionary, individual-level adaptationist perspective – into a relatively comprehensive and coherent theory. We think such an integrative effort is needed because despite all of the progress that has been made in evolutionary psychology towards understanding various aspects of group cooperation, these findings have not been presented in any kind of comprehensive theoretical package. This lack of integration makes it harder to draw out the most important insights from the less important ones (especially for a specific context such as organizational behaviour), and also harder to communicate these findings efficiently to other academics and to the people in organizations who would most benefit from applying the findings.

As we discuss ATCG, we provide examples of how this theory can be applied to achieve better understanding, prediction, and promotion of cooperation in modern human organizations, and ways in which it compliments and diverges from the predictions of existing theories from evolutionary and social science. According to the philosopher of science Imre Lakatos (1978), an advance in scientific theory occurs when a new theory is introduced that makes all of the same predictions as the existing theory or theories, but adds additional, novel predictions. We believe that by this standard, ATCG constitutes scientific progress. While ATCG shares some predictions with pre-existing theories from mainstream organizational behavior and social science, it also generates a variety of unique predictions about how people will cooperate in organizations.

The sketch of ATCG that follows is divided up into three main sections. In Sect. 2, we discuss the fundamental issue of how ancestral humans gained individual fitness advantages by engaging in group cooperation. In Sect. 3, we examine the most important cooperative strategy that is engaged in by members of productive groups, “reciprocal altruism”, as well as the free rider problem that can derail this strategy and wreck productivity. In Sect. 4, we look at how cooperative behavior changes depending on individual differences, sex differences, and differences in the class of resource being shared. In our conclusion we review how ATCG overlaps with and diverges from existing theories of organizational cooperation.

2 How Cooperation Benefits Individual Fitness

2.1 Darwin’s Focus on Individuals

Darwin’s theory of adaptation by natural selection (1859) focused on individuals: natural selection endows individuals with adaptations that improve their “fitness” (their ability to survive and reproduce). In considering how humans are adapted to cooperate in groups, it is crucial to maintain this individual-level focus, and to ask: how did cooperation benefit the fitness of individual cooperators in ancestral environments (Alexander 1987)? It is this individual-level focus of Darwinian theory that has caused cooperative behavior to often seem profoundly puzzling from an evolutionary perspective. Darwin himself noted that cooperative (or “altruistic”) acts, such as a bee’s suicidal sting in defense of its hive, posed a major challenge to his theory. If cooperative acts benefit the fitness of others at the expense of the cooperator, then non-cooperators (also known as “cheaters”, “defectors” or “free riders”) will always achieve higher payoffs, and thus exploit cooperators to extinction. Ever since Darwin, the evolution of cooperation has been considered a central problem – or indeed *the* central problem – of behavioral biology (Wilson 1975).

Over the past several decades, however, biologists have made significant progress towards solving this central problem by producing several theories of cooperation, including two that have become especially well-established. The first is “kin selection” (Hamilton 1964), a theory of gene-level cooperation that explains altruism among close genetic kin. The second is “reciprocal altruism” (Trivers 1971), which explains mutually beneficial exchange between interactants who are not necessarily genetically related. These two theories are now routinely used to solve Darwin’s puzzle of cooperation. Kin selection is important to a vast variety of species, including humans, while reciprocal altruism is important to humans (who possess, as discussed below, the social cognitive skills to engage in reciprocity successfully) but relatively unimportant to most other species (Dugatkin 1997; Stevens and Hauser 2004; West et al. 2007). ATCG is designed to explain cooperation in groups of *non*-relatives, and although kin selection theory would not therefore appear to apply, it is relevant to a deep theoretical understanding of such cooperation (because kin altruism and reciprocal altruism probably both evolved via the same fundamental process of genic self-favoritism; see Price 2006a). Nevertheless, ATCG can be described and applied effectively without much reference to kin selection, so for the sake of efficiency we will not discuss this theory further. On the other hand, ATCG is more directly founded on Trivers' (1971) reciprocal altruism, and this theory is discussed in more detail below.

Having pointed out the importance of the individual-level perspective, we should note that there is a history of confusion and controversy surrounding this perspective. Despite the progress that has made in explaining how cooperation benefits individual fitness, some theorists maintain that individual-level theories are insufficient to account for the complexity of cooperation in human groups, and that some kind of group selection theory is required (Boyd and Richerson 1988; Wilson and Sober 1994; Gintis 2000; Gintis et al. 2003; Wilson and Wilson 2007). A purely group selectionist theory would predict that individual cooperative behavior evolved to benefit the average fitness of the group as a whole, as opposed to the cooperator's own individual fitness, and thus is a radically different perspective from that of the individual-level theory. For example, while the individual-level theory predicts that individuals will work in organizations in order to receive compensation and benefit themselves, group selection predicts that they will work for free in order to benefit the organization.

Group selection has long been a controversial topic in behavioral biology. Darwin (1871) himself even considered whether group selection could have played some role in the evolution of human moral sentiments, and throughout much of the twentieth century "naïve" group selectionist theories – focusing on how a behavior evolved to benefit the group or species, without considering how it affected the individual – were common in biology (Wilson and Wilson 2007). This "naïve" period ended when biologist George Williams published his influential critique of group selection, which drew attention to the special conditions that it requires, and emphasized that ordinary individual-level hypotheses should be examined first, before resorting to more exotic, higher-level alternatives (Williams 1966). In more recent years, however, group selection has made something of a comeback, in relatively sophisticated forms such as multilevel selection, which theorizes that selection has important effects simultaneously at multiple levels, including intragenomic, individual, and group levels (Wilson and Wilson 2007).

We agree with the multilevel selectionists that in studies of any kind of behavior, it is always wise to consider whether multilevel selection theory could enhance one's ability to predict the features of that behavior. However at this stage we do not see any advantages, in terms of improving ATCG's predictive power, in adopting the theoretical view that cooperative behavior in groups of non-relatives evolved to produce benefits at any level other than that of individual fitness. While ATCG makes many predictions that assume selection occurred at the individual level, it makes none which assume selection occurred at the group (or any other) level. Moreover, individual selection is the simplest and least exotic level of selection that one can examine in the course of an adaptationist analysis

(Williams 1966). Therefore, in keeping with Occam's razor and with Williams' (1966, p. v) dictum that "adaptation should be attributed to no higher a level or organization than is demanded by the evidence", our chapter maintains an individual-level focus.

Before leaving the topic of group selection behind, we should emphasize that all of ATCG's predictions that are presented throughout this chapter follow from the individual-level adaptationist perspective, while as far as we can tell, not a single one of them would follow from a purely group selectionist perspective. The irrelevance here of the purely group selectionist perspective should be apparent in the very beginning (i.e. the present section) of this chapter, as we elaborate on ATCG's foundational premise that cooperation evolved because it allowed cooperators to gain individual fitness advantages. Of course, the drastically divergent predictions of these two approaches are offered a litmus test by how things really work in the real world. As we will show, predictions that have been made from the individual-level perspective have so far been widely supported.

2.2 *Cooperation Evolved Because It Produced Synergistic Benefits for Cooperative Individuals*

ATCG takes account of ethnographic and archaeological evidence suggesting that in the environments in which humans evolved, cooperating in groups (for purposes of hunting, warfare, shelter construction, predator defense, etc.) afforded individuals benefits that they could not have obtained by acting alone (Lee and DeVore 1968; Alexander 1987; Kelly 1995; Keeley 1996). If you could acquire 5 lb of rabbit meat by hunting alone, as opposed to 50 lb of mammoth meat by participating in a group hunt, then cooperation would have offered a ten-fold advantage, holding effort and all other costs constant. Of course, the costs of cooperation cannot be overlooked. Some of these costs would also be present in a solitary activity (e.g. expenditure of time and energy), but others would have been unique to cooperation (e.g. coordination and social interaction costs). A member of a group mammoth hunt, in contrast to a lone rabbit hunter, has to worry about such things as meeting his co-members at a certain time, coordinating his movements with those of his co-members during the hunt, and ensuring that he receives a fair share of the meat – not to mention avoiding getting trampled to death. But as long as the synergistic benefits of cooperation provided the individual with benefits that outweighed these costs, then cooperation would have offered an individual fitness advantage. ATCG assumes that opportunities to engage in individually adaptive cooperation arose regularly in ancestral environments, and therefore that the human mind evolved to become skilled at recognizing and taking advantage of these opportunities.

2.3 Social Status is a Key Second-Order Benefit of Cooperation

ATCG also notes that the benefits of cooperation can involve much more than just a share of the first-order benefit that the interaction produces (e.g., mammoth meat). Even if a hunting party member had no need for mammoth meat, he could still acquire a second-order benefit from cooperation. For example, he might learn about the hunting techniques of skilled co-members, or gain a chance to practice his own techniques. But the second-order benefit he could have acquired that is most relevant to our discussion is social status. By social status, we simply mean the power to bestow benefits, or inflict harm, on other people. By helping the group bring down a mammoth, for example, a skilled hunter could prove his willingness and ability to generate value (meat) for others. Others would benefit from having this hunter in their group in future interactions, and would suffer if he left the group or refused to help them hunt. This dependence of others would make the hunter high-status (i.e., powerful [Emerson 1962]), and in order to remain within his favour, others would be motivated to act to benefit (and to avoid harming) him. His social status could thus serve as a magnet for many kinds of economic resources. Further, this association between status and resources would have made the hunter more sexually attractive to females, which would have increased his access to reproductive resources as well.

The links that are drawn in the above example between hunting and status, and between status and sexual attractiveness, are not just theoretical. Field studies show that hunting skill is associated positively with social status and reproductive success in hunter-gatherer societies (review in Smith 2004). More generally, male social status relates positively to reproductive success in premodern societies (Chagnon 1979, 1988; Betzig 1986), and females in all kinds of societies tend to find higher status men more attractive (Buss 1989; review in Davies and Shackelford 2008). But the main point of the above example is to illustrate a central proposition of ATCG: by cooperating in groups, an individual can make himself valuable to others and thus obtain the crucial resource of social status. Even if that individual has no interest in the first-order resource that the group is producing, the prospect of acquiring status might make him regard participation as worthwhile.

Just as social status was a highly relevant second-order benefit of cooperation in ancestral groups, so it is in modern organizations. These organizations face a basic challenge of motivating employees to contribute to the production of resources that are not for their own consumption. Employees of a biotechnology firm, for example, may need to cooperate to design a new artificial leg, even if most of them are not going to use this product themselves. The method of motivating employees that is used in most organizations is to offer them social status in exchange for their help in producing the first-order resource. And just as in the ancestral past, higher status contributors – those on whom production most depends – attract greater economic compensation, in order to convince them to remain in the organization and to continue to contribute.

2.4 Synergistic Cooperation Is Inherently Advantageous, But There Is Nothing Inherently Synergistic About Cooperation

ATCG proposes that evolution designed people not just for cooperation, but for cooperation that brought individual benefits. As noted above, for cooperation to be individually-adaptive, it must be synergistic. If Person X is a good hunter who can obtain 5 lb of rabbit meat by hunting alone, versus 5 lb of shared deer meat by hunting in a group, then cooperation offers no first-order synergistic benefits for X. There might be second-order benefits to cooperating (e.g. the opportunity to acquire status), but these would need to be high enough to overcome the automatic costs of cooperation (e.g. coordination costs); otherwise, the adaptive choice for X would be to hunt alone. And if cooperation actually caused X's share of the first-order resource to decrease – if X could obtain more meat by hunting alone than he could via cooperation – then cooperation's likelihood of being the adaptive choice for X would go down even further.

Of course, even if cooperation were maladaptive for X, it could be adaptive for some of X's potential interaction partners. If Person Y could obtain no meat by hunting alone, versus some meat by hunting in a group with X, then Y would have an interest in convincing X to join the hunt. The best way for Y to do this would be to offer X a relatively large share of first- or second-order benefits that would compensate X for his relatively large contribution, and thus make cooperation adaptive for X. We'll discuss the importance of these kinds of benefit-to-contribution ratios, and their relevance to modern organizational contexts, later in this chapter. But for now, we want to focus on the idea that while synergistic cooperation is inherently advantageous, there is nothing inherently synergistic about cooperation.

2.5 Synergistic Cooperation (or the Lack Thereof) in Real Organizations

As the result of trends in organizational practices such as the increased popularity of work teams (Douglas and Gardner 2004), many organizations strive to cultivate a culture of cooperation and communication in which group action is seen as being inherently superior to individual action (Hall 2007; for a military example, see Rielly 2000). This enthusiasm for cooperation is to some extent understandable: cooperation can often be genuinely productive, sometimes astoundingly so, and many people reflexively assume cooperation to be a "good thing" wherever it appears. However, cooperation can also be imposed on individuals who would be more productive if permitted to produce alone. For example, many organizations encourage their employees to generate ideas in brainstorming groups of interacting individuals (Rietzschel et al. 2006), despite substantial evidence that "nominal groups" – consisting of individuals who work alone to generate ideas that are then pooled – generate more ideas, and more high-quality ideas, than groups of interacting individuals (Diehl and Stroebe 1987; Rietzschel et al. 2006).

As examples of the kind of non-synergistic cooperation that is routinely encouraged in organizations, consider an employee who by herself could come up with a brilliant marketing strategy, but who must compromise her idea in order to accommodate the inferior and counterproductive contributions of her team members; or consider three employees who must incur significant coordination and communication costs in order to jointly write a report that turns out no better than what any one of them could have written alone. And most members of organizations will, at one time or another, have had to serve on a committee that seemed to reach decisions and take actions much more slowly and ineffectively than an individual could have done. For employees trapped in non-synergistic cooperative interactions, enthusiasm for cooperation may be buoyed by the expectation of some second-order reward ("this committee is a waste of time, but serving on it will look good on my résumé"). But even if this second order justification is forthcoming, these employees' respect for their employer will likely fall due to their perception that management is encouraging employees to engage in pointless and counterproductive cooperation. Employees may also tolerate situations of non-synergistic cooperation in order to avoid appearing as uncooperative or arrogant; they may fear that if they point out that cooperation is counterproductive, they will appear as poor team players – that is, as though they want to shirk their responsibilities, or as though they think they are too talented to have to compromise with team members. Or they may simply be afraid to contradict their manager's judgment that cooperation is the best approach, or just lack the data to conclude that one strategy is better than the other. Whatever reason an employee may have for remaining in non-synergistic interactions, if he could avoid such interactions without fear of negative consequences, then it would increase productivity both for himself and for his organization.

ATCG's recognition that adaptive cooperation must produce individual-level synergistic benefits is an essential first step to untangling the motives for cooperation in the real world. However, it is not yet a solution to the puzzle of cooperation, because it explains only why individuals would be motivated to cooperate in the first place. Even if they are so motivated, how do they ensure that they are receiving an adequate level of compensation, and that they are not being exploited by others in their group? To address these questions, we need to consider the role of reciprocal altruism as the dominant cooperative strategy in groups.

3 Promoting Reciprocity and Avoiding Free Riders

3.1 Can Reciprocal Altruism Explain Cooperation in Groups?

As noted in Sect. 2, Trivers' (1971) theory of reciprocal altruism is the leading evolutionary explanation for the evolution of cooperation among genetic nonrelatives. Reciprocal altruism has been applied most commonly to interactions between two individuals. For example, if person X can pay a small cost to provide a big benefit to person Y, and Y can later pay a small cost to provide a big benefit to X, then the exchange interaction will be mutually beneficial; X and Y will have each paid a small cost in exchange for a big benefit. The risk to the individual in such an interaction is that your partner will prove to be a cheater: if your "altruism" is not reciprocated, then you will have maladaptively paid a cost for no benefit. Thus, while reciprocity offers big advantages to those who can find reliable partners, it also involves the risk of getting paired with a cheater (Cosmides and Tooby 2005). In order to engage in reciprocity successfully, an organism must have a high level of cognitive sophistication, in order to recognize and remember cheaters and to avoid interacting with them. Humans definitely do possess the requisite cognitive abilities, but the extent to which other species do is unclear (Cosmides and Tooby 2005; West et al. 2007; Stevens and Hauser 2004; for a review of the mixed evidence regarding primate reciprocity, see Silk 2005).

While the theory of reciprocal altruism has been used relatively uncontroversially to explain the evolution of cooperation in two-person interactions in a wide range of disciplines from biology to anthropology to economics (Trivers 2006), its applicability to *n*-person (group) interactions has engendered more disagreement. This applicability is important to ATCG and to this chapter, because organizations involve *n*-person interactions, that is, multiple people working together to fulfil some group goal. The ability of reciprocity to evolve in such groups depends on several factors. One of these factors is the type of reciprocity strategy involved: for example "continuous" reciprocity strategies, which match the mean co-member contribution, evolve more successfully under many conditions than do "discrete", all-or-nothing reciprocity strategies (which contribute fully if a threshold percentage of co-members contribute, but otherwise contribute nothing at all; Johnson et al. 2008; Takezawa and Price 2010). Another factor is the size of the group: reciprocity evolves more easily in small groups (e.g., fewer than ten members) than in large groups (Boyd and Richerson 1988; Takezawa and Price 2010). Reciprocity's disadvantageousness in large groups is due to the fact that as groups get larger, the probability increases that groups will be infiltrated by "free riders" (the term assigned to cheaters in cooperative group contexts).

Some researchers have suggested that because reciprocity does not evolve well in large groups, an explanation besides reciprocity is needed to explain *n*-person cooperation (Boyd and Richerson 1988; Henrich 2004). However, reciprocity's disadvantageousness in large groups would probably not have been an obstacle to its evolution in ancestral human groups, which tended to be small. According to a comprehensive survey of foraging societies (Kelly 1995), the average hunter-gatherer band consists of about 25 people, of which seven or eight are full-time adult foragers. Given the sexual division of labor, the average *n*-person interaction will involve half of these adults, that is, 3–4 people – a group size which is well within the range in which reciprocity could evolve. For this reason, ATCG agrees with the perspective of evolutionary psychologists who have suggested that the best evolutionary explanation for organizational cooperation is *n*-person reciprocity (Price 2006a; Tooby et al. 2006). Although we work in large groups today, we may nevertheless act *as if* we are in small groups, because our cognitive machinery for cooperation evolved in small groups, not large ones.

3.2 Reciprocity in Groups: Striving for "Fair" Compensation

So if ATCG predicts that the average group member will behave as a reciprocal altruist, what does that mean exactly? It means that in exchange for his contribution to fulfilment of the group's goal, he will expect to receive a share of group benefits that is proportional to the relative size of his contribution. For example, if he has contributed the most to bringing down a mammoth, then he will expect to receive the best share of mammoth meat out of anyone in the group, or some second-order reward of equivalent magnitude (for example, the biggest increase in social status out of anyone in the group). ATCG predicts that if the group member perceives his own benefit-to-contribution ratio to be at least as large as those obtained by his co-members, then he should perceive his level of compensation to be "fair", and he should be motivated to continue cooperating; if, on the other hand, he perceives this ratio to be relatively small, then he should experience a sense of unfairness and lose motivation to continue cooperating. A worker who is reliable and hard working but gets no recognition or reward for such behavior will soon slack off. Consistent with this prediction, a standard finding in behavioral economics is that on average, group members are more willing to contribute to public good production when they perceive that their benefit-to-contribution ratios are no less than those of co-members (Ledyard 1995; Croson 2007; Fischbacher et al. 2001; Kurzban and Houser 2005). Behavioral economists often refer to such reciprocal altruism as "conditional cooperation" (Fischbacher et al. 2001).

In pursuing a fair benefit-to-contribution ratio, the cooperator is accomplishing two goals. First, he is ensuring that he is getting as substantial a return as possible on his investment of cooperative effort. Second, he is avoiding being exploited by free riders (i.e., members with relatively high benefit-to-contribution ratios). We will discuss each of these two goals in turn.

3.3 Why Pursue Fairness? Maximizing the Advantage of Being a Cooperator

To the extent that the cooperator's effort is benefitting group co-members, he has power to negotiate the terms of the relationship. If his co-members refuse to grant him benefits that are proportional to the size of his contribution, he may reduce effort, refuse to continue to contribute, or leave the group. ATCG predicts that he will strive for a level of compensation that is at least commensurate with the exchange value of the services he provides to co-members. (He may well strive for more compensation than is fair, but his motivation to do so will depend on the consequences of free riding; see discussion later in this section).

In a well-managed group – one in which rewards are allocated fairly – higher contributors should reap greater benefits and should thus be advantaged over lower contributors. Members may thus engage in “competitive altruism” (Roberts 1998), that is, compete with co-members to be seen as the highest contributors to group goals, and those seen as the most altruistic should receive the greatest rewards. By competing to be the most altruistic member of the group, cooperators behave just as “self-interestedly” as any free rider; the difference is that while the free rider’s self-interest benefits himself while harming the group, the competitive altruist’s self-interest benefits both himself *and* the group. The predictions of competitive altruism theory, which are shared with ATCG, have been supported in experimental and field studies. For example, among Amazonian Shuar hunter-horticulturalists, villagers who work the hardest in cooperative tasks are allocated the highest social status (Price 2003, 2006a), and a similar link between altruism and status has been found in studies of British students (Hardy and Van Vugt 2006). Barclay and Willer (2007) also found that economic game participants compete to be more generous than others, in order to increase the likelihood that they will be chosen for potentially lucrative cooperative partnerships.

In order to motivate employees to behave in group-beneficial ways, then, managers must allocate rewards fairly, and allow employees to compete for these rewards by contributing in ways that most benefit the organization. If an employee makes a contribution that benefits the organization, for example by introducing a product improvement or new marketing strategy, a manager should never assume that the employee was selflessly motivated or is indifferent about being recognized and rewarded for this contribution, even if that employee modestly plays down the extent of his or her own contribution. If an employee does not receive some individual-level benefit that is commensurate with the value of his or her contribution, the employee will probably feel angry and exploited and lose motivation to cooperate (see below discussion of the exploitation problem). Further, to the extent that this lack of fairness is observed by others in the organization, it will send a message to these others that they have little incentive to act in pro-organization ways.

On the other hand, because a group’s cooperative goals may sometimes conflict with the competitive aspirations of its individual members, a delicate balance must be maintained between the “competitive” and “altruistic” aspects of group cooperation, lest the former overwhelm the latter. An inherent risk in groups characterized by competitive altruism is that individual members will so strongly desire to contribute highly to group goals, in order to outcompete co-members for the rewards of contribution, that their contributions will actually have a negative impact on group productivity. A desire for personal glory, for example, may lead a employee (especially, for reasons discussed in Sect. 4 below, a male employee) to engage in group-damaging behaviors such as interrupting his co-members at meetings, denigrating his co-members’ contributions to a group project, or pursuing a group leadership position for which he is under-qualified. All of these may invoke the dislike of colleagues and undermine morale and cooperation. In order to dissuade competitive altruists from becoming overly competitive, managers should always ensure that status rewards are based not on individual performance per se, but on the extent to which this performance has helped the group achieve its goals. Moreover, the rules must be transparent so that the incentive is visible to all and does not come as a surprise or appear unique to the recipient.

Interestingly, the fact that excessive status-seeking can threaten group goals is recognized in small-scale societies (Boehm 2001). Among Ju/'hoansi hunter gatherers in Botswana, good hunters achieve high status because they help secure meat for other group members. However, in order to prevent good hunters from becoming too oriented towards self-glorification as opposed to group-provisioning, group members make a practice of "insulting the meat", where they systematically denigrate the game that the hunter brings home (Lee 1993). That is not to suggest that hunters do not see through this ruse, nor that ritual insults would be the best way to curb excessive status-seeking in modern organizations. However, the fact that this problem is recognized by hunter-gatherers does suggest that it is fundamental to human nature: individuals are adapted to compete for status by cooperating in groups, and in order for their cooperative efforts to succeed, their competitive impulses must be continuously kept in check.

3.4 Why Pursue Fairness? Neutralizing Free Riders

The second goal the cooperator accomplishes by striving for a fair benefit-to-contribution ratio is avoiding being exploited by free riders (i.e., members with relatively high benefit-to-contribution ratios, who reap the benefits of others' efforts and contribute little themselves). To understand why this exploitation problem is such a serious concern for cooperators, we will start out by considering why free riders exist in the first place.

Imagine an ancestral hunter who joins a group mammoth hunt because he would gain more meat than he could by chasing rabbits alone. While it would be better for the co-members if the hunter contributed more while taking less mammoth meat in return, it would be better for the hunter to contribute less while taking more meat. The members who would reap the highest net benefits in this interaction – and who would therefore gain the highest fitness advantages – would be the free riders who contributed the least while taking the most. Each member can thus potentially gain a *free rider advantage* (Olson 1965; Hardin 1968). Experimental and field evidence from all types of societies – from hunter-gatherers to Western business organizations – attests to the universality of the free rider problem: when group members have the opportunity to acquire the free rider advantage, many will do so, as long as they do not expect to get caught (Albanese and Van Fleet 1985; Kidwell and Bennett 1993; Ostrom 1990; Andreoni 1988; Fehr and Gächter 2000; Price 2006a).

In addition to having to decide whether to seek the free rider advantage themselves, ancestral group members also had to avoid being exploited by co-members who did free ride or attempted to free ride. Members who failed to solve this *exploitation problem* would have been at an adaptive disadvantage relative to free riders, so genes for nonchalance in the face of this problem tended to disappear from ancestral gene pools. A basic finding of mathematical models of the evolution of cooperation is that when free rider problems are allowed to proliferate, cooperators eventually get exploited to extinction (Hamilton 1964; Henrich 2004). If cooperators perceive that they are facing an exploitation problem, and that the only way that they can reduce their own exploitation is by refusing to contribute further, then that is what they will do. Cross-cultural evidence confirms the prediction that cooperators react to exploitation by reducing their own contributions, and that as a result, unchecked free riding leads to the disintegration of group cooperation (Ostrom 1990). This disintegration process can be clearly observed in laboratory experiments in group cooperation. At first, people start out with high levels of cooperation, but with each round people become less and less cooperative (Ledyard 1995; Fehr and Gächter 2000; Croson 2007). This decay occurs because once some members begin free riding, their co-members respond by ratcheting down their own contributions, in order to mitigate their own exploitation. Free riders, in turn, then lower their own contributions further, in order to maintain their advantage. As this negatively reciprocal process progresses, levels of cooperation dwindle towards zero. It's obvious to an outsider that everyone would have been better off if all had continued to contribute, but from any one participant's perspective, it is disadvantageous to continue to cooperate if others are not.

Social scientists have been aware of free rider problem for decades, due especially to two highly influential publications that flagged the importance and prevalence of the "collective action problem" and the "tragedy of the commons" (Olson 1965; Hardin 1968). Thus, ATCG's focus on this problem is nothing new. However, despite widespread awareness of this problem, many mainstream organizational behavior theories have more or less overlooked it (for example equity theory, as noted below). While it may be easy to preach and promote cooperation, it is hard to sustain it unless you tackle the free rider problem. ATCG's individual-level adaptationist perspective not only affirms the centrality of this problem to organizational cooperation (Tooby et al. 2006), but also, as detailed below, allows ATCG to shed new light on the problem and propose workable solutions for how the free-rider problem can be solved.

3.5 The Consequences Problem: Punishment and Ostracization of Free Riders

If cooperators withhold their contributions in order to solve the exploitation problem, group cooperation decays. They may successfully avoid exploitation, but this only worsens the prospects for cooperation. One way to solve the exploitation problem while avoiding this decay would be to neutralize or reverse the free rider advantage for others, by imposing some kind of punitive or reputational cost on free riders, or by excluding them from the interaction (Price et al. 2002). The gravity of this *consequences problem* will depend on the extent to which free riders' co-members (or other interested parties) are willing and able to impose these consequences.

Cross-cultural evidence from experimental and real-world groups suggests that when given opportunities to impose consequences on free riders, members do so (Ostrom 2000). These consequences frequently take the form of monetary fines (Yamagishi 1986; Fehr and Gächter 2000; Price 2006a; Nikiforakis 2008) and social costs like ostracization (Cinyabuguma et al. 2005; Sheldon et al. 2000; Page et al. 2005; Barclay and Willer 2007). When such consequences are imposed, free riding can be deterred, and groups can avoid the collapse of cooperation that unsanctioned free riding induces. (Note that punishment in groups can itself involve a [second-order] free rider problem; for a discussion of how evolution may solve this problem, see Price 2003). This evidence is consistent with ATCG's prediction that in order for a group to sustain cooperative productivity, members will need some mechanism for imposing negative consequences on free riders. ATCG also predicts that the group's highest contributors will be the most likely to support the imposition of these consequences, because they will be the most vulnerable to the exploitation problem. This is supported by empirical evidence. For example, higher contributors exhibit more punitive sentiment towards free riders (Price et al. 2002; Shinada, Yamagishi and Ohmura 2004; Price 2005) and people who participate more frequently in cooperative interactions are more likely to base their moral judgements of others on the extent to which these others have engaged in free riding (Price 2006b).

The process by which cooperators choose to interact with each other while avoiding free riders is known in biology and evolutionary psychology as positive assortation or partner choice (Hamilton 1964; Price 2006a; Barclay and Willer 2007; Johnson et al. 2008). ATCG predicts that members who are willing to cooperate reciprocally should tend to prefer, seek, and retain co-members who are also willing to cooperate reciprocally. In other words, cooperators should stick together and ostracize free riders. Evidence for positive assortation has been consistently produced by group cooperation experiments: when participants are permitted to choose their interaction partners, based on information about potential partners' contribution levels in previous interactions, then relatively cooperative individuals choose each other and form relatively productive groups (Ehrhart and Keser 1999; Sheldon et al. 2000; Page et al. 2005; Barclay and Willer 2007). The free riders prefer cooperators too (if they did not, they would end up with no one to exploit), but with partnerships being based on mutual choice, they end up getting left out in the cold.

3.6 Solving the Free Rider Problem in Real Organizations

Free riding spreads infectiously and can be hard to stamp out once established. ATCG suggests that managers ought to take free riding seriously, and work to solve any free rider problem that may threaten the health of their organization. It also suggests that the best way for managers to solve the free rider problem, and thus solve the exploitation problem for high contributors, is to make employees plainly aware that there will be a consequences problem for those who pursue a free rider advantage. Efforts can focus on both detection and punishment, both of which are necessary for an effective deterrent. Employees must expect that these consequences will be consistent enough and severe enough to neutralize or reverse the free rider advantage. However that does not mean that the most effective way for managers to solve such problems will usually be through the direct imposition of harsh punishments. The threat of coercion can do more harm than good, if it "crowds out" voluntarily cooperative behavior (Titmuss 1970; Vollan 2008): employees who are motivated to cooperate without any threat of punishment may resent the unnecessary coercion and actually cooperate (or excel) less when threatened than they otherwise would. Direct punishment can also backfire if it is administered unjustly, for example in a manner suggesting that the punisher is motivated by his own overt selfishness as opposed to concern for the common good (Fehr and Rockenbach 2002). Finally, direct punishment can cause anger, resentment, and a desire for retaliation among the punished. In public goods games, for example, a significant proportion of free riders who are punished will retaliate by attempting to punish the person who punished them (Cinyabuguma et al. 2006; Nikiforakis 2008).

Despite the risks and costs associated with administering direct punishment, it may sometimes be the most appropriate and effective way to deal with egregious cases of free riding. However, there are also more low key methods for solving free rider problems or possibly even precluding them entirely. In order to effectively introduce a consequences problem, the key is to think broadly about what will deter would-be free riders. Even in the absence of direct punitive costs, adjustments can be made to organizational environments that will make employees perceive that free riding will not pay. Below are a number of ways to help solve the free rider problem by increasing the salience of free rider detection and/or punishment.

3.6.1 Solution One: Cognitive Cues of Detection

Experiments suggest that free riding can be reduced even through the use of relatively subtle cues that invoke our evolved cognitive mechanisms associated with cooperation. For example, by featuring stylized depictions of eyes as screen wallpaper on the computers used by economic game participants; eye-like representations suggest (not necessarily consciously) a risk of detection and thus apparently make participants more wary of the consequences problem (Haley and Fessler 2005; Bateson et al. 2006; Burnham and Hare 2007). The depictions of eyes used in these studies were crude representations; no rational person would mistake them for real human eyes that could actually see and monitor behavior. Nevertheless, these depictions were sufficient to reduce free riding. While unorthodox, these results suggest that an office décor containing eye-like depictions (e.g., in screen wallpaper or integrated within artwork) might unobtrusively generate cognitive cues that lead to reduced free riding. Recall that human cooperation evolved in small groups that were much more intimate than the sprawling organizations of modern societies. Thus there is a problematic “mismatch” between our evolved cognitive mechanisms and the environments of modern organizations. These organizations demand high levels of cooperation but usually do not adequately simulate the environments to which these cognitive mechanisms are adapted. One way of closing the gap is by reinstating some of the missing features of the environments in which those mechanisms evolved. Compared to existing theories of organizational behavior, ATCG is unique in proposing that organizations can enhance productivity by strategically reconstructing key elements of human ancestral environments. Further, as the eye studies show, these elements do not need to actually function as they did in ancestral environments (i.e., eye depictions do not need to actually monitor behavior), or even be particularly life-like, in order to affect behavior.

3.6.2 Solution Two: Mutual Monitoring and Peer Evaluation

Just as depictions of eyes can increase cooperation by suggesting that one’s behavior is being monitored, actual monitoring should also be an effective way to minimize free riding. It is much easier to get away with free riding if your co-members cannot verify the extent of your work effort, and a major (and underappreciated) advantage of open plan offices is that when employees cannot wall themselves off from one another, they can more easily engage in mutual monitoring. Peer evaluations are another way to promote mutual monitoring; if members of a group project are given opportunities to evaluate each other’s contributions, for example, it provides a voice for high contributors and thus lessens their vulnerability to exploitation.

3.6.3 Solution Three: Small Groups

Recall that reciprocity is more evolutionary stable in small groups, that is, fewer than about ten members (Boyd and Richerson 1988; Takezawa and Price 2010), and that human adaptations for cooperation probably evolved in groups that were no larger than this. Small groups should enhance cooperativeness by allowing for more effective mutual monitoring, because monitoring becomes more difficult, and eventually becomes impossible, as groups become larger. Thus in smaller groups free riders have a greater risk of being detected, and high contributors have more reason to believe that their contributions are being noticed and appreciated by other group members. The fact that reciprocity is easier to achieve in small groups is probably a major reason why small work teams (again, of no more than about ten members) appear to be most effective (Govindarajan and Gupta 2001).

3.6.4 Solution Four: Positive Assortation (Partner Choice)

Another effective way to regulate free riding in self-directed work teams might be to allow the more cooperative members of these teams to positively assort. Managers, instead of monitoring contributions and penalizing free riders themselves, could try leaving these tasks to team members. If employees are given freedom to select their own cooperative partners, high-contributing team members can follow their instincts to partner with other high contributors and thus avoid free riders. The result will likely be a relatively productive group of members who are free to contribute fully, without fear of the exploitation problem. Of course this process will probably also create some relatively unproductive groups, consisting of less cooperative members who have been shunned. Ideally, however, this unproductivity will be a short-term cost leading to long-term benefits; the ostracization of uncooperative members will raise their awareness of their reputational problem and may convince them to change their ways – or flag them for evaluation, training, or dismissal.

3.6.5 Solution Five: Whistle Blowing

Managers should also take care to not downplay the concerns of employees who voice unhappiness about the extent of others' free riding. As noted above, an organization's highest contributors will have the most to lose from others' free riding, and will thus be more likely to detect, and experience punitive sentiment towards, free riders (Price et al. 2002; Shinada et al. 2004; Price 2005, 2006b). By ignoring and failing to act on employee concerns about free riders, a manager will risk alienating the organization's most valuable employees, and will seem to lend tacit approval to the exploitation of these employees by free riders. Cooperation can collapse quickly and easily if free riders take hold, so early warning systems should be highly valued.

Finally, managers should remember that they themselves are as vulnerable as lower-level employees to being tempted by the free rider advantage. Free riding in organizations is usually seen as a problem that occurs at sub-managerial levels (Albanese and Van Fleet 1985; Kidwell and Bennett 1993), but there is no theoretical reason to expect that free riding should be more prevalent at these levels, as managers are as capable as anyone of acquiring disproportionately high benefit-to-contribution ratios, especially if they have good people below them producing work that can be passed off as their own. The perception of managerial free riding may increase under poor economic conditions, because when organizations fail, managerial contributions will more likely be perceived as low or negative, even as managerial compensation remains high. A good deal of public outrage throughout the recent financial crisis has been targeted specifically at managers who reaped huge rewards for making hugely *negative* contributions to organizational goals. For example, Sir Fred Goodwin received an annual pension of £700,000 after leading RBS to the largest annual corporate loss in UK history (Treanor 2009).

This ‘massive reward for massive failure’ pattern is a grotesque parody of the reciprocity rule that people use to assess the fairness of compensation, i.e., “reward should be proportional to contribution”. Thus bankers like Sir Fred are perceived as supremely exploitative free riders. Since managers cannot be relied upon to police their own free riding, this task must fall to stakeholders whose interests lie in promoting the success of the organization as a whole, and who realize that free riding at any level is a threat to that success.

3.7 Is ATCG More Predictive than Equity Theory?

As noted above, ATCG assumes that in order to cooperate adaptively, group members must ensure that their benefit-to-contribution ratios are no smaller than those of co-members. Readers who are already familiar with equity theory (Adams 1963, 1965) may recognize that this focus on the benefit-to-contribution ratio is essentially similar to Adams’ emphasis on the relationship of “outcomes” to “inputs.” As suggested by this similarity, ATCG and equity theory do have much in common; however they also have some fundamental differences. Before comparing the two theories explicitly, we will first present a brief review of equity theory.

Equity theory (Adams 1963, 1965) is one of the best-known and most successful theories in the field of organizational behavior: when Miner (2003) asked 71 organizational behavior scholars to rank the importance of 73 organizational behavior theories, equity theory finished in third place overall, and was the top-finishing theory of cooperative behavior. (Equity theory has also been broadened to apply to social relationships in general, e.g. marriages [Walster et al. 1978]). Simply stated, equity theory predicts that a member of an organization (referred to by Adams as “Person”) will assess the ratio of the benefit that he receives from his job (his “outcome”) to the contribution that he makes to his organization (his “input”), and compare this ratio to some referent individual or group (“Other”). Other will often be Person’s organizational co-members (although Other may also be something quite different, for example Person in a former job). Adams considers equity theory to be a special case of cognitive dissonance theory, a widely-studied psychological phenomenon in which people attempt to minimize the perceived discrepancy between their desires and their actual experience (Festinger 1957; Cooper 2007). As such, equity theory’s fundamental prediction is that Person will be content if his own ratio is similar to Other’s ratio, and distressed if these ratios are different, because the latter situation should produce more perceived dissonance.

If Person does perceive dissonant ratios, then he will attempt to make them less dissonant – that is, more equitable – by adjusting the outcomes/inputs of himself and/or of Other. Person’s attempts to increase equity will be motivated by the emotion of anger if Person is disadvantaged by the inequity, and by the emotion of guilt if Person is advantaged by the inequity. Therefore if Person perceives that Other is making the same salary (outcome) in exchange for less work effort (input), then Person will be motivated by anger to rectify this inequity by reducing his own effort or extracting increased effort from Other, or by convincing management to raise his own salary or lower Other's salary. By the same token (and this is equity theory's most extraordinary prediction), if Person perceives that his own salary is higher than Other's, even though their effort levels are equal, then Person will be motivated by guilt to strive to increase his own effort, lower Other's effort, reduce his own salary, or increase Other's salary. Equity theory predicts aversion to self-advantageous inequity because of its roots in cognitive dissonance theory: self-advantageous inequity is just as dissonant as self-disadvantageous inequity, and should therefore be just as distressing.

Despite predicting that Person will seek to avoid self-advantageous inequity, equity theory also predicts that Person will be more tolerant of such unfairness than he will be of self-disadvantageous inequity. In other words, equity theory is somewhat asymmetrical in that while it predicts that Person will object both to being underrewarded and to being overrewarded, it also predicts more vigorous objection to underreward than to overreward. The theory cannot gracefully account for this asymmetry, because its dissonance theory foundations offer little insight about why underreward should cause more distress than overreward. Adams deals with the asymmetry by suggesting that overreward situations may seem more tolerable due to Person's egocentric bias: "Person is motivated to minimize his costs and to maximize his gains" (Adams 1965: 284). However if Person is thus motivated, then why does equity theory predict in the first place that Person should *avoid* rather than *seek* overreward situations? This bolting-on of egocentric bias does not seem to be an internally consistent way of dealing with the asymmetry, and egocentric bias is probably best seen as only an auxiliary or ad hoc hypothesis (Lakatos 1978), rather than a core hypothesis, of equity theory.

3.8 Efforts to Rescue Equity Theory in Situations of Overreward

Equity theory is regarded as a successful theory in large part because its prediction of aversion to underreward has received strong empirical support (Mowday and Colwell 2003; Colquitt et al. 2005). However, a consistent criticism of equity theory is that its prediction of aversion to overreward has received less support (Bolino and Turnley 2008): while people usually object strenuously to self-disadvantageous inequity, they do not reliably do so to self-advantageous inequity. In order to explain this lack of aversion to overreward, many researchers have implicitly or explicitly invoked Adams' ad hoc egocentric bias hypothesis (Greenberg 1983; Thompson and Loewenstein 1992; Diekmann et al. 1997; Leung et al. 2004).

An alternative approach to explain the lack of aversion to overreward is to suggest that individuals vary in term of their "equity sensitivity" (Huseman et al. 1985; 1987; Miles et al. 1989; Akan et al. 2009). Equity sensitivity research suggests that people can be divided up into three classes, based on how they score on a continuous measure of equity sensitivity: a relatively rare class of "benevolent" individuals, who prefer outcome-to-input ratios that are lower than co-members (underreward), coexists with more common classes of "equity sensitive" individuals, who prefer ratios that are equal to co-members, and "entitled" individuals, who prefer ratios that are higher than co-members (overreward). From this perspective, free riders would most likely come from the "entitled" class. This classification scheme is basically similar to those proposed by evolutionary-oriented behavioral economics researchers (Fischbacher et al. 2001; Kurzban and Houser 2005), whose empirical findings suggest that while most people, when playing cooperation games, can be classified as reciprocal altruists (who usually cooperate as long as co-members cooperate, similar to equity sensitives), a minority behave as free riders (who usually do not cooperate, similar to entitleds), and an even smaller minority behave as unconditional cooperators (who usually cooperate even when co-members do not, similar to benevolents).

3.9 Predictions of ATCG That Differ from Those of Equity Theory

The refinements to equity theory mentioned above make some progress towards helping equity theory explain the lack of aversion to overreward. By proposing that in addition to seeking equity, many people exhibit egocentric bias, and some people behave as entitleds who prefer overreward, equity theory is better able to explain why free riding is such a universal problem in groups. Still, these refinements do not put equity theory on a par with ATCG, in terms of being able to make predictions and provide solutions to the free rider problem. ATCG's advantages in this regard are of three kinds.

3.9.1 Prediction One: The Free Rider Problem Can Be Solved Via Social Consequences

First, ATCG correctly predicts how people will change their cooperative behavior in response to external social influences. The only mechanisms proposed by equity theory for what motivates individual responses to inequity are the emotions of guilt and anger. For example, while benevolents are predicted to experience relatively low anger upon being underrewarded, entitleds are predicted to experience relatively low guilt upon being overrewarded (Miles et al. 1989). Individuals are portrayed as having fixed equity sensitivity orientations that are regulated internally by emotions, and little attention is given to the idea that people are capable of changing their behavior (let alone switching orientations) in response to external social influences. Thus, if you are the manager of an organization that is bedeviled with too many entitleds, there isn't much you can do except either expect the organization to fail, or else try to replace the entitleds with benevolents or equity sensitives. ATCG, on the other hand, predicts that group members will become interested in changing their behavior depending on social influences, especially those that deter free riding.

3.9.2 Prediction Two: The Emergence of a Particular Cooperative Strategy Will Depend on the Frequencies of Other Strategies

ATCG's second advantage over equity theory is that it predicts the circumstances under which a particular kind of cooperative strategy will emerge in an organization. Equity sensitivity theory simply assigns people to different equity sensitivity categories, without considering the dynamics of how these categories should interact with one another, or the conditions under which any particular category should emerge as dominant in an organization. ATCG, in contrast, is capable of making some principled predictions along these lines. These predictions, which specify how any cooperative strategy (i.e. reciprocity, free riding, or unconditional cooperation) can emerge as a frequency-dependent adaptive response to the presence of other strategies, will be discussed in Sect. 4.

3.9.3 Prediction Three: More Competitive Individuals Will Be More Pro-equity/Anti-equality

ATCG's third advantage over equity theory is that it offers insights about what kinds of individuals will most favour the *equity* distribution rule (under which the highest contributors obtain the greatest rewards) as opposed to the *equality* distribution rule (under which everyone receives the same reward). While equity theory makes no predictions about the preference for equity over equality, ATCG predicts that individuals who have more to gain from engaging in competition will be relatively pro-equity and anti-equality. This prediction will be discussed in Sect. 4, where we focus on individual and sex differences.

4 How Cooperation is Affected by Differences Among Individuals, Differences Between Sexes, and Differences Among Resources

In Sect. 3, we sketched a general overview of ATCG's perspective on reciprocity in groups. In this section we will investigate how individuals will vary in their cooperative behavior, depending on their strategic orientation and their competitiveness. We will then discuss ATCG's predictions about how the sexes will differ in terms of cooperative behavior. Finally, we will explain how ATCG's predictions about resource-sharing vary, when different classes of resources – specifically, windfall and surplus resources – are being shared.

4.1 The Frequency Dependence of Cooperation

As noted above, both equity sensitivity and evolutionary theorists have predicted that individuals will vary in the kinds of cooperative strategies they play. However, only evolutionary theory, and not equity sensitivity theory, provides a solid basis for predicting how particular variables will influence this individual variation. ATCG incorporates this evolutionary view and the predictions that it makes. In order to explain this view, we must first describe why the advantageousness of any cooperative strategy is frequency dependent.

Evolutionary game theory (Maynard Smith 1982) suggests that the adaptiveness of a cooperative strategy in a population often depends on the frequency of other strategies in the same population (Boyd and Lorberbaum 1987; Lomborg 1996; Hauert et al. 2002). Consider the following rock-paper-scissors scenario, which is illustrated in Fig. 1.

In a population of free riders (F), reciprocators (R) – who cooperate as long as they can verify that their partners are cooperating – have an advantage, because only they can gain the benefits of cooperation (assuming that the benefits of cooperation are greater than the costs of verifying partner cooperativeness, and that reciprocators can exclude free riders from the benefits of cooperation). Eventually the population will become dominated by reciprocators. Once the reciprocators gain supremacy, however, they become vulnerable to an invasion of 'unconditional cooperators' (U), who always cooperate, even without verifying partner cooperativeness. While unconditional cooperators gain the same benefits from cooperation as reciprocators, they avoid the reciprocators' verification costs (such verification is wasteful in this environment, because there are no free riders). However, the more the unconditional cooperators come to dominate the population,

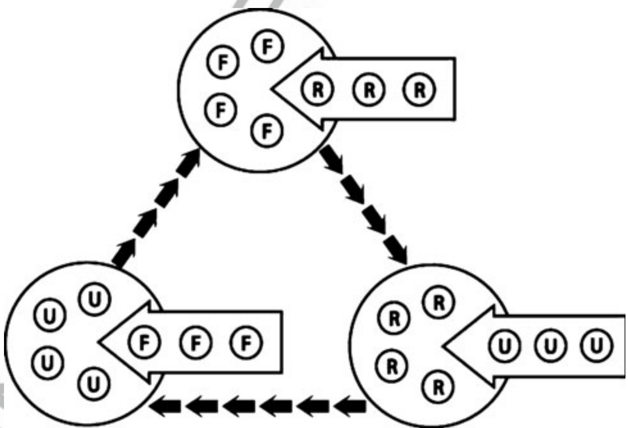

Fig. 1 The cycle of frequency-dependent for three cooperative strategies: free riding (F), reciprocity (R), and unconditional cooperation (U). At the *top* of the diagram, a population dominated by F is invaded by R, who is advantaged over F due to its ability to gain the benefits of cooperation (and to exclude F from these benefits). At the *bottom right*, an R-dominated population is invaded by U, who is advantaged over R due to its ability to gain the benefits of cooperation, without paying the costs of monitoring and verifying partner cooperativeness. At the *bottom left*, a U-dominated population is invaded by F, who is advantaged because it can exploit U's over-trusting cooperativeness. After F becomes dominant, the cycle repeats itself

the more the population becomes vulnerable to an invasion of free riders, because unconditional cooperators are easily exploited (Nowak and Sigmund 1992).

ATCG incorporates the logic of the above rock-paper-scissors scenario, and predicts that the likelihood that a strategy will be pursued in an organization will depend on the frequencies of other strategies in that organization. ATCG is at present agnostic, however, about whether the different strategies in the above scenario represent different individuals that always play the same strategy (i.e., different polymorphisms) or the same individuals played flexible strategies. Some researchers have suggested that the former scenario is more likely, and that fixed polymorphic strategies are maintained in populations because across all social environments of shifting strategy frequencies, each strategy will be adaptive on average (Kurzban and Houser 2005; Cesarini et al. 2008). On the other hand, it seems as though the best possible individual strategy would be a flexible one (Boyd and Lorberbaum 1987) that played (1) reciprocator in a population of free riders, while excluding free riders from the benefits of cooperation, (2) unconditional cooperator in a population of reciprocators, and (3) free rider in a population of unconditional cooperators. To what extent is an individual capable of switching strategies according to this pattern? That question has not yet been thoroughly addressed by research. But regardless of whether individuals are best seen as fixed as opposed to flexible cooperative strategists, ATCG makes three points here that are of particular relevance to managers.

4.1.1 First Point for Managers: Strategic Behavior Can Be Altered

First, even if people are fixed strategists, evidence reviewed above suggests that group members do adjust their cooperative behavior somewhat, depending on how they expect co-members will behave. For example, would-be free riders become more cooperative when they perceive they may be ostracized for free riding, and reciprocators become less cooperative in the presence of free riders. These adjustments may not map on particularly well to the rock-paper-scissors dynamics described above; for example, a free rider who starts acting like a reciprocator out of fear of being ostracized may not be “switching strategies” so much as suspending his free riding until the threat of ostracization has passed. Nevertheless, the fact that members make these adjustments does demonstrate that social influences – especially, imposition of the consequences problem on would–be free riders – can be used to enhance group productivity, as ATCG (but not equity theory) predicts.

4.1.2 Second Point for Managers: Shifts in Employee Cooperative Behavior Can Be Predicted, Based on the Frequencies of Strategies Within an Organization

A second point of relevance to managers is that regardless of whether people are fixed or flexible strategists, the rock-paper-scissors scenario predicts that particular strategies are likely to emerge and become dominant in particular organizational environments. For example, imagine an organization in which insufficient effort is made to monitor employee contributions, and to ensure that the greatest rewards go to the highest contributors to organizational goals. Low contributors can obtain high rewards, for example, by convincing management that they have contributed more than they actually have. Because it is not necessary to actually contribute in order to get ahead, would-be high contributors lose their motivation to contribute, and free riding emerges as the dominant strategy. (Throughout this example, the emergence of a new dominant strategy could be due to either current employees who switch their strategies, or else to an influx of new employees – who may be attracted to the organizational culture because it affords their strategy an advantage).

In order to rectify this situation, management will need to begin neutralizing the free rider advantage by allocating higher rewards to higher contributors. This introduction of fair compensation policies will give reciprocity an advantage over free riding, and reciprocity will become the dominant strategy. Over time, employees will become increasingly trusting that their contributions will be rewarded proportionately. The more they trust in this outcome, the less necessary they should believe it is to constantly monitor and verify that their own benefit-to-contribution ratios are no lower than co-members. Such monitoring efforts are wasteful when everyone else truly is reciprocating, so unconditional cooperation will emerge as the dominant strategy. The more members cooperate unconditionally, however, the more opportunity co-members will have to exploit them. This may explain why, although a high level of trust is generally assumed to be beneficial in organizations (Dirks and Ferrin 2001), "too much" trust appears to be detrimental to work team effectiveness (Langfred 2004). Unverified trust will create fresh opportunities for co-members to adopt free riding techniques, for example to exaggerate the extent of their own unmonitored contribution level. If an organizational climate of too much trust allows free riding to emerge as the dominant strategy, the cycle will have come full-circle, and reciprocity will again need to be restored.

4.1.3 Third Point for Managers: Cooperation is Always Ultimately Vulnerable

The above example contains a practical warning: even in an organization in which rewards are allocated extremely fairly, the stability of cooperation is always ultimately vulnerable. A manager might rightfully take pride in the high levels of trust that he observes in his organization, but he should always keep in mind that climates of unconditional cooperation are vulnerable to being invaded and undermined by free riders. By the same token, however, even an organization that has decayed into a free rider's paradise can be rehabilitated, provided that management is willing to make the effort to change the culture such that individual contributions to organizational goals are monitored and rewarded proportionately.

4.2 Competitiveness and a Preference for Equity over Equality

So far our chapter has focused on one kind of distribution rule in particular: the *equity rule*, which specifies that individuals receive rewards in direct proportion to their contributions. We have focused on this rule because it leads to the most economically productive groups (Deutsch 1975), due to the fact that it most effectively solves problems of cooperation (especially, the free rider problem) that hinder productivity. However there are, of course, other distribution rules in human societies, and two other common ones are the *equality rule*, under which everyone receives the same amount, and the *need rule*, under which the needier receive more (Deutsch 1975; Romaine and Schmidt 2009). Equity and equality have received more research attention than need, and are probably more relevant than need in organizational contexts, so we will focus here on equity and equality.

Whether an individual benefits more from equity or equality depends on that individual's competitiveness, that is, on how much that individual can gain by engaging in competition. Two main factors determine an individual's competitiveness: the individual's sex (as we will discuss in the next section), and the individual's likelihood of winning that competition. A more competitive group member will benefit more from equity than equality because only equity will give him an opportunity to gain, via competitive altruism, an advantage over co-members. For example, an individual who is highly capable of contributing to a group productive effort would stand to be highly rewarded in an equity system, and would do better under equity than under equality. A member who has little ability to engage in competitive altruism, on the other hand, would more likely do better under equality.

Research on how individual competitive ability affects attitudes toward equity and equality has tended to focus on the level of the nation-state or of society as a whole. For example, studies focusing on preferences for national governments that are more oriented towards equity or meritocracy (e.g., capitalism) versus equality (e.g., communism) have found that citizens who are better able to acquire resources, such as higher-income and better-educated citizens, are relatively supportive of the rule of equity (Ritzman and Tomaskovic-Devey 1992; Kunovich and Slomczynski 2007). Further, research on "social dominance orientation" has found that members of ethnic majorities, as well as higher-income individuals, tend to be more generally approving of inequality among groups in society (Pratto et al. 2006). Studies such as these suggest that individuals tend to prefer the distribution rule which advantages them. However, these studies do not directly examine possible relationships between specific biological traits and a pro-equity/anti-equality orientation.

ATCG offers novel predictions here: pro-equity/anti-equality sentiment will be expressed relatively highly by individuals who display traits that would have enhanced individual competiveness in ancestral environments. In making this prediction, ATCG could potentially cast new light on the issue of who prefers equity. For example, ATCG predicts that males with relatively great upper body strength will be relatively pro-equity/anti-equality. The logic of this prediction is similar to that used by Sell et al. (2009), who show that males with greater upper body strength express more support for political aggression (e.g., for military action by their own country). Sell et al. explain this result by noting that in ancestral environments, stronger males could have benefited relatively highly from the use of aggression. Of course, even though upper body strength has little impact on who wins wars in modern environments, the evolved psychology persists. Similarly, stronger males in ancestral environments would have had more to gain from equity and more to lose from equality, because their physical power would have made them relatively capable of contributing to group productive efforts. Therefore, ATCG predicts them to be relatively pro-equity and anti-equality in modern environments, even though physical strength is, in many modern organizations, less important than it was ancestrally for engaging in competitive altruism.

Besides physical strength, other ancestral correlates of competitiveness that ATCG predicts will relate positively to pro-equity/anti-equality orientation include testosterone level, and measures of good health and physical condition such as physical attractiveness and bilateral facial and bodily symmetry. Higher testosterone levels are associated with increased competitive status-seeking behavior in males (Dabbs 1997, 1998), and physical attractiveness and symmetry are both used as general indexes of biological quality (Gangestad et al. 1994; Brown et al. 2008). All of these variables have been shown to affect some aspects of behavior in economic games. For example, more symmetrical males make lower offers in an economic game (Zaatari and Trivers 2007), while higher-testosterone men are more likely to reject low offers (Burnham 2007). Physical attractiveness has shown no consistent relationship with behavior in these games (for inconsistent results see Mulford et al. 1998; Solnick and Schweitzer 1999; Takahashi et al. 2006). Taken together, these results do not allow one to assess whether these physical correlates of ancestral competitiveness are associated (be it positively or negatively) with level of "general cooperativeness", and they do not test the hypothesis that these physical correlates are associated positively with pro-equity/anti-equality orientation. However, these results do imply that there are links between these physical correlates and the psychological mechanisms which govern cooperative behavior, and ATCG suggests some compelling hypotheses about what these links should be, and how they should impact support for the equity rule in organizations.

4.3 Sex Differences

So far in Sect. 4 we have focused on individual difference variables that affect cooperativeness in both sexes. Now we will examine differences in cooperativeness that distinguish the sexes from each other.

ATCG incorporates the standard evolutionary approach to explaining sexually dimorphic traits, and thus provides a solid basis for predicting sex differences in cooperative behavior. According to the theory of parental investment and sexual selection (Darwin 1871; Trivers 1972), sex differences evolve because the sexes are selected to make different-sized investments in the production of offspring. In most species, males are the lesser-investing sex; for example, while the minimum investment that most male mammals must make in order to reproduce is a trivial amount of time and sperm, most female mammals must make a minimal investment of a long period of gestation and lactation. As a result, males have the potential to reproduce at a much faster rate than do females, and the reproductive success of males (unlike that of females) is limited mainly by mating opportunities. Because mating opportunities benefit males more than females, and because higher status males get more mating opportunities, selection on males tends to strongly favour the ability to succeed in status competition. Therefore in most species, especially mammals and primates, (including humans) males compete for status more vigorously than do females (Daly and Wilson 1988; Kruger and Nesse 2006, 2007; Graves, 2010). And just as males are, on average, better-designed than females for status competition, females are, on average, better-designed than males for parental investment.

One implication of these evolved sex differences is that male and female employees, in evaluating the fairness of their benefit-to-contribution ratios, will tend to differ in the forms of benefit they most value. Because females are relatively more oriented towards parental investment, family-friendly policies tend to be valued more by females than by males (Scandura and Lankau 1997; Kim 2008). Benefits that come in the form of generous parental leave policies and flexible work schedules, for example, will be valued more highly by females than by males.

An even more important result of these sex differences is that human males (like the lesser-investing sex in many species) should tend to be more motivated than females to compete for social status. Males manifest this tendency during childhood and continue to display it throughout their adult lives (Geary 2002; Browne 2006). Studies in experimental psychology and economics have routinely found that males are more interested than females in competitive behaviour (review in Croson and Gneezy 2009). For example, when engaged in tasks such as solving puzzles and running on a track, male performance is enhanced when the tasks are performed in competition with others, while female performance is not (Gneezy et al. 2003; Gneezy and Rustichini 2004); and when given a choice about what kind of compensation scheme they prefer, males are more likely than females to choose a competitive scheme (e.g., winner take all) as opposed to a non-competitive one (e.g., piece rate) (Niederle and Vesterlund 2007). Male competitiveness is also evident in studies that have focused explicitly on cooperation. Van Vugt et al. (2007) found that males increased their in-group cooperation significantly in response to competition from rival groups, whereas females were relatively unaffected by this competition.

The increased competitiveness of human males should make them more pro-equity and anti-equality, for reasons outlined in the previous section of this chapter: because ancestral males had more to gain than females from status competition, they also had more to gain than females from the rule of equity and less to gain from the rule of equality. The fact that males do tend to be more pro-equity than females, and that females tend to be more pro-equality than males, has been recognized for decades. Studies have found consistently that when allocating resources, males tend to use the equity rule and females tend to use the equality rule (Vinacke 1969; Major and Deaux 1982; review in Inness et al. 2004). This sex difference has usually been explained in terms of different socialization pressures on males and females (Inness et al. 2004). However, because ATCG explains variation in pro-equity/anti-equality orientation in terms of variation in competitiveness, as opposed to sex differences per se, ATCG predicts not just between-sex differences in this orientation, but also within-sex differences depending on other factors (as noted above). Further, because ATCG attributes sex difference in pro-equity/anti-equality orientation primarily to biological adaptation, as opposed to socialization, it predicts that this difference would be difficult to eradicate via socialization alone. Further evidence against the socialization hypothesis is that differences in cooperative behavior between boys and girls emerge at a very young age (Ellis et al. 2008). For example, boys more often play team games involving larger groups, are angrier when rules are broken, and have more transient friendships, whereas girls have more exclusive friendships. Although the sex difference in competitive status-striving has occasionally been reflected upon in the mainstream organizational behaviour literature (for example, in the context of salary negotiation [Stevens et al. 1993]), it is widely underappreciated in the field (Sandelands 2002). Which factors may account for the neglect of this sex difference? It has not been due to a failure on the part of organizational researchers to appreciate the general importance of status enhancement as an incentive in organizations; indeed, they have appreciated its importance for decades (Clark and Wilson 1961). Nor has it been due to a general reluctance among organizational researchers to investigate sex differences; indeed, according to a review by Ely and Padavic (2007), no less than 131 articles discussing sex differences appeared in the top four management journals between 1984 and 2003.

Instead, neglect of this sex difference has probably been due to two other factors: first, the general political thorniness of the topic (see below); and second, the fact that evolutionary considerations have not been a traditional component of any topic in organizational behavior, including sex differences. For example, of those 131 management articles on sex differences, none were recorded by Ely and Padavic as having taken an evolutionary theoretical perspective. It is no coincidence that the field's most extensive and straightforward discussions of sex differences in status-striving have appeared in a special issue of *Journal of Organizational Behavior* devoted to Darwinian perspectives on organizations (Browne 2006; Colarelli et al. 2006). Organizational researchers would benefit by taking a more evolutionary perspective on this topic, as there is a clear Darwinian rationale for why males should be relatively preoccupied with competition and status, and this sex difference probably generates a variety of important effects in organizational contexts.

4.3.1 Negative Reactions to Status Reductions, Especially Among Males

One of these important effects is that employees, and particularly male employees, should be sensitive to perceived social slights regarding the value of their contributions to cooperative endeavors. Evolutionary psychologists have long recognized that males are relatively likely to react negatively and sometimes violently to insults to their status, even when these insults seem relatively trivial (Daly and Wilson 1988; Goldstein 2002; Nisbett and Cohen 1996; Wrangham and Wilson 2004). The social dynamics of a typical organization will provide regular opportunities for an employee to feel that his or her status has been slighted in some way. Such insults may be explicit, for example being demoted, fired, or passed over for a promotion, but in group cooperative interactions they will more often be subtle, for example sensing that the recommendations you made in a meeting were ignored, or that your contributions to a group project were not adequately recognized. Differences in how negatively males and females react to such insults could lead to sex differences in variables that are important to organizational behavior researchers such as motivation, job satisfaction, and desire for retributive justice.

The potential of status reductions to elicit strong negative reactions, particularly among males, is one reason why status must be allocated with great care. Although status rewards may often seem relatively cheap to administer compared to other kinds of incentives (e.g., financial ones), status is nevertheless a scare resource. Status allocation events are zero-sum games, as any enhancement in the rank of one particular member will produce a drop in the *relative* status of at least one co-member (relative, that is, to the ascendant member), and thus may be perceived as insulting by the co-member(s). To help minimize the chances that a status reallocation event will be perceived as insulting, care should be taken to convince all group members that the reallocation has been equitably based on the extent to which members have been contributing to group goals. Peer reviews might even be used in the judgment, to generate the impression that the decision reflects a common census rather than arbitrary favoritism.

4.3.2 Positive Reactions to Status Enhancement, Especially Among Males

The flip side of males reacting more negatively to status-lowering insults and demotions is that they should also be relatively motivated to strive for status-enhancing rewards. Such rewards could include material status symbols like a higher salary or bigger office, but could also include social indicators such as public recognition for one's achievements or a higher assigned rank in an office hierarchy. The view that males should on average be relatively motivated to chase such rewards implies that the underrepresentation of females in top management positions may be due not just to sexist discrimination, but to a reduced motivation on the part of females to compete aggressively for these jobs (Browne 2006; this issue is also relevant to female political candidates, e.g., Clift and Brazaitis 2003). This observation may seem controversial, as it would seem to suggest that women do not desire such positions as strongly as do men, which might seem to justify their underrepresentation. However, a few considerations must be kept in mind here.

First, as with many scientific statements about mean group differences, this is probably a case of overlapping normal distributions, which is consistent with the expectation that many females will be *more* status-oriented than many men. Second, predicting that males will on average be more motivated to compete for high-status positions is not the same thing as predicting that they will be more effective on average in such positions; desiring a job is not the same thing, of course, as being competent to perform it. Accordingly, the observation that males tend to more competitively pursue status says nothing about the desirability of male overrepresentation in top management (indeed, it gives us reasons to assess it more critically). This observation does suggest, however, which steps an organization might take in order to increase female representation in high-status positions. In particular, it suggests that an open competition for such jobs, in which an organization waits to see which candidates throw their hat into the ring and most aggressively promote themselves, might not be the best way to attract the most qualified female candidates (or indeed many qualified male candidates). Such competitions may self-select for a large pool of males, and females who are relatively male-like in terms of competitive status-striving (Rhoads 2004). However, a larger pool of qualified females might be generated if such candidates are actively scouted out and recruited, instead of being expected to aggressively pursue the jobs on their own.

4.4 Different Sharing Expectations for Windfall and Surplus Resources

We will conclude Sect. 4 by pointing out that expectations about how a group's resources should be shared will be influenced not just by fairness considerations and by differences among individuals and between sexes, but also by the abundance and availability of the resource. In discussing ATCG's predictions about resource-sharing so far, we have been focusing on resources that are deliberately produced by concerted organizational effort. In these situations, as we have seen, the prevailing view of fairness tends to be that only someone who contributed to production should receive a share of the resource, and higher contributors should receive larger shares. ATCG identifies two kinds of resources, however, that people tend to believe should be shared more widely, generously and equally.

The first of these resources are windfall resources, that is, resources that are unpredictable in terms of availability. ATCG agrees with the perspective that when the availability of a resource is relatively unpredictable, individual-level selection favors widespread voluntarily sharing (Kaplan and Hill 1985; Andras et al. 2007). This sharing rule appears to be the product of a risk-reduction psychological adaptation: if a resource's availability is unpredictable, then chance determines who acquires it. Thus, any one person is just as likely to benefit from the widespread sharing rule as to be obligated by it. Support for this theory has been produced in studies such as Kaplan and Hill (1985) and Kaplan et al. (1990), who found that more unpredictable resources were shared more widely by Ache foragers. Similarly, Kameda et al. (2002) found that in a series of laboratory and vignette experiments, people who acquired money as the result of chance were more willing to share it widely, and were expected by others to share it more widely.

Although the evidence in favour of windfall resources being widely shared is compelling, some research suggests that other factors can emerge as being more important influences on how widely a resource is shared. Bliege Bird et al.'s (2002) study of Meriam foragers suggests that a resource's abundance, as opposed to its unpredictability, is a more important predictor of how generous people are with it. In their study, when an individual possessed a surplus of a food resource such as fish or turtle, he was more likely to share it widely. ATCG would predict this result, because the less an individual needs to consume a resource himself, the more he can afford to exchange it for other resources, such as social status. For example, Bliege Bird et al. (2002) suggest that sharing allows individuals to broadcast a costly signal of the qualities that enabled them to forage successfully; thus, their sharing increases their social status by making them seem more attractive to potential mates and allies.

ATCG's perspective on windfall and surplus resources can help illuminate some practical issues about how the fairness of compensation procedures are evaluated in organizations. Managers should keep in mind that when organizations acquire resources that are unexpected, or more than the organization is perceived to "need", employees will probably feel relatively entitled to a share of these resources. If an umbrella-making company has a particularly profitable quarter due to a freakishly rainy summer, it would good for employee satisfaction to widely distribute the benefits of this windfall. And if a company's profits have far exceeded its budgeted needs, then widespread sharing with employees would again be well-advised. What's more, managers who hoard resources for themselves will be perceived as particularly selfish if these resources are of the windfall and/or surplus kind. Consider, for instance, the recent public outrage over the size of banker bonuses. The unpredictable quality of bonuses probably makes the public regard them to some extent as windfall resources. Moreover, bonuses are perceived as surplus – not needed for the bank's operating costs or to pay the bankers' already-generous salaries. These bonuses are perceived as being concentrated in the hands of a few elite earners, as opposed to being shared generously throughout a larger community – not shared, for example, with the society which kept many of the banks afloat throughout the crisis (although these bonuses are usually taxed, being taxed is not perceived as voluntary sharing), or even with lower-level employees of the banks themselves. Thus banker compensation, which the public already perceived as basically unfair (e.g. due to outsized rewards, and as discussed in Sect. 3, the practice of "reward for failure"), seems even more unfair because it often takes the form of unpredictable surpluses that are not voluntarily shared.

5 Conclusion

The Adaptationist Theory of Cooperation in Groups (ATCG) is a synthetic theory that draws together the contributions of a large number of researchers. Most of these researchers have been able, by adopting an individual-level adaptationist perspective, to make predictions about cooperation in groups that go beyond those that are made by existing theories in social and organizational science. That said, ATCG also shares predictions with several previous theories. In this conclusion, we will briefly review some of the main ways in which ATCG compliments and diverges from existing theories of cooperation in groups.

First of all, it may seem ironic, but the theory of cooperation that ATCG probably has the least in common with is another evolutionary theory, the purely group selectionist perspective (Gintis 2000). All of ATCG's predictions follow from the basic premise that cooperation evolved because individual cooperators receive fitness advantages; without this premise, ATCG has no reason to predict behavioral dynamics such as reciprocity, competitive altruism, free riding, the frequency dependence of cooperative strategies, and individual and sex differences in cooperative behavior. Further, although a multilevel selectionist perspective (Wilson and Wilson 2007) could accommodate these individual-level processes better than a purely group selectionist process could, we see no added value, in terms of improving ATCG's predictive power, in adopting a multilevel perspective at this stage of theory development.

ATCG has a good bit more in common with equity theory (Adams 1963), with its focus on input-to-outcome (benefit-to-contribution) ratios, and with equity sensitivity theory (Huseman et al. 1985), which recognizes individual variation in the preference for equity. However, ATCG improves on equity theory's ad hoc and minimal attention to the free rider problem by recognizing this problem as the central impediment to productivity in groups. Further, because equity theory and equity sensitivity theory focus on the internal emotional regulation of cooperative behavior, they do not offer clear solutions to the free rider problem; ATCG on the other hand does offer solutions, by predicting that free riding will be mitigated by imposition of external social consequences (or by cues which suggest that such consequences are forthcoming). And while equity sensitivity theory predicts that different kinds of cooperative strategies will exist in a population, ATCG goes much further by predicting the dynamics of the process by which any one cooperative strategy can emerge as dominant in an organization, depending on the frequencies of other strategies.

ATCG also predicts that individuals with greater competitive ability should do better under equity systems as opposed to equality systems, and so should hold relatively pro-equity/anti-equality attitudes. With this prediction, ATCG distinguishes itself further from equity theory and equity sensitivity theory, but finds some common ground with theories which predict that individuals who are better able to compete for resources in modern societies will exhibit more support for meritocracy and social inequality (Ritzman and Tomaskovic-Devey 1992; Kunovich and Slomczynski 2007; Pratto et al., 2006). However, ATCG goes beyond these theories as well, by predicting that traits that were conducive to competitive ability in ancestral environments should lead to increased pro-equity/anti-equality orientation in modern environments, regardless of the extent to which these traits increase competitive ability in modern environments. By defining competitive ability in terms of ancestrally-relevant criteria, ATCG can identify novel variables (e.g., aspects of biological formidability such as strength and attractiveness) that may impact preferences for equity over equality.

ATCG also has features in common with theories that have recognized the centrality of the free rider problem (Olson 1965; Hardin 1968). However because ATCG focuses on the evolutionary dynamics that allow the free riding strategy to either flourish or perish, it has arrived at predictions about this problem that other theories have not made. For example, ATCG predicts that organizations will be most vulnerable to an invasion of the free riding strategy when levels of trust within the organization are at their highest, and least vulnerable when reciprocal altruism has been allowed to emerge as the dominant strategy within the organization. ATCG also places a uniquely strong emphasis on solutions to the free rider problem such as punishment and ostracism of free riders, and positive assortation among cooperators, and makes a variety of novel predictions about how these solutions will work. For example, ATCG predicts that because higher contributors are relatively personally disadvantaged by free riders, they will be relatively likely to detect them and advocate their punishment. It also predicts that if you allow people to choose their own interaction partners as they assort into cooperative groups, then more cooperative members will mutually choose one another while excluding less cooperative members. Finally, ATCG predicts that cues that in ancestral environments would have indicated that one's cooperative behavior was being monitored, such as eye-like depictions, will increase cooperative behavior in modern environments, even though people rationally "know" that these depictions cannot actually see.

ATCG focuses on the centrality of social status as a second-order benefit of cooperation, and on the fact that in a well-managed group in which reciprocity is the dominant strategy, group members are in competition with one another to contribute the most to group goals. It therefore makes predictions about the relationship between cooperation and status that other theories have not explicitly made. Namely, ATCG predicts that through the process of competitive altruism, the highest contributors will achieve the highest social status within the group. Further, because the competitive altruist's ultimate goal is to compete for high status, and his altruistic efforts are just a means to that end, there is always the risk that he will put his own competitive goals ahead of the group's actual best interests, and as a result end up harming the group (e.g., by finagling a high-status role that someone else could have performed more competently).

ATCG's theoretical foundations in evolutionary biology, which incorporate parental investment and sexual selection theory (Darwin 1871; Trivers 1972), provide a solid basis on which to predict sex differences that are highly relevant in organizational contexts, such as men's relatively strong interest in competitive status striving and women's relatively strong interest in parental investment. Some implications of these sex differences have been explained by other social science theories, for example, the fact that males are more pro-equity/anti-equality than females has been explained in terms of socialization pressures. ATCG's perspective on these sex differences, however, suggests that they would not be as easy to eradicate as most socialization theories would predict, and furthermore offers specific ways to manipulate these concerns for the good of the organization. Other implications of these sex differences – for example, ATCG's prediction that males will react more negatively than females to status reductions – do not seem to be clearly specified by any other existing theory.

Finally, because ATCG adopts the view that people are adapted to share windfall resources more widely than predictable, deliberately produced resources (Kaplan and Hill 1985), and to share surplus resources more widely than essential resources (Bliege Bird et al. 2002), it predicts how the sharing expectations that emerge in organizations will be affected by resource predictability and availability. These predictions do not seem to be made by any existing theory in organizational science.

Before ending, if we are permitted a more speculative and ambitious claim, it may be no coincidence that the Darwinian focus on individual selection resonates with the economic self-interest model that underlies the insights of Adam Smith and free-market capitalism. Neither justifies the other, of course (that would be the naturalistic fallacy), but they appear to share some fundamental characteristics in common. An interesting question for future research is whether, perhaps, free-market capitalism has succeeded where communism has failed because human brains are better adapted to the former.

In conclusion, we hope we have shown in this chapter how the work of many evolutionary researchers can be pulled together in order to produce a model of human cooperation in groups that is relatively coherent, predictive, and useful in terms of its applied value to real-life organizations. By highlighting the features that ATCG shares in common with existing theories, as well as the novel predictions that ATCG makes, we have tried to demonstrate that the individual-level adaptationist perspective has contributed to scientific advancement in our understating of organizational cooperation. We trust that this perspective will continue to generate new insights about such cooperation in the future, and that it will ultimately lead to a further refined and comprehensive theory.

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