

The Evolution of Teamwork, Cooperation and Risk

Peter Andras and John Lazarus

Our aims in this chapter are twofold. First, we place teamwork in the context of the evolutionary analysis of cooperation and altruism. This allows us to predict the evolutionary scenarios likely to have favoured the evolution of team work, the likely origins of human teamwork and the biases to be predicted in team thinking. Second, we examine the influences of environmental risk – conceptualized as both environmental adversity and uncertainty - on cooperation in the organic world and describe a new model to explain these influences. We conclude by drawing conclusions about the role of environmental risk in the emergence of human cooperation and teamwork.

1. The evolution of teamwork and team reasoning

If teamwork is a strategy that follows from team reasoning (*sensu* Colman, 2003; Sugden, this volume) then the function of teamwork can be said to be to maximize utility for the team as a whole. This goal is reached by a particular combination of actions by members of the team. Since the goal of maximizing utility for the team may compromise utility for (at least some of) its constituent individuals, teamwork may require cooperative or altruistic acts by team members. In this section we examine the various selective mechanisms for cooperation and altruism distinguished by evolutionary biology and ask which of these mechanisms might result in teamwork as defined here. We ask, in other words: how does teamwork evolve?

We are concerned here largely with functional and evolutionary questions concerning teamwork, cooperation and altruism, and not with questions of motivation, development, intention or psychological mechanism (see Tinbergen, 1963, for a classic account of these distinctions). In evolutionary biology, functional questions about behaviour are concerned with the consequences of action and ask how action might be adaptive; how it might solve some problem important to the organism's survival or reproductive success, and thus to its Darwinian fitness. Adaptations inevitably have both benefits and costs, and natural selection results in changes in the organism over time that hone its adaptations towards the optimal condition of maximum fitness, or net benefit (i.e., benefit minus cost), although Darwin (1872) himself appreciated that there is no guarantee that the optimal state will be reached. Consequently, the building blocks of functional analysis are the benefits and costs of action measured in the currency of fitness. Cooperation and altruism are defined functionally in evolutionary biology, therefore, simply in terms of their resultant benefit and cost. Cooperation is defined as a social action resulting in a benefit both to the actor and to the recipient of the act, while altruism is defined as an act that benefits the recipient at a cost to the actor. These are the definitions we use in discussing the evolution and function of cooperation and altruism.

We can distinguish, in principle, between two kinds of cooperation. In the first, sometimes called mutualism, all individuals involved in the interaction benefit but none benefits at the expense of others. A simple example is group living, which reduces predation risk for all in the group by (with some simplification) 'diluting' the risk of capture by the number in the group. A second example is group hunting by wolves in which only by cooperative hunting is it possible to bring down a prey many times larger than an individual wolf. By not

cooperating – not joining the group, or not joining the hunt - the individual loses out. In the second kind of cooperation the individual benefits directly by taking the non-cooperative option. In the Prisoners' Dilemma game, for example (see Sugden, this volume, for details), the alternative to cooperation is defection, which always gives the defector a greater payoff and the other player a worse payoff. The latter type of cooperation has been of greater interest to psychologists and economists since it seems more strategic - payoff depends on the choice made by the other party. It also invokes a range of phenomena in humans – such as cheating, trust, reciprocity, fairness, sanction, retribution, punishment, guilt, forgiveness and reconciliation - that raise complex questions concerned with social decision making, emotions and ethics:

This distinction is more apparent than real, however, since the first type of cooperation will often provide opportunities for differential benefit. Even in the simple case of gregariousness an individual may seek an advantage by attempting to gain a safer position in the centre of the group, protected from predatory attack by more peripheral individuals and increasing their risk by its move towards the centre. In the group hunt some may hang back and not pull their weight, but still take a share of the spoils, influencing the payoffs to those involved.

Wherever there is room for strategic choice we expect to find it exploited, with effects on all players in the action.

1.1 How might teamwork evolve?

Group selection

Until the 1960s it was commonly believed that natural selection could act at the level of the

group or species. In this climate Wynne-Edwards (1962) argued that altruism would be selected if it aided population survival by preventing overexploitation of resources. He drew the analogy of the advantage of setting fishing limits to maintain fish stocks for the long-term benefit of all fishing fleets. Groups - rather than individuals - were seen as the unit of selection, with more successful groups surviving at the expense of the less successful. Modeling of group selection has continued and group selection has been proposed as a mechanism for the origin of human cooperation (Sober and Wilson, 1998). The problem that group selection has to overcome in explaining cooperation is that a selfish individual would have a fitness advantage in a group of altruists working for the good of the group, so that selfishness would be favoured by selection and spread through the population. Egoists can further undermine the group selection of group-directed altruism by moving to new, perhaps largely altruistic, groups and seeding them with selfishness (Maynard Smith, 1964, 1976). Whether group selection has been a significant force in evolution has been hotly debated.

This controversy aside, group selection is a candidate mechanism for the evolution of teamwork, the team being equivalent to the group whose fitness - rather than that of its constituent individuals - is the target of selection.

Kin selection

Relatives share genes by common descent. Genes influencing social behaviour between relatives (e.g., parental care, sibling rivalry) therefore have the chance of influencing the replication of those same genes in other individuals. In this case the evolutionary fate of the behaviour in question is determined by its consequences for the fitness of both parties, since both bear the relevant genetic material. The behaviour is favoured by natural selection as long

as it results in the genes that influence it – *regardless of the body they are inhabiting* – collectively having a greater chance of replication into the next generation. The unit upon which natural selection acts in this case is therefore the gene rather than the individual and the pair of relatives concerned are a team, since selection is expected to result in actions whose consequences enhance their combined fitness. In the case of interactions between kin, natural selection therefore favours teamwork, since the team's optimal solution coincides with that of the gene, and the positive social relationships between kin are readily understood in evolutionary terms.

The argument can be quantified. The benefit arising from cooperative and altruistic behaviour relies on the beneficiary bearing the gene responsible for the cooperation or altruism. The probability of this occurring, for any gene, is readily calculated for different relatives from the knowledge that a particular parental allele (i.e., version of a gene) has a probability of 0.5 (i.e., a 50-50 chance) of being passed to an offspring, and that siblings have the same probability of sharing an allele by common descent from a parent (Hamilton, 1964). This probability reflects the closeness of kinship between the individuals and is termed the *coefficient of relatedness, r*.

Now, suppose an altruistic act produces a cost C to the actor and a benefit B to the recipient relative, and the coefficient of relatedness between them is r . The gene promoting altruism will be benefited if the relative contains it, which it does with probability r . So, on average, the benefit of such acts to the relevant gene is equal to Br . For natural selection to favour the altruistic act its benefit must outweigh its cost, so that the condition favouring altruism between relatives can be expressed as $Br > C$ (Hamilton, 1964), and the payoff to the team is

$Br + C$. For altruism between full sibs ($r = 0.5$) to be favoured, for example, the benefit must be greater than twice the cost.

Individual selection and reciprocity

The first attempt to understand the evolution of cooperation and altruism between unrelated individuals by individual selection was based on reciprocity. Trivers (1971) pointed out that if altruistic acts were exchanged between two individuals, with benefits exceeding costs, then both parties would receive a net benefit after a pair of reciprocated interactions. Such an exchange would thus fit the definition of teamwork. The problem for the evolution of reciprocity by this means, as Trivers realised, is same one that threatens to undermine the establishment of all cooperative relationships, that of cheating. The recipient of the first altruistic act gains a higher pay off by not reciprocating than by reciprocating.

Trivers' (1971) ideas were combined with games theory and evolutionary modeling (Maynard Smith, 1982) by Axelrod and Hamilton (1981, Axelrod, 1984) to explore the evolutionary fate of various strategies in the iterated Prisoners' Dilemma. Axelrod and Hamilton sought an evolutionarily stable strategy or state (ESS); one in which a single strategy increases in frequency over generations in the simulated population until it becomes and remains the sole strategy (or, alternatively, a mixture of different strategies remain stable at fixed frequencies). Stable states are of interest for the obvious reason that, by definition, they are the states that endure and are expected to be seen in nature. An ESS that emerged in this and related work was 'Tit-for-Tat' (and similar strategies: Boyd and Lorberbaum, 1987), that started by cooperating and then matched the partner's last move (cooperation or defect), so that a population of Tit-for-Tat strategists would always cooperate. Given the pay-off

structure of the Prisoners' Dilemma Tit-for-Tat strategists are exhibiting teamwork (see also Sugden, this volume).

Beyond reciprocity

This work was just the start of two productive decades of theoretical and empirical work on the evolution of cooperation and altruism, with an increasing emphasis on attempting to understand the origins of human cooperative and altruistic acts when reciprocity is not expected (Fehr and Fischbacher, 2003). There is a current emphasis on explaining human altruism and trustworthiness as strategies for building the kind of reputation that brings rewards in the longer term (Frank, 1988; Milinski, et al., 2001, 2002), so that ultimately altruism increases fitness. Examples here are charitable giving, tipping waiters and generous acts to strangers and others from whom reciprocation is unlikely. For a reputation to be enhanced by such acts they must be observed by others (and result in 'indirect reciprocity' by third parties), which limits reputation building as a full explanation. Related to this proposal concerning reputation it has been suggested that cooperation could constitute an honest signal of an individual's quality as a mate or coalition partner, and thus results in future rewarding alliances (Roberts, 1998; Gintis et al., 2001). For both reputation building and honest signaling such one-sided, one-off, acts of giving would not seem to count as teamwork.

Where human teamwork can emerge successfully in a context that goes beyond simple reciprocity is in real life common pool resource groups, such as fisheries and grazing commons (Ostrom 1990), and in small group simulations of these same organizations (Ostrom, et al., 1992), but these have not received direct evolutionary analysis. Trust and a

belief in fairness (e.g., Fehr & Rockenbach 2003) are important determinants of success.

1.2 The origins of human teamwork

Having examined how teamwork might evolve as a result of general selective processes applying to many animal groups we turn to the evolutionary origins of human teamwork. Humans have a particularly rich cooperative life (Fehr and Fischbacher, 2003), although before accepting ourselves as superior as a consequence we should consider whether our cooperative sophistication is any greater than, say, our refinement for violence or sexual activity when compared to other species. That aside, where should we look to understand the evolutionary origins of our own brand of teamwork, apart from the general evolutionary processes already described?

Important influences on the evolution of human teamwork are likely to have been the small social groups in which early humans lived, and our capacity for forming long-term relationships. Caporeal et al. (1989, p. 683), for example, propose that behaviour, defined here as teamwork: ‘evolved under selection pressures on small groups for developing and maintaining group membership and for predicting and controlling the behavior of other group members’. They and many other psychologists and economists have found, in experimental games, that individual decisions are less selfish, more fair, and closer to teamwork outcomes than predicted by rational egoism (e.g., Colman, 2003).

Frank (1988) argues that the rewards available from trusting, long-term, loving or commercial relationships have favoured the evolution of the kind of non-verbal commitment signals that are difficult to fake and that allow us to assess character and reliably predict, after

a short interaction, whether another person will cooperate or defect in an experimental game (Frank et al., 1993). It is these cooperators, Frank argues, who are more likely to be selected as long-term partners.

1.3 From teamwork to team reasoning

We now consider the contribution that evolutionary thinking might make to understanding the kinds of reasoning that result in human teamwork (Lazarus, 2003). Understanding the modes of reasoning employed is an interesting and unsolved issue precisely because they do not result in rationally selfish behaviour (Colman, 2003).

The above analysis of selection processes and evolutionary origins suggests the existence of the following biases in reasoning, or emotional influence, that would favour team thinking (together with their selective source):

- Consideration for welfare of the group as a whole (group selection); this is the most problematic proposal due to the uncertainties connected with group selection. Caporeal et al.'s (1989) scenario described above seems to employ group selection.
- Consideration for kin (kin selection).
- Concern for reciprocity, extending to concerns with trust, fairness, punishment, forgiveness and reconciliation (reciprocal altruism).
- Concern for reputation.
- Impressing potential partners; correlated with personal quality.
- Concern for commitment.

This list provides some testable predictions of the reasoning biases involved in team thinking.

Decision making in real-life economic team contexts may reflect evolved predispositions, and may tap motivations at work also in the economically elementary scenarios of the psychological laboratory. For example, studies of the way in which communities govern their own use of common pool resources (CPRs), such as grazing pastures (Ostrom 1990), may be revealing evolved influences on cooperative decision making, and even evolved modes of reasoning, since the hunting and gathering activities of early humans also have CPR properties. Successful CPR decisions are characterized by: a clear in-group/out-group distinction; resource provision in proportion to need, and sharing of costs in proportion to ability to pay; and graded punishments for the greedy (Ostrom 1990). Whether these characteristics apply to decision making in other kinds of cooperative relationship is open to evolutionary psychological and empirical analysis.

Finally, it falls within an evolutionary psychological view to accept that human teamwork results from the maladaptive application of reasoning in a novel environment that was adaptive in the ‘environment of evolutionary adaptedness’ of early humans.

2. Cooperation and environmental risk

In the remainder of the chapter we consider a single issue – risk – that has important impacts on cooperative behaviour and therefore on teamwork. Risk comes in two forms: adversity and uncertainty (Daly and Wilson, 2002). We can describe the environment as being more risky

if something about it – such as resources, physical structure, climate, competitors or predators - is more *adverse* in the sense of decreasing Darwinian fitness or some currency of human value. However, risk can also refer to the *uncertainty* or unpredictability of some phenomenon (Gigerenzer, 2002). Elsewhere we show that there can be a positive relationship between these two aspects of risk (Andras, Lazarus and Roberts, in prep.).

In this section we review natural examples of cooperation and altruism between various organisms that demonstrate what seems to be a widespread tendency for pro-social behaviour to be enhanced under conditions of increased risk. In most cases risk is expressed as adversity but there are also examples of uncertainty effects. In the following section we present a model that explores one way in which these effects might be explained. We conclude the chapter by drawing conclusions about the role of environmental risk in the emergence of human cooperation and teamwork.

2.1 Bacterial colonies

In response to certain environmental stressors bacteria form various multi-cellular structures such as biofilms and mushroom bodies (Greenberg, 2003) that develop as a result of cellular communication by, for example, the secretion or membrane expression of signalling molecules. For example, in the presence of antibiotics the bacterium *Pseudomonas aeruginosa* is likely to form a biofilm structure that boosts its antibiotic resistance (Drenkard and Ausubel, 2002) - presumably to the mutual benefit of all individuals - and is responsible for the development of antibiotic resistant lung infection in hospitalized patients (O'Toole, 2002). Biofilm formation can be prevented by triggering twitching behaviour, in which daughter cells move rapidly away from each other after cell division (Singh et al., 2002). The

twitching behaviour can be switched on by environmental factors, like the presence of lactoferrin, a common constituent of human external secretions (Singh et al., 2002).

In the case of the amoeba *Dictyostelium discoideum* starvation results in the formation of a slug with the participation of tens of thousands of cells (Strassmann et al., 2000). Around 20% of the slug formation altruistically develops into a non-viable stalk, supporting the rest of the cell colony. If starved cells are mixed with non-starved ones, the non-starved cells are likely to cheat during colony formation by participating less in the stalk component of the slug (Strassmann et al., 2000).

Unicellular organisms are thus able to form multi-cellular structures in the presence of environmental stress factors (e.g., antibiotics, lack of nutrients) by communicating about the nature of the environment. Such multi-cellular biofilms, mushroom bodies and slugs are cooperative structures, enhancing fitness in the presence of environmental stressors.

2.2 Cooperation among plants

A recent analysis of plant communities living at alpine and sub-alpine ranges in many parts of the world shows that competition for resources is more characteristic of sub-alpine plant communities, while cooperation is more typical in alpine habitats (Callaway et al., 2002). In alpine conditions the plants live under greater environmental stress, and thus risk. Alpine plants produce significantly more biomass if they live close to other plants, receiving mutual protection from the wind, for example. Conversely, sub-alpine plants produce less biomass if they grow together with other plants, suffering relatively more from competitive interactions and benefiting less from cooperation.

2.3 Social feeding of worms

The roundworm *Caenorhabditis elegans* feeds on bacteria. When meeting lawns of bacteria the worms may slow down to increase their bacterial intake. Alternatively they may continue moving and occupy a position at the boundary of the bacterial lawn, letting other worms also feed. The behaviour of the worms depends on two neurons which play an important role in sensing nociceptive (tissue damage) signals (Sokolowski, 2002). If the worms live in a crowded environment the two neurons trigger the social response in the worms (de Bono et al., 2002) leading to the sharing of resources. If the neurons are destroyed the worm continues its solitary feeding behaviour, irrespective of crowding. Thus *C. elegans* worms form cooperative social structures in response to environmental stress (crowding). The control of the social behaviour by critical nociceptive neurons indicates that the perception of environmental stress is crucial for the triggering of social behaviour.

2.4 Cooperation in fish schools

Small fish subject to predation (e.g., guppies, *Poecilia reticulata*) often live in schools. The size of fish schools shows strong dependence on the risk of predation. In environments characterized by a high number of predatory fish the size of the fish schools is large, while in environments with few predators the school sizes are significantly smaller (Farr, 1975; Seghers, 1974).

The analysis of sexual behaviour of guppies shows similar results (Evans and Magurran, 1999). In the presence of many predators male guppies perform relatively few courtship

actions and produce a small amount of sperm. In environments with few predators the males are more likely to display courtship behaviour and produce significantly more sperm. This shows that males compete less in high predation risk environments.

2.5 Mole rat societies

The African mole-rats (*Bathyergidae*) show a variety of social organisations. Some species of the family live a mainly solitary life style, while others live as eusocial colonies (Spinks et al., 2000). Colonies of the common mole-rat (*Cryptomys hottentotus hottentotus*) are larger in arid areas and smaller in mesic (moderately moist) areas. The movement of individual animals between colonies is also less frequent in arid than in mesic areas.

Larger and less variable communities provide the opportunity for the sharing of resources (e.g., food) with more individuals and for the existence of repeated meetings with known individuals, a facilitating factor for the development of cooperative relationships. Arid areas present stronger ecological constraints and greater foraging risks than mesic areas. This indicates that greater environmental risk results in more cooperative behaviour in these communities.

2.6 Human cooperation

Early humans lived in hunter-gatherer communities, in which typically men hunted game and women gathered seeds and other plant parts. Investigation of an existing hunter-gatherer society shows that during the dry season hunter-gatherer communities are larger and fewer in number in a given area, and smaller in size and more numerous in the same area in the wet

season (Hawkes et al., 2001). This indicates that more adverse conditions trigger the formation of larger groups.

Evidence also shows that men share hunted game after successful hunts (Kaplan and Hill, 1985; Hawkes et al., 2001). Considering the small likelihood of successfully capturing big game, by sharing the meat it is guaranteed that the members of the community have the opportunity to eat regularly a small amount of highly nutritious food. In this context the cooperative sharing of meat reduces the risk of lacking highly nutritious food, a risk imposed by the environment on the community.

Anecdotal reports of civil wars, front lines in wars and natural calamities (e.g., earthquakes, flooding, hurricanes) show that cooperation and group cohesiveness among humans increases very much in such situations. For example, in civil war situations local populations supportive of the military or paramilitary forces are willing voluntarily to collect food and clothing for the fighters. Also a supportive civil population is ready to take the risk of hiding friendly fighters and even to organize their escape. This anecdotal evidence is supported by research both at the macrosocial level of international and interethnic relations and at the microsocial level of small interactive groups (reviewed by Hogg, 1992) and suggests that human cooperation increases under conditions of external threat and intergroup conflict.

Kameda et al. (2002) investigated human cooperative behaviour using lottery games. They found that when gains were more uncertain the willingness for cooperative sharing and the expectation of cooperative sharing was significantly greater than when the gains were less uncertain. A real world example of human cooperation responding positively to

environmental uncertainty is the greater endurance of common pool resource groups, such as fisheries and grazing commons, where environmental uncertainty is greater (Ostrom, 1990).

2.7 The role of communication

In the above examples the organisms concerned communicate with each other and this communication provides the foundation for the cooperative and altruistic behaviour. For example, in the case of bacteria the individuals communicate by having appropriate proteins incorporated into their outer membrane, and in the case of humans individuals communicate using language and non-verbal communication. Such communications reflect environmental resources and risk factors: for example, the presence of antibiotics triggers protein communications between bacteria, and the opportunity to hunt down big game, or the presence of a predator, triggers communication between hunter-gatherer humans.

3. Environmental risk and cooperation: a model

A recent simulation model of the evolution of cooperative behaviour between selfish agents shows that the higher the perceived environmental uncertainty the higher is the likelihood of cooperation between the selfish agents (Andras et al., 2003). This model simulated the evolution of societies of simple agents playing a cooperation/cheating game to generate resources that were spent on living costs. The results show that when the process generating the new resources has a larger variance (i.e., environmental uncertainty is higher) the stable evolved likelihood of cooperation between two agents is also higher.

This modeling work shows that an important factor determining collaboration between selfish individuals is the perceived or subjective uncertainty of the environment. Other modeling results of ours show that more adverse environments are perceived to be more uncertain (Andras, Lazarus and Roberts, in prep.). Together these results indicate that one way to increase cooperation in communities of individuals is for them to perceive their environment to be more adverse or more uncertain.

This work examined directly the impact of environmental uncertainty (in the form of resource variance) on the evolutionary stability of cooperation, using evolutionary simulation methods and a particular model of cooperation. In the models described here we take a different approach. We start by assuming that, compared to non-cooperation, mutual cooperation brings greater (or in one case, and in the limit, equal) benefits to the individual. Our results can then be applied to any model or empirically known situation, where this is the case.

We then ask how the advantage of behaving cooperatively, as opposed to non-cooperatively, varies with risk, where risk is defined first as adversity and then as uncertainty. The major assumption of the models is that as the quality of the environment improves the benefit to the individual increases with a diminishing returns function. The models are conceived in evolutionary terms so that benefits and costs are considered to be influences on Darwinian fitness. Equivalently, however, the models could describe a human subjective view of quality and benefit (utility) and thus predict cooperation as a function of rational decision-making (whether or not one wished to explain rationality in evolutionary terms).

Let:

q = some dimension of environmental quality (e.g. resource, predation risk, temperature)

$B(q)$ = benefit (= fitness increase) to individual as a function of q .

C = cooperate

nC = not cooperate

$dB = B(q, C) - B(q, nC)$ = the increment in fitness due to cooperation as opposed to non-cooperation, as a function of q .

3.1 Model 1

Assume that:

1. $B(q)$ is a diminishing returns function.
2. $dB = B(q, C) - B(q, nC) > 0$ for all q ; i.e. conditions (derivable from various models, for example, or empirically demonstrated) for which cooperation always pays.
3. $B(q, C)$ and $B(q, nC)$ converge as q increases from its lowest value.

The model is shown graphically in Figure 1. The first assumption above is biologically very plausible, and is assumed in many behavioural ecological models. It follows the assumption that fitness will increase with environmental features - such as resources, suitability of the abiotic environment or freedom from predation - smoothly and asymptotically to some maximum value. The second assumption is fundamental to the model. The third assumption follows if non-cooperators can achieve the same asymptotic fitness as the cooperators at some level of q . We return to the second and third assumptions in Model 2.

FIGURE 1 ABOUT HERE

First, consider risk as adversity. Figure 1 shows directly that as adversity increases (i.e., as the quality of environment declines) the marginal benefit of cooperation over non-cooperation (dB) increases. For existing models of cooperation it will generally follow that the proportion of cooperators in the population at stability will also increase with adversity (if cooperation is not already fixed in the population) or that the individual's level of cooperative investment will increase (e.g., Roberts and Sherratt, 1998). We ignore any further dynamics between the level of adversity and stability conditions for cooperation.

Second, consider risk as uncertainty, where uncertainty is measured in terms of the variance of q . The model assumptions mean that if $f(q)$ is the C curve (i.e., $f(q)=B(q,C)$) and $g(q)$ is the nC curve (i.e., $g(q)=B(q,nC)$) then:

$$4. f(q) > g(q)$$

$$5. 0 < f'(q) < g'(q)$$

$$6. 0 > f''(q) > g''(q)$$

In other words, the two curves should be diminishing return functions such that their difference is acceleratingly decreasing.

We now show that if $p(q)$ is the probability distribution of q , then in the high variance case, where the range of existing environmental qualities is greater, $f(q)-g(q)=dB$ has a larger mean value over the interval of interest than the same mean value for the low variance case. In other words, the benefit of cooperation increases with variance (uncertainty).

We denote by m the mid-point of the interval, then the two end points can be written as $m-v$ and $m+v$, where $2v$ is the width of the distribution of environmental quality. We wish to show that if $r(v)$ is the mean value of $f(q)-g(q)$ over $[m-v, m+v]$ then the $r(v)$ is an increasing function. This means that if v is larger the mean value is larger. The $r(v)$ being increasing is equivalent to $r'(v) > 0$.

$$a(q) = f(q) - g(q)$$

$$r(v) = \frac{\int_{m-v}^{m+v} a(q) \cdot p(q) dq}{\int_{m-v}^{m+v} p(q) dq}$$

$$r'(v) = (p(m+v) + p(m-v)) \left(\frac{a(m+v) \cdot p(m+v) + a(m-v) \cdot p(m-v)}{p(m+v) + p(m-v)} - \frac{\int_{m-v}^{m+v} a(q) \cdot p(q) dq}{\int_{m-v}^{m+v} p(q) dq} \right)$$

If $a''(q) = f''(q) - g''(q) > 0$, i.e., $a(q)$ is convex we get

$\exists \mu \in [m-v, m+v]$ such that

if $AP'(q) = a(q) \cdot p(q)$ and $P'(q) = p(q)$ then

$$\frac{\int_{m-v}^{m+v} a(q) \cdot p(q) dq}{\int_{m-v}^{m+v} p(q) dq} = \frac{AP(m+v) - AP(m-v)}{P(m+v) - P(m-v)} = \frac{AP'(\mu)}{P'(\mu)} = \frac{a(\mu) \cdot p(\mu)}{p(\mu)} = a(\mu)$$

$$a''(q) > 0 \Rightarrow \lambda \cdot a(m+v) + (1-\lambda) \cdot a(m-v) > a(\mu), \forall \mu \in [m-v, m+v], \lambda \in [0,1] \Rightarrow$$

$$\frac{p(m+v)}{p(m+v) + p(m-v)} a(m+v) + \frac{p(m-v)}{p(m+v) + p(m-v)} a(m-v) > a(\mu), \forall \mu \in [m-v, m+v]$$

$$\Rightarrow r'(v) > 0$$

This shows that indeed, for any probability distribution over the q values, if the difference function between C and nC is convex (assumptions 4-6 above) then if v is larger the average value of the difference between C and nC is larger.

As argued for adversity, for existing models of cooperation it will generally follow that the proportion of cooperators in the population at stability will also increase with uncertainty (if cooperation is not already fixed) or that the individual's level of cooperative investment will increase. Again, we ignore any further dynamics between the level of uncertainty and stability conditions for cooperation.

3.2 Model 2

Abandoning the third assumption of Model 1, suppose instead that the benefit functions of cooperators and non-cooperators at first *diverge* as q increases, before converging (see Figure 2). In the limit assume that assumption two is also violated, so that at the lowest environmental quality cooperators and non-cooperators have *equal* and minimal fitness. Then, in the poor quality zone (considered alone) to the left of the point q^* , at which cooperator and non-cooperator benefits maximally diverge (see Figure 2), the conclusions of the model for the influence of adversity on dB are reversed. If the population exists across environmental qualities both less than and greater than q^* , cooperation is then most beneficial at the intermediate environmental quality q^* , rather than increasing monotonically with adversity.

FIGURE 2 ABOUT HERE

The conditions under which the benefit of cooperation (dB) increases with uncertainty are not simple to specify. This is first because the results for Model 1 apply here in reverse for $q < q^*$, and second because the relationship between dB and uncertainty depends on how the population is distributed across environments above and below q^* .

Although in general terms one cannot readily choose between the two models, if our examples in section 2 are representative it would seem that Model 1 is the more common representation of reality. Accepting this assumption, our modeling here would suggest that the common facilitative effect of adversity and uncertainty on cooperation may, at the functional level, be due in part simply to a diminishing returns function of environmental influences on fitness. Selection is then expected to act on proximate mechanisms so that cooperation is enhanced in conditions of greater adversity and uncertainty.

This result complements the predictions of our other models (Andras et al., 2003; Andras, Lazarus and Roberts, in prep.), which are not directly concerned with the shape of the functional relationship between environmental quality and fitness benefit.

4. Risk and teamwork

Whether cooperation in human societies can flourish successfully without sanctions imposed from outside the group is an old question but there is reason for optimism, from both real life, common pool resource groups (Ostrom 1990) and experimental games (Ostrom, et al., 1992). To the extent that the threat of sanctions decreases the perceived uncertainty of the environment – a predictable sanction reducing uncertainty more than the unpredictable

possibility of an equivalently costly reprisal - one message of this chapter is that such predictability may also decrease the willingness of individuals to cooperate. At the same time, where the spontaneous level of cooperation is low, imposing rules and enforcing cooperative behaviour may increase cooperative acts in the short term, but is less likely to lead to the longer-term establishment of cooperative motivation and team thinking.

It is important to understand the basis for the voluntary adherence to behaviour that can lead to the formation of teams. Empirical evidence (Fukuyama, 1996) indicates that trust between humans plays an essential role in the emergence of voluntary cooperation. In the context of our discussion we can view trust as the expectation that rules of behaviour will be followed by individuals within the community. If such expectations are high, and they are reinforced by practice, it is likely that the rules will be closely adhered to, and the formation of cooperative groups, including teams, is likely. If the adherence to rules is imposed by sanctions their implicit meaning is that such adherence is not expected with confidence. This is likely to reduce trust between individuals and with it the likelihood of cooperation and team formation.

Note

Sections 2 and 4 of the chapter were written largely by PA. Section 1 was written by JL, who is also responsible for the model in section 3 (except for the variance proofs, which are the work of PA).

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Figure legends

Figure 1. Model 1. Benefit (B) to cooperators (C) and non-cooperators (nC) as a function of environmental quality (q). The two functions converge from the lowest value of q .

Figure 2. Model 2. Benefit (B) to cooperators (C) and non-cooperators (nC) as a function of environmental quality (q). The two functions at first diverge and then converge from the lowest value of q . The two functions may or may not extend (dotted lines) to the lowest value of q (where they meet).