Review

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Collective action problem in heterogeneous groups

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I review the theoretical and experimental literature on the collective action problem in groups whose members differ in various characteristics affecting individual costs, benefits and preferences in collective actions. I focus on evolutionary models that predict how individual efforts and fitnesses, group efforts and the amount of produced collective goods depend on the group's size and heterogeneity, as well as on the benefit and cost functions and parameters. I consider collective actions that aim to overcome the challenges from nature or win competition with neighbouring groups of co-specifics. I show that the largest contributors towards production of collective goods will typically be group members with the highest stake in it or for whom the effort is least costly, or those who have the largest capability or initial endowment. Under some conditions, such group members end up with smaller net pay-offs than the rest of the group. That is, they effectively behave as altruists. With weak nonlinearity in benefit and cost functions, the group effort typically decreases with group size and increases with within-group heterogeneity. With strong nonlinearity in benefit and cost functions, these patterns are reversed. I discuss the implications of theoretical results for animal behaviour, human origins and psychology.

1. Background

Group living, which is widespread in animals, has both fitness benefits and costs, thus group-living species have developed various adaptations for dealing with their social environments [1–3]. Group-living animals necessarily have to coordinate many of their activities such as eating, sleeping or moving. In some species, individuals also actively collaborate with their group-mates, for example in territorial defence, hunting or breeding. In particular, our ancestors were involved in collective large-game hunting and between-group conflicts over territories, mating and other resources. Because of the economy of scale, within-group collaboration can be very profitable, especially for humans. In modern humans, collaboration happens at all levels of human society.

Group-living implies interdependence, collective actions, shared benefits and shared costs. Interdependence and shared interests, however, do not eliminate conflicts of interests of group-mates. Even when cooperation benefits all partners, they will probably end up not cooperating because they can see the advantages of free-riding or fear the dangers of being exploited by others who may choose to free-ride. As a consequence, defection becomes a dominant strategy in the Prisoner's Dilemma [4], individuals withdraw their efforts in production of a collective good [5], or members of a commune fail to exercise self-restraint in exploitation of a communal resource, destroying it as a result [6]. Adam Smith's powerful metaphor of the 'invisible hand' emphasizes unintended social benefits that can result from individuals' pursuit of personal interests. However, in the words of Russell Hardin, when engaged in collective actions '...all too often we are less helped by the benevolent invisible hand than we are injured by the malevolent back of that hand; that is, in seeking private interests, we fail to secure greater collective interests' [7, p. 6].

How various social dilemmas, i.e. conflicts between individual and collective interests, can be resolved has been a subject of intense observational, experimental and theoretical work across a variety of scientific disciplines including economics,

evolutionary biology, anthropology and psychology. Here, I will be concerned with one particular set of social dilemmas—the collective action problem (CAP) within the context of collective goods production [5,7]. This is a situation when group members can make an individually costly effort towards achieving some group-beneficial goals (e.g. hunting a large game or defending the territory) but because individuals potentially can receive the benefits without having contributed to their production, they have an incentive to reduce their effort or withdraw it completely. If enough individuals fail to contribute, the collective benefit is not produced and everybody suffers.

Systematic theoretical studies of collective action started 50 years ago with a publication of Mancur Olson's book *The Logic of Collective Action* in 1965 [5]. Olson's book offered three main insights/hypotheses:

— the group-size paradox: collective goods provisioning decreases with the group size;
— exploitation of the great by the small: the largest beneficiary of the collective good bears a disproportionately large burden of its production; and
— selective incentives (i.e. reward and/or punishment) and institutional designs can help large groups overcome the CAP.

Olson's *Logic* has had a tremendous impact on a diversity of social sciences (see [7–12] for summaries of more recent work). However, it appears to be somewhat ignored in evolutionary biology. (According to the Web of Science database, the book has been cited more than 7500 times. Of these, less than 1% is in the evolutionary biology literature.) Nevertheless, the ideas from economics have percolated into theoretical evolutionary biology and have been developed both further and independently into an impressive array of new directions. By now, it is well appreciated that increasing the group size typically makes cooperation more difficult (Olson's first main insight) and that punishment is an efficient way to promote cooperation (a part of Olson's third main insight). However, the effects of within-group heterogeneity (Olson's second main insight) are much less understood.

(a) Review goals

My general goal here is to review the theoretical work on the CAP that might be particularly interesting and relevant for behavioural evolutionary biologists, anthropologists and psychologists. The important role of the CAP in undermining within-group cooperation in between-group territorial conflicts is well recognized by evolutionary primatologists [13–19] as well as by some other behavioural biologists [20–23]. In the anthropological literature, the existence of the CAP in between-group conflicts [24–26] as well as in hunting and other types of collective production [27–29] is also well acknowledged. In particular, the facts that foragers apparently have 'limited needs' and that their work efforts are surprisingly modest have been linked to their culture of sharing, which makes food and other objects public goods [27,30]. Earlier discussions by Hawkes [27] and Nunn & Lewis [15] used simple two-player games to illustrate the CAP. While there is indeed a substantial theoretical literature on dyadic interactions [31], two-player games are not necessarily very informative about multiplayer dynamics. I will be looking at collective actions involving more than two individuals simultaneously in further sections.

An inherent feature of most animal and human groups involved in collective activities is their heterogeneity. Group members may differ in how much they value the collective good, how many resources they have, how much cost they pay per unit of effort and so on. Olson [5] argued that this heterogeneity would often lead to the situations where 'there is a systematic tendency for 'exploitation' of the great by the small' (p. 29). That is, some individuals (e.g. those with the highest stake in the collective good or for whom the effort would be least costly, or those who have the largest initial endowment) would contribute all the effort while the rest of the group-mates will free-ride contributing nothing. (In Olson's terminology, a group with individuals whose benefits from a collective action exceed the associated costs even if they are solely borne by these individuals is a 'privileged group'.) Subsequent theoretical work, mostly in the economics literature, explored this issue in detail (see below). However, as noted earlier, the insights from this work have not been applied much to biological and anthropological problems (although the potential importance of within-group heterogeneity in biological CAPs was recognized by Nunn & Lewis [13,15]). Below I will discuss the relevant theoretical and experimental results in detail.

Even though the amount of work on the CAP published in the economics literature is enormous, there are certain limitations on its applicability to biological questions. While the analysis of economics models typically focuses on Nash equilibria (NE, at which individuals aim to maximize their absolute gain), biological models usually study evolutionarily stable strategies (ESS, at which natural selection maximizes the individuals' relative gain). NE and ESS can lead to rather different predictions [32–34]. Economics models often ignore the question how individuals can identify an appropriate NE, whereas in evolutionary models the question of convergence to an ESS is of primary importance. Moreover, many NE identified by game theory methods are evolutionarily irrelevant [35, ch. 5]. Economics models also typically ignore many evolutionary factors, such as group selection, genetic relatedness, spatial structure and migration, which all can significantly affect evolved social behaviour. These considerations imply that additional studies of biologically inspired models are often needed.

My main focus will be on models relevant for evolutionary biology within a broad cross-specific perspective. I will pay special attention to the evolution of social instincts, that is, genetically based propensities that govern the behaviour of individuals in social interactions. As first argued by Darwin [36], social instincts have evolved by natural and sexual selection. In modern perspective, these instinctive social behaviours are plastic, resulting from the interaction of the genotype with the social environment [37]. Within this framework, individual behavioural strategies change by random mutation (and recombination). However, some of the conclusions emerging from using this approach may also be valid for other strategy revision protocols used in evolutionary game theory, such as learning or myopic optimization [38].

(b) Alternative approaches

There are a number of alternative theoretical approaches for studying collective actions which will not be covered in this study. I briefly discuss them here. I will be concentrating on

models describing the CAP in situations when group members pay individual costs to share group benefits. For discussions of models describing the 'tragedy of the commons' [6], when group members receive individual benefits but share costs, see e.g. [39–43]; some relevant empirical evidence on the effects of heterogeneity is reviewed in [44,45]. I will consider models focusing on NE and ESS; for related work using other equilibrium concepts, e.g. those that include errors in decision-making or learning, see [38,46–50]. I will focus on models explicitly allowing for a single type of individual effort such as voluntarily contributing to production of a collective good. More complex models that allow for multiple types of individual efforts simultaneously (e.g. contributing to production and punishing defectors [51–54]) are outside of the scope of my review. I will assume that groups are formed exogenously. For recent reviews on endogenous coalition formation in the theoretical and biological literatures, see [55] and [56], respectively. In the models to be discussed, exact spatial arrangement of groups is largely irrelevant. Public goods games (PGG) in spatially structured populations have been recently reviewed in Perc et al. [57].

In models to be discussed below, individuals will make their decisions about the actions to take simultaneously. There is, however, an alternative approach to modelling collective actions which explicitly assumes that individuals make decisions about their efforts sequentially [9,58–64]. In this case, the group behaviour may exhibit a threshold effect: once there is a critical mass of contributors, everybody else also starts contributing. The 'first movers' can be individuals with the highest interest in the collective good. In some of these models, group members are basing their decisions not (only) on the benefit/cost considerations but rather on a simple behavioural rule: contribute and/or participate if a certain number or proportion of other individuals are already participating ('bandwagon effect') [58]. These models have been used for describing social mobilization, formation and diffusion of social movements, spread of social unrest and contagion through social networks while allowing for stochasticity in decision-making, effects of learning beneficial strategies and a possibility that some individuals (e.g. 'organizers') promote cooperative behaviour of others [59,61–63,65,66]. This work is outside of the scope of my review.

(c) Review structure

The literature on multiplayer evolutionary games and collective action is quite diverse [67,68]. In the case of dyadic interactions with just two discrete strategies, all possible games can be classified in an unambiguous way. With continuous strategies and/or with multiple players such a classification becomes much more difficult [69,70]. Rather than trying to use such a classification, I will structure my discussion around two general types of social interactions which I will call 'us versus nature' games and 'us versus them' games [71]. These games correspond to two general types of collective actions in which our ancestors were almost certainly engaged. The first type includes group activities such as defence from predators, some types of hunting or food collection, use of fire, etc. The success of a particular group in these activities largely does not depend on the actions of neighbouring groups. The second type includes direct conflicts and/or competition with other groups over territory and other resources including mating. The success of a particular group

in an 'us versus them' game definitely depends on the actions of other neighbouring groups. The outcomes of both types of collective actions strongly affect individual reproduction as well as group survival. 'Us versus nature' games comprise typical collective action models with linear or nonlinear pay-off functions [72–75]. 'Us versus them' games correspond to models of between-group contests in economics theory [76].

Below I start by outlining a general approach for modelling collective actions in evolutionary biology. Then I consider 'us versus nature' and 'us versus them' games separately. For each type of games, I summarize results on homogeneous groups before discussing the behaviour of models describing heterogeneous groups. I will illustrate analytical results using a series of numerical examples based on a simple model linking the two types of games. I will also review relevant experimental economics research.

2. Mathematical models and their predictions

Let us consider a population of individuals subdivided into G groups each of size n individuals. Assume that individual i in group j makes an effort x_{ij} towards the group's success in a collective action. Effort x_{ij} can be treated as a binary variable (e.g. taking only two values: 0 and 1) or a non-negative continuous variable. Individual efforts of group members are aggregated into a group effort X_j. Following the economics literature, I will call the function converting individual efforts $x_{1j}, \ldots, x_{nj}$ into group effort X_j the *impact function*. The most common impact function in the literature is linear:

$$X_j = \sum_i x_{ij}. \tag{2.1a}$$

Two other examples are the 'weakest-link' when X_j is equal to the minimum of x_{ij} values in the group and the 'best-shot' when X_j is equal to the maximum of x_{ij} values. In some models, individuals differ in their strengths and/or capabilities s_i and the impact function is defined as $X_j = \sum_i s_i x_{ij}$, so that individuals with largest s_i values have the largest effect on X_j [77,78]. Some work uses the 'constant elasticity of substitution' (CES) impact function [79,80]

$$X_j = \left(\sum_i x_{ij}^{1/\alpha} \right)^{\alpha}, \tag{2.1b}$$

which will play an important role in discussions below. Here α is a non-negative parameter which can be interpreted as a measure of within-group synergicity or collaborative ability [71]. If collaborative ability α is very small ($\alpha \ll 1$), the group is only as efficient as its member with the largest effort ($X_j \approx \max_i(x_{ij})$). Increasing collaborative ability α while keeping individual efforts the same increases the group effort X_j. If all group members make an equal effort x, then $X_j = n^{\alpha} x$. The latter function is related to the Lanchester–Osipov model used in military research [81,82] and also in evolutionary biology [83,84].

I will specify the individual pay-off as

$$f_{ij} = f_{ij,0} + b_{ij} P_j - c_{ij} x_{ij}. \tag{2.2}$$

Here, $f_{ij,0}$ is a baseline pay-off, b_{ij} the value of group j's success to individual i and c_{ij} the cost parameter for this individual. Function P_j is a non-decreasing function of X_j and, potentially, of other groups' efforts; it gives the normalized value of the resource produced by group j as a result of

collective effort; we normalize P_j relative to a maximum possible reward size ($0 \leq P_j \leq 1$) so that it measures the success of collective action (actual or expected). Using economics terminology, I will call this function the *production function* in us versus nature games and *contest success function* in us versus them games. In some models, one assumes that individual i in group j gets share v_{ij} of the total prize B_j, so that $b_{ij} = v_{ij}B_j$. If group members share the reward equally, $v_{ij} = 1/n$. In equation (2.2), the benefit and cost terms contribute additively to individual pay-off. More complex functions can also be used (for example, multiplicative [39,85]). Note also that equation (2.2) assumes that individual cost, $c_{ij}x_{ij}$, is linear in individual effort x_{ij} but nonlinear functions are also used often (see below).

Individual pay-offs define individual fitness (i.e. reproductive success) w_{ij}. There are different ways to specify w_{ij}. For example, when individuals compete over the whole population

$$w_{ij} = \frac{f_{ij}}{\bar{f}}, \qquad (2.3a)$$

where $\bar{f}$ is the average pay-off in the whole population. Assuming that group j contributes a share S_j of offspring to the next generation and that individuals compete for reproductive success within the groups, $w_{ij} = S_j(f_{ij}/\bar{f_j})$, where $\bar{f_j}$ is the average pay-off in group j. With high-risk collective actions and between-group competition, group extinction becomes possible. If the probability that group j survives between-group competition and contributes to the next generation is proportional to the degree of success P_j in a collective action and the spots of groups going extinct are repopulated by duplicating surviving groups, then

$$w_{ij} = \frac{P_j}{\bar{P}} \frac{f_{ij}}{\bar{f_j}}, \qquad (2.3b)$$

where $\bar{P}$ is the average of P_j.

These models describe multi-level selection operating at both within- and between-group levels [86]. Group-level selection favours large individual efforts x_{ij} (which would increase the probability/degree of group success P_j), while individual-level selection favours low efforts x_{ij} (which would reduce the individual costs term cx_{ij}) creating an incentive to free-ride. What makes it beneficial to free-ride is that all group members share the benefit of high P_j values at least partially independently of their individual contributions to the group's success. Using fitness function (2.3a) implies that groups are formed randomly each generation. In the case of animal and human groups, this assumption is difficult to justify biologically, but it leads to simpler mathematics and has been used in the majority of theoretical papers on cooperation in evolutionary biology. Fitness function (2.3b) is more appropriate if groups retain their identity from generation to generation as is the case in most biological populations.

(a) Us versus nature games

In us versus nature games, the probability/degree P_j of group j success depends on the group effort X_j but does not depend on the efforts of other groups. Most published modelling work corresponds to fitness function (2.3a) and uses an assumption (implicitly or explicitly) that groups are formed randomly at the beginning of each generation.

(i) Homogeneous groups

First, I discuss the evolutionary dynamics in the case when groups are homogeneous (see [31,68] for recent thorough reviews). In such groups, we can set $f_{ij,0} = 1$, $b_{ij} = b$ and $c_{ij} = c$. In the simplest case of linear impact and production functions, also known as an N-player Prisoner's Dilemma game, $f_i = 1 + (k/n)X - cx_i$, where k is a reward factor (by which the group contribution X is multiplied before the reward is divided between n group members). (Here and below I drop subscript j specifying the group both for simplicity of notation and also because economics models usually focus on a single group while evolutionary biology models usually assume that groups have identical structure). In this model, group members would jointly benefit if they all make a positive effort x as long as $k > c$. However, the logic of the Prisoner's Dilemma prevents this from happening [31] and the groups end up contributing nothing (unless the reward is very high, $k > nc$, so that the pay-off from one's own action, k/n exceeds the cost c).

Although the N-player Prisoner's Dilemma game is the most popular model for studying cooperation in groups, it is by no means the only reasonable model [68]. In the Volunteer's Dilemma model [72], it is assumed that a single volunteer can produce a collective good of value b to everybody (which corresponds to a step production function). Naturally, each group member prefers others to pay the cost of production. In this model, if $b > c$, there is a symmetric mixed equilibrium with the probability of defection being $(c/b)^{1/(n-1)} < 1$. Weesie & Franzen [87] showed that cost sharing among contributors increases the probability of volunteering. Archetti [74] has generalized this model in a number of directions including cases when individual benefit is an S-shaped function of the total number of volunteers and when group members are genetically related. The latter factor increases the probability of volunteering.

The Volunteer's Dilemma is related to the Snowdrift game as well as to the Hawk–Dove and Chicken games [31], in all of which cooperation is a preferable strategy if the opponent does not cooperate. Zheng *et al*. [88] studied an N-person Snowdrift game with cost sharing among contributors. They showed that cooperators can be maintained in the population at a small frequency (approximately $1/n$ with large n). Similar conclusions emerge in a version of an N-person Stag Hunt game in which it pays to contribute to a public good if there is a certain number of other contributors [89]. For generalizations to other types of production functions, finite population size and variable population size, see e.g. [90–93]. All of the above work assumed binary individual efforts, i.e. x_{ij} could be only 0 or 1. If individuals' efforts are continuous and costs and/or benefits are certain nonlinear functions of the efforts, then at a NE group members are predicted to make a certain non-zero effort [94–96]. Doebeli *et al*. [97] studied a continuous multi-player Snowdrift game with quadratic production and cost functions. They showed that under some conditions, the population evolves either to a monomorphic state where everybody contributes a small effort or it evolves, via an evolutionary branching [98], to a dimorphic state where some individuals contribute a large effort while the rest free-ride. Frank [85] studied a model with multiplicative interactions of individual costs and group benefits. In his model, it is beneficial to make an effort if nobody else in the group

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contributes. Frank showed that individuals always make a positive contribution which is inversely proportional to the group size. Allowing for within-group genetic relatedness or an accelerated increase in costs and benefits with efforts increases individual efforts [85].

A general prediction of nonlinear models of homogeneous groups is thus that under some conditions groups will produce collective goods. With discrete strategies, there will be a small proportion of contributors while the rest will free-ride. With continuous strategies, the groups will be represented either by mild cooperators (i.e. individuals making small contributions) or by a mixture of a small number of cooperators making substantial contributions and a large number of defectors. Increasing group size typically decreases within-group cooperation.

(ii) Heterogeneous groups

Within-group heterogeneity can be introduced in a number of different ways. Earlier work (reviewed in [8]) focused on heterogeneity in initial endowment/wealth of group members and used linear impact, production and cost functions. This corresponds to pay-off being written as $f_i = f_{i,0} + (k/n)X - cx_i$, where $f_{i,0}$ is the baseline pay-off (endowment) of individual i. An earlier theoretical study [99] predicted an increase in total public good production as the distribution of endowments becomes more unequal. Andreoni [100] showed that at a NE, the contributors will include only the wealthiest individuals (i.e. individuals with $f_{i,0}$ larger than a certain threshold). In the limit of a very large group size, there will be just a single contributor—the wealthiest group member. These results, which supports Olson's logic, are conditioned on the use of linear functions. In Frank's model [85] with multiplicative interactions of costs and benefits, individuals contribute proportionally to their endowments, whereas the group effort does not depend on the distribution of endowments. Moreover, in his model all individuals have an equal fitness/pay-off at equilibrium, independently of their initial endowment.

A substantial effort has focused on models with heterogeneity in valuation b_i and cost c_i parameters. With some nonlinear production and/or cost functions, all group members are predicted to make a contribution and the group effort does not necessarily increase with within-group inequality/heterogeneity; see [79] and [101] for examples with $n = 2$. McGinty & Milam [102] analysed a case with an arbitrary group size assuming quadratic benefit and cost functions. They predicted that individuals will contribute in proportion to their ratios, b_i/c_i, of valuation to cost parameters. Some recent work analysed an asymmetric version of the Volunteer's Dilemma assuming that individuals differ with respect to how much they value the public good (b_i) and how much cost (c_i) each would pay to produce it. In particular, Diekmann [73] identified a mixed strategy equilibrium at which the probability of defection is proportional to b_i/c_i, so that 'strong' players (i.e. with higher valuation and/or lower cost) will be more likely to defect (see [103]). This solution is counterintuitive in that it directly contradicts Olson's conjecture about the exploitation of the great by the small. He et al. [104] generalized results in [73] for the case of genetically related individuals in a simplified version in which there is one 'strong' player, with benefit and cost

parameters b_s and c_s, and $n-1$ identical 'weak' players, with parameters b_w and c_w, where $b_s/c_s > b_w/c_w$. They showed that genetic relatedness between group-mates increases cooperation. In a follow-up paper, however, He et al. [105] argued that the mixed equilibrium identified by Diekmann [73] is evolutionary unstable. They also showed the existence of two other ESSs. At one ESS, the collective good is produced by the strong player while all $n-1$ weak players defect. At the other ESS, the strong player always defects while weak players defect with a certain probability. He et al. [105] argued that the former equilibrium has a larger domain of attraction and therefore is more relevant biologically.

A general, and intuitive, conclusion of this body of work is that individual efforts increase with individual benefit/cost ratios and endowments. Linear models exhibit a threshold effect so that group members contribute to production only if they are above a certain minimum value in a relevant characteristic. In nonlinear models, all individuals contribute but to a different extent, with some contributions being very low. Group efforts usually increase with within-group inequality but there are exceptions.

(iii) Examples

I will attempt to illustrate and clarify the above diversity of theoretical results using a simple model as a reference point. Besides its simplicity, this model also allows for comparisons between us versus nature games and us versus them games to be discussed below. Specifically, I define the degree of success (production function) for group j by a saturating function

$$P_j = \frac{X_j}{X_j + X_0}, \tag{2.4}$$

[71]. Here, X_0 is a parameter specifying the group effort X_j at which the degree of success is 50%; the larger X_0, the more group effort X_j is needed to secure the success. I will call X_0 the half-success effort. I will assume that within each group individuals have equal baseline pay-offs, $f_{i,0} = 1$, but differ in valuation b_i and cost c_i parameters and that groups have identical distributions of these parameters among their members. Below I will consider how the predicted individual efforts, pay-offs and fertilities, group efforts and degree of success in producing the collective good depend on the group size, within-group heterogeneity, half-success efforts, the shape of impact and cost functions, and benefit and cost parameters. I will present analytical results and will also illustrate them numerically.

In deriving analytical approximations, I used an invasion analysis/adaptive dynamics approximation assuming that within-population genetic variation is very low ([98,106]; see [71,77] for applications of these methods to similar models). Numerical simulations show that theoretical conclusions remain valid at a qualitative level even in the presence of some genetic variation. The derivations are straightforward, so to save space I do not show them here. The equations I do show assume, for simplicity, that the number of groups G is very large.

In analytical approximations, models' behaviour depends on certain individual-specific benefit-to-cost ratios, which I will denote as r_i. To describe the effects of within-group heterogeneity in r_i, it is convenient to use a heterogeneity measure based on the notion of the generalized mean.
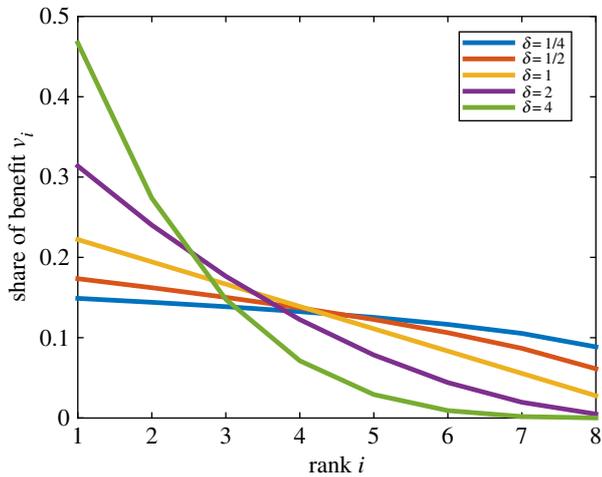
Figure 1. Dependence of the share of benefit v_i going to an individual of rank i on parameter δ in the models used in numerical simulations with $n = 8$. $\sum v_i = 1$. (Online version in colour.)

Given a set of individual characteristics $r_1, \ldots, r_n$ and a parameter q, the generalized mean is $M_q = \left((1/n) \sum_i r_i^{1/q} \right)^q$. In this notation, the arithmetic mean is M_1, the harmonic mean is M_{-1} and so on. Below I will use a normalized version of the generalized mean, $H_q = M_q/M_1$. If all individuals are identical (i.e. $r_i = r$), $H_q = 1$ for all q. As one introduces variation in r_i, H_q decreases if $q > 1$, but increases if $q < 1$. Parameter H_q thus captures the effects of within-group heterogeneity. (It also depends on the group size n, but this dependence is relatively weak).

In numerical simulations, following Gavrilets & Fortunato [77], I posit that individuals have identical cost parameters ($c_i = 1$) but differ in benefit parameters. I specify the latter as $b_i = v_i B$. I assume the total benefit per group B is fixed and that individuals are ranked according to the share v_i of B they receive. This share is set to be proportional to a power function of individual rank i: $v_i \sim (n + 1 - i)^\delta$. Here δ is a parameter measuring the degree of inequality: with $\delta = 0$, all shares are equal to $1/n$ and the groups are egalitarian; with $\delta = 1$, share v_i is a linear function of individual rank i; and with $\delta > 1$, it is a decreasing, concave-up function of rank. In simulations, I used five values of $\delta = 0.25, 0.5, 1, 2$ and 4. The ranks were assigned randomly at the beginning of the generation (e.g. based on strengths). Figure 1 illustrates the effect of δ on shares v_i. For simplicity of interpretation, in my numerical results within-group heterogeneity will be captured by δ rather than by H_q. In implementing the model numerically, I assumed, following earlier work [84,77,107], that individual efforts at each rank were controlled by different loci, so that in each individual only one locus was expressed, corresponding to his rank. Generations were discrete and non-overlapping. I allowed for mutation, free recombination and migration. There were two sexes but only one of them (males) was engaged in collective actions. Group selection was captured by making each group in the new generation to independently descend from a group in the previous generation with probability proportional to P_j. In surviving groups, each female produced two offspring while reproductive success of males was proportional to their pay-off f_{ij}. In models with no group extinction, all offspring dispersed randomly and groups were formed randomly at the beginning of each generation. In models with group extinctions, male offspring stayed in their native groups while females dispersed randomly (as in chimpanzees and probably our ancestors [108]). See Gavrilets & Fortunato [77] for additional details of simulation methods.

Basic model. First, consider the case with no group extinction (i.e. using fitness function (2.3a)) and linear cost and impact functions. It is useful to define parameters $r_i = b_i/(c_i X_0)$ equal to the individual benefit divided by the cost at half-success effort, and use a normalized group effort $Z = X/X_0$. Let individuals be ranked according to r_i and there be no ties. In this model, the population evolves to a state at which within each group only an individual with the highest benefit to cost ratio, r_1, can make an effort while all other group-mates always contribute nothing. Rank-1 individual contributes only if $r_1 > 1$; his effort (and that of the group) then is $Z = \sqrt{r_1} - 1$. Note that the condition $r_1 > 1$ can be rewritten as a requirement for the share of the reward going to the rank-1 individual to be high enough: $v_1 > v_{crit} = c_1 X_0/B$. In this case, the highest valuator benefits from producing the collective good even if acting alone.

Figure 2a illustrates these results for the case of no variation in cost parameters ($c_i = 1$). The figure shows that the group effort increases with increasing within-group inequality and decreasing group size; both these factors increase the share of the highest valuator v_1. With $n = 8$ and low inequality or with $n = 16$, contributions are practically absent except for small 'noise' due to recurrent mutation. Allowing for group extinction (i.e. using fitness function (2.3b)) changes the dynamics considerably (figure 2b). Now, all individuals with valuations above a certain threshold v_{crit} make non-zero contributions which increase linearly with their valuations v_i. The group effort X weakly depends on within-group heterogeneity and group size. Note that in spite of within-group inequality in shares of the reward, variation in fertilities is relatively modest, both with and without group extinction. Note also that under some conditions the highest valuator has lower fertility than his 'subordinate' group-mates (e.g. with group extinction).

Nonlinear costs. Second, assume that the cost term in pay-off equation (2.2) is $-cx_{ij}^\gamma$ with $\gamma > 1$. This implies that costs of small efforts are insignificant but costs rapidly increase as efforts become larger. This model's behaviour is qualitatively different from that with linear costs. Now, the relevant benefit-to-cost ratios are $r_i = b_i/(c_i X_0^2)$ and $R = \sum r_i$. (Note that with no variation in individual costs, i.e. if $c_i = c$, R is equal to the total benefit $B = \sum b_i$ divided by the total cost at half-success rate cX_0^2.) There is no minimum valuation anymore for making a contribution and each individual makes a positive effort proportional to $r_i^{1/(\gamma-1)}$. The normalized group effort Z increases monotonically with the product of the benefit-to-cost ratio R, a power function of group size, $n^{\gamma-2}$, and heterogeneity parameter $H_{\gamma-1}$ computed using r_i values. (Specifically, Z solves the equation $\gamma Z^{\gamma-1}(Z+1)^2 = Rn^{\gamma-2}V_{\gamma-1}$.) With quadratic costs (i.e. if $\gamma = 2$), the group effort depends neither on the group size nor on within-group heterogeneity, and individual contributions are linearly proportional to r_i. With $1 < \gamma < 2$, the group effort decreases with group size n and increases with variation in r_i. With, $\gamma > 2$, the situation is reversed: the group effort increases with group size n and decreases with variation in r_i.

Figure 3a,b illustrates these results for the case of no variation in cost parameters ($c_i = 1$). Allowing for group extinction (i.e. using fitness function (2.3b)) increases individual efforts (figure 3c,d). The effects of within-group inequality greatly decrease, while those of the group size diminish for $\gamma = 1.5$, but are augmented for $\gamma = 2.5$.
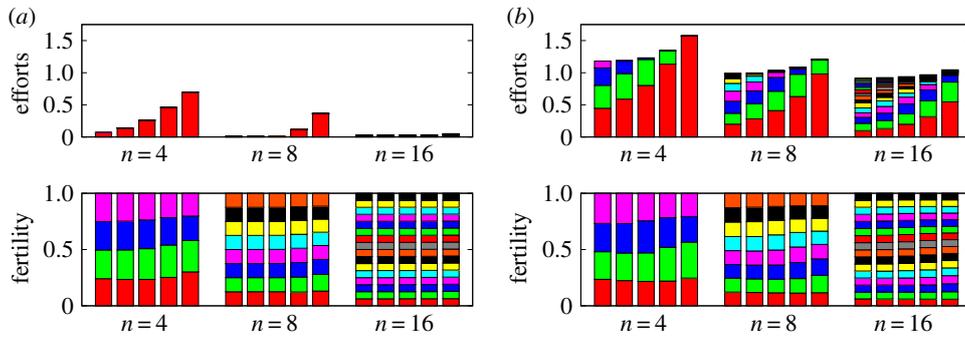
Figure 2. Collective action in the 'us versus nature' game with production function (2.4) without (*a*) and with (*b*) group extinction. Additive impact and cost functions. Summary results over all runs for one set of parameters, with $B = 4$, $X_0 = 1$, $c = 1$, $G = 1000$. For each run, the values are averages over individuals of rank i in all groups in the population. Colours show the relevant amounts for individuals of different ranks, from the rank-1 individual at the bottom (red) to the rank-n individual at the top. Each set of bars corresponds to a specific value of group size n. Each bar within a set corresponds to a specific value of within-group inequality δ, from the smallest on the left ($\delta = 0.25$; low inequality) to the largest on the right ($\delta = 4$; high inequality). Top half of graphs: individual efforts x_i; the total height of each bar gives the group effort. Bottom half of graphs: fertilities, i.e. individual shares of reproduction ($f_i / \sum f_j$). (Online version in colour.)
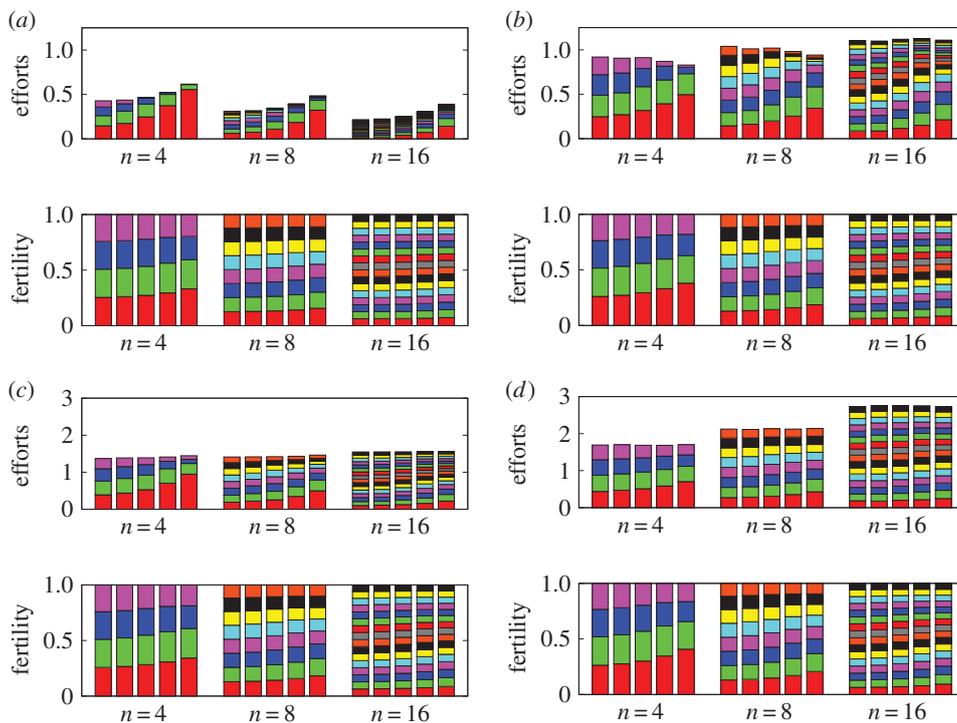

Figure 3. Effects of nonlinear costs in the 'us versus nature' game. First column (*a,c*): $\gamma = 1.5$, second column (*b,d*): $\gamma = 2.5$. (*a,b*) No group extinction, (*c,d*) with group extinction. (Online version in colour.)

Synergicity. Third, instead of an additive impact function let us use the CES function (2.1*b*) with collaborative ability α. The behaviour of this model depends on the benefit-to-cost parameters $r_i = b_i/(c_i X_0)$ and $R = \sum r_i$, a power function of group size $n^{\alpha-2}$ and heterogeneity parameter $H_{\alpha-1}$ computed using the corresponding r_i values. If $Rn^{\alpha-2}H_{\alpha-1} < 1$, the groups make no effort. Otherwise individual contributions are proportional to $r_i^{\alpha/(\alpha-1)}$ and the normalized group effort $Z = \sqrt{Rn^{\alpha-2}H_{\alpha-1}} - 1$. In a special case of $\alpha = 2$, the group effort does not depend on the group's size or heterogeneity, and individual contributions are proportional to r_i^2. With $1 < \alpha < 2$, the group effort decreases with group size n and increases with variation in valuations v_i. With, $\alpha > 2$, the situation is reversed: the group effort increases with group size n and decreases with variation in valuations v_i.

Figure 4*a,b* illustrates these results for the case of no variation in cost parameters ($c_i = 1$). With group extinction (i.e. using

fitness function 2.3*b*), individual efforts greatly increase (figure 4*c,d*). The effects of within-group inequality greatly decrease, while those of group size diminish for $\alpha = 1.5$, but are augmented for $\alpha = 2.5$. Note that with synergicity (i.e. with $\alpha > 1$), groups can make significant total effort with much smaller individual efforts, which explains why the height of bars in figure 4 is smaller than that in figure 3.

Conclusions on examples. In the basic model, individuals defect if rewards are small but cooperate in securing big rewards. Increasing the reward size causes an increase in the efforts of high valuators but it can also decrease the efforts of low valuators who would increasingly free-ride. Increasing inequality decreases the efforts of low valuators but this is overcompensated by increased efforts of high valuators. As a result, with linear cost and impact functions, the group effort increases with inequality and decreases with group size. With linear costs, there is a threshold effect:
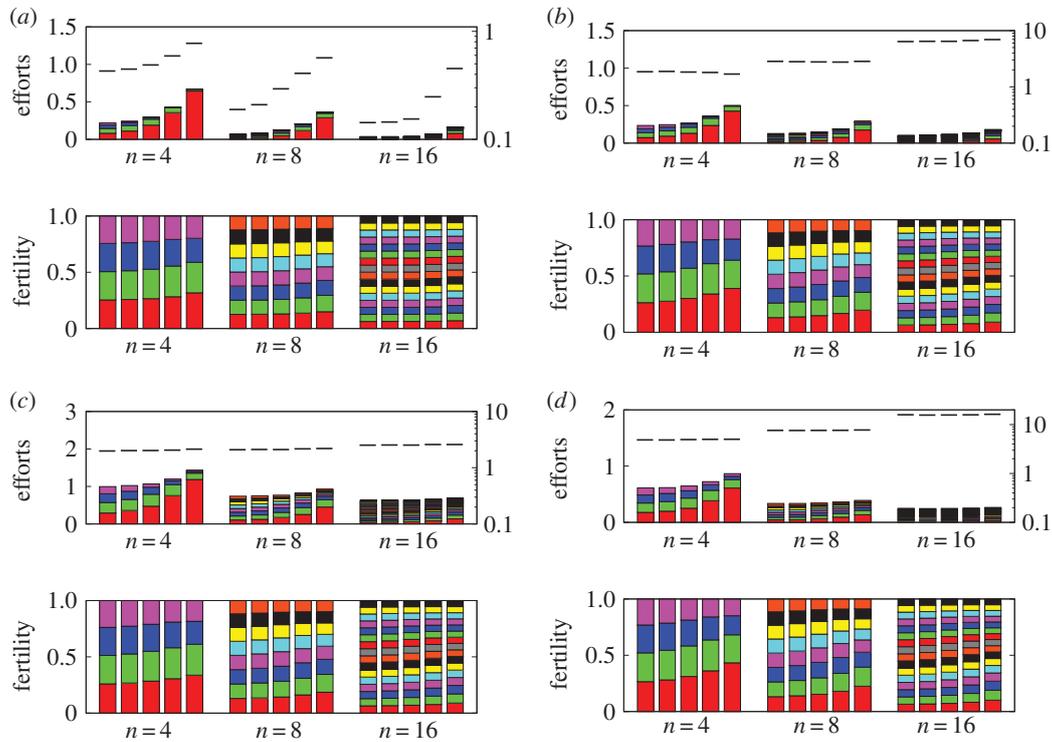
Figure 4. Effects of synergicity in the 'us versus nature' game. First column (a,c): $\alpha = 1.5$, second column (b,d): $\alpha = 2.5$. (a,b) No group extinction, (c,d) with group extinction. The dashes show the group effort on the logarithmic scale specified on the right y-axis. (Online version in colour.)

individuals contribute only if their valuation is above a certain critical value. In nonlinear models, all individuals contribute to public goods production. With linear costs, there is high dispersion of efforts within groups. However, this dispersion is reduced with quadratic costs and, especially, with synergicity. With highly nonlinear cost and benefit functions, the group effort can increase with group size and can decrease with inequality. Allowing for group extinction results in two main effects. First, all group members contribute proportionally to their valuations. Second, individual and group efforts as well as the degree/probabilities of success significantly increase. In most cases, individual share of reproduction grows with rank/valuation. But there are some cases where highest valuators (who are simultaneously the biggest contributors) have lower fertility than other individuals because of the costs paid.

(iv) Experimental games

Us versus nature games with homogeneous groups have been studied intensively in experiments. In linear PGG, contributions typically show a continuous decline [109]. However, in nonlinear PGG, contributions are often maintained at intermediate values, as predicted by models [96].

There has been also a substantial effort to study PGG with heterogeneous groups. However, the results are somewhat inconsistent because of differences in implementation and various social, historical or other factors [102,110,111]. In an early review of experimental work on PGG, Ledyard [109] concluded that asymmetry of benefits had negative effects on contributions. Fisher et al. [112] showed that individuals with lower valuation to cost ratios v_i/c_i contribute less than those with high values of this ratio, as predicted by the theory. Chan et al. [113] provided some experimental support for an increase in public good provision with inequality in wealth, again as predicted. However, in the experiment conducted

by Buckley & Croson [110], less wealthy individuals contributed the same absolute amount (or more as a percentage of their income) as the more wealthy. In Anderson et al. [111], inequality reduced contributions to a public good for all group members, regardless of their relative position. In Reuben & Riedl [114], individuals differed in their valuation v_i of reward. With no punishment of free-riders, total contributions were higher with inequality. Punishment did not significantly increase total earnings but strongly increased inequality at the cost of low-benefit members. Consequently, with punishment, low-benefit members did not benefit from being part of a privileged group. Secilmis & Güran [115] studied the effects of differences in endowment. They observed higher average contributions in egalitarian groups. With inequality, high-endowment individuals contributed more in the absolute sense but approximately the same percentage of their endowment; contributions by individuals with the same endowment decreased with increasing group inequality. Diekmann and co-workers [116,117] studied the asymmetric Volunteer's Dilemma with punishment. In their experiments, within-group social dynamics led to a state where punishment was mostly administered by individuals for whom it was less costly. Kölle [78] allowed for differences in valuation v_i and capabilities/strengths s_i. Without punishment, heterogeneity in valuations did not increase the average effort but that in capabilities did increase it. Punishment was much more effective with variation in capabilities than with that in valuations or with no variation. As noted above, with quadratic benefit and cost functions, individuals are predicted to contribute in proportion to their benefit to cost ratios. Experimental results by McGinty & Milam [102] largely support this prediction.

(b) Us versus them games

A limitation of Olson's theory is that he considered the CAP as a phenomenon within a single group assuming that

external threat to the group does not exist or can be treated as constant [118]. Here I review the us versus them games that explicitly capture the effects of other groups on the degree/probability P_j of the focal group's success. The most commonly used function for specifying P_j in us versus them games in the economics literature is the Tullock contest success function

$$P_j = \frac{X_j}{\sum X_k}, \qquad (2.5)$$

[76,119,120], which is also used in evolutionary biology models [34,84,107,121–123]. Note that the denominator in the equation above can be written as $X_j + \sum_{k \neq j} X_k$. This implies that functions (2.4) and (2.5) become identical if we interpret half-success parameter X_0 as the total effort of all other groups in the population, $\sum_{j \neq i} X_j$.

(i) Homogeneous groups

Katz *et al.* [124] (see also [76,125]) studied a conflict between two groups for a prize. They assumed that individual costs grew linearly with the efforts and that the reward was divided equally within the winning group. They also allowed for differences in group sizes and in how groups valued the prize. A conclusion of their analysis is that at a NE, the group in which individuals have a higher valuation of the prize, will expend more effort and will have a higher probability of winning. This implies that a smaller group in which individuals have higher valuation of the prize (because, in the case of success, each group member would get a larger amount) will have a higher probability of winning. This is another example of Olson's group size paradox but in the context of between-group contests. With multiple groups of equal size n, each of which values the prize equally, the equilibrium group effort is $X = B/nc$ [76]. Individual contributions are not defined uniquely, but if each group member contributes equally, $x = X/n$. However, if individual costs are certain nonlinear functions of efforts, an increase in the group size can raise the group effort [126].

So far, I have discussed models with endogenously specified valuations/shares. It is also possible that individual shares are defined by outcomes of an additional within-group conflict. Such nested or multi-level contests have also been studied [118,123,127–130] with a general conclusion that external conflicts cause increasing within-group cooperation and reduced free-riding.

(ii) Heterogeneous groups

Baik [131] generalized the Katz *et al.* [124] model for a case of a multi-group contest in which group members differ in their valuations (or shares) of the prize (see also [76]). His prediction is that within each group only an individual with the highest valuation of the prize will make a positive contribution while the rest will contribute nothing. This result implies that neither the group size nor the distribution of valuations among $n - 1$ other group members matter. However, if individual efforts are limited from above by a certain exogenously specified value, then multiple individuals can become contributors within each group and alternative equilibria with different sets of contributors become possible [34,131,132]. Epstein & Mealem [133] studied a contest between two groups. They showed that if individual costs are specific nonlinear functions of individual efforts, then all group members contribute in

proportion to their valuations and free-riding is reduced. Similar behaviour is predicted for the CES impact function [101,134]. In the case of weak-link contests, analysis predicts multiple equilibria including those with no free-riding at all [135]. In best-shot contests, there can be 'perverse equilibria' in which the highest valuation players completely free-ride on others by exerting no effort [132]. Allowing for group extinction results in that multiple individuals with highest valuations start contributing rather than a single individual [77]. The latter paper also predicts an increased group effort with within-group inequality and reduced net benefit (fertility) of high valuators relative to their free-riding group-mates (see below and also [136]). Choi *et al.* [137] studied a model of a contest between two groups of size $n = 2$ in the presence of both within-group power asymmetry and conflict over the share of the reward. They showed that high within-group inequality can increase the group effort in external conflict but the effect depends on the degree of synergicity of individual contributions.

(iii) Examples

To illustrate and extend these results, I will use contest success function (2.5) assuming no variation in baseline pay-offs ($f_{i,0} = 1$), but within-group heterogeneity in benefit and cost parameters which I will write as $b_i G$ and c_i. (The reason for scaling the benefit parameter by G is that with similar group efforts $P_j \approx 1/G$, so that the expected benefit per group is b_i as in 'us versus nature' games.)

Basic model. Consider the basic model with linear impact and cost functions, and no group selection [131]. In this model, the relevant benefit-to-cost ratios are $r_i = b_i/c_i$; only the individual with the highest r_i value always makes an effort $x_1 = r_1$ while all other group-mates always free-ride. Figure 5a illustrates this model numerically for the case of equal costs ($c_i = 1$). As predicted, there is a single contributor—the highest valuator—whose effort increases with within-group inequality. Note a sharp decline in fertility of the highest valuator with inequality which can be substantially smaller than that of other individuals. That is, the highest valuator behaves as an altruist.

Adding group extinction to the basic model by using pay-off function (2.3b) leads to a model studied by Gavrilets & Fortunato [77]. As mentioned above, in their model, there is a threshold valuation v_{crit} so that only individuals with $v_i > v_{crit}$ will contribute at ESS while all other group-mates will free-ride. The group effort increases with inequality. Fitness of high valuators can be smaller than that of low valuators in spite of the fact that the former are getting the biggest share of the reward. Under some conditions, fitness of the highest valuators can be very close to zero so that they can be viewed as effectively sacrificing themselves for the benefit of their groups. Figure 5b illustrates this model numerically assuming all $c_i = 1$.

The behaviour of the highest valuators may seem altruistic but, as explained in [77], actually it is not. For example, in the case of hierarchical groups, dominant individuals maximize their fitness by contributing; given the subordinates do not contribute at all, dominants will not be better off by reducing their contribution. Thus, the non-contributors are indeed free-riding, but the contributors are not altruistic; paradoxically, they are acting in their own interest by contributing to the collective good. What is driving their
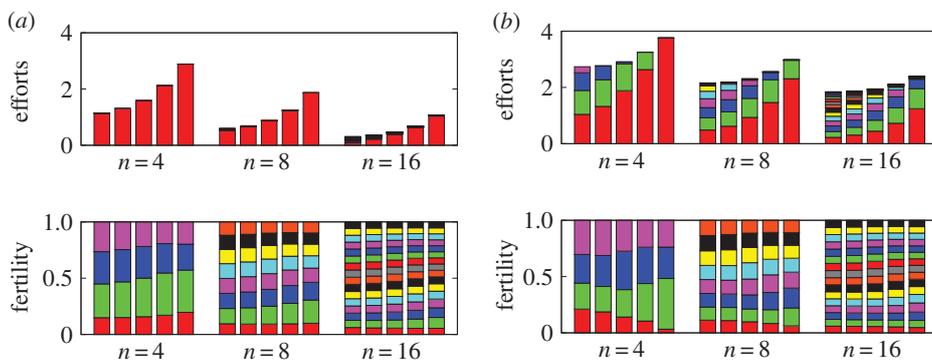
Figure 5. Collective action in the 'us versus them' game with production function (2.5) without (*a*) and with (*b*) group extinction. Additive impact function, linear costs function. (Online version in colour.)
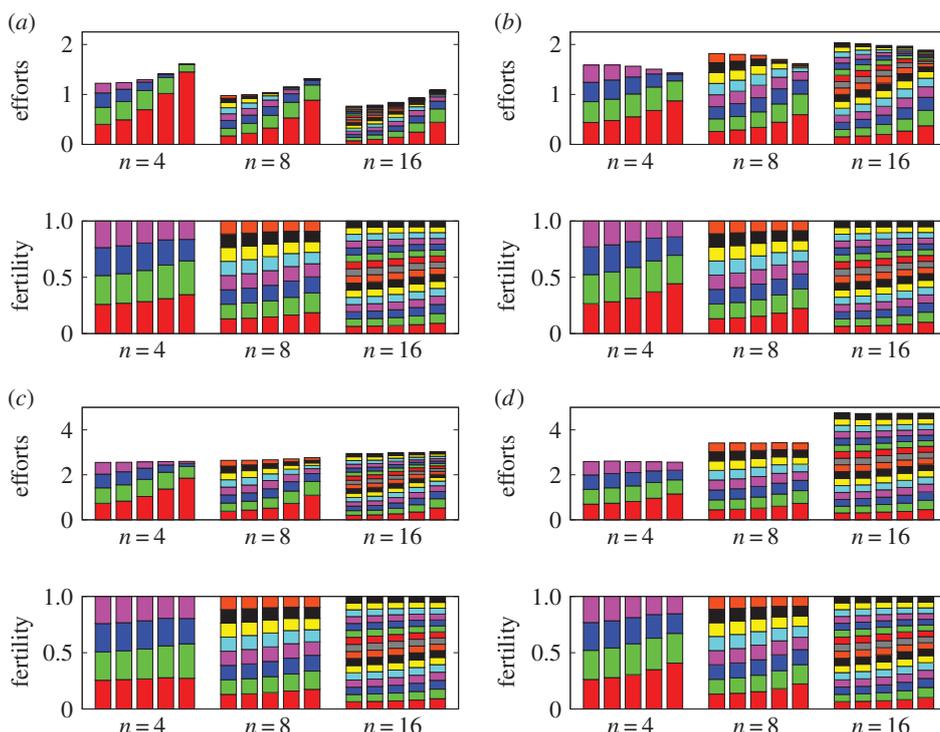

Figure 6. Effects of nonlinear costs in the 'us versus them' game. First column (*a,c*): $\gamma = 1.5$, second column (*b,d*): $\gamma = 2$, second column $\gamma = 2.5$. (*a,b*) No group extinction, (*c,d*) with group extinction. (Online version in colour.)

contribution is that they are essentially competing with their counterparts in other groups rather than with their own group-mates.

Nonlinear costs. Assuming nonlinear costs term $-cx_{ij}^{\gamma}$ has a qualitatively similar effect to that in us versus nature games. The relevant benefit-to-cost ratios are $r_i = b_i/c_i$ and $R = \sum r_i$. The group effort X solves the equation $\gamma X^{\gamma} = Rn^{\gamma-2}V_{\gamma-1}$ with individual efforts being proportional to $r_i^{1/(\gamma-1)}$. For example, with $\gamma = 2$, at an ESS the group effort is $X = \sqrt{R/2}$ and each group member contributes: $x_i = (r_i/R)X$. Note that X does not depend on the distribution of r_i within the group or the group size n. The total cost spent by the group is $cX^2 = B/2$, that is, one-half the overall benefit. Individual pay-offs depend linearly on valuations. With $1 < \gamma < 2$, the group effort decreases with group size n and increases with variation in valuations v_i. With $\gamma > 2$, the situation is reversed.

Figure 6*a,b* illustrates these results numerically for the case of equal costs parameters ($c_i = 1$). Allowing for group extinction (i.e. using fitness function (2.3*b*)) results in increasing individual efforts (figure 6*c,d*). The effects of within-group inequality greatly decrease, while those of group size diminish for $\gamma = 1.5$, but are augmented for $\gamma = 2.5$.

Synergicity. Using impact function (2.1*b*) has a qualitatively similar effect to that in us versus nature games. The predicted group effort X is $X = Rn^{\alpha-2}V_{\alpha-1}$ and individual efforts are proportional to $r_i^{\alpha/(\alpha-1)}$. For example, if $\alpha = 2$, the group effort at ESS is $X = R$ and each group member contributes effort $x_i = r_i^2 X$. The total cost paid by the group is $C = B\sum r_i^2$ which is minimized in egalitarian groups (i.e. with $r_i = 1/n$). Individual pay-offs are $f_i = 1 + Br_i(1 - v_i)$. With $1 < \alpha < 2$, the group effort decreases with group size n. With $\alpha > 2$, the situation is reversed.

Figure 7*a,b* illustrates this model numerically for the case of equal costs parameters ($c_i = 1$). The effects of allowing for group extinction are similar to those in other models (figure 7*c,d*).

Conclusions on examples. Overall, the behaviour of these models parallels that of us versus nature models considered
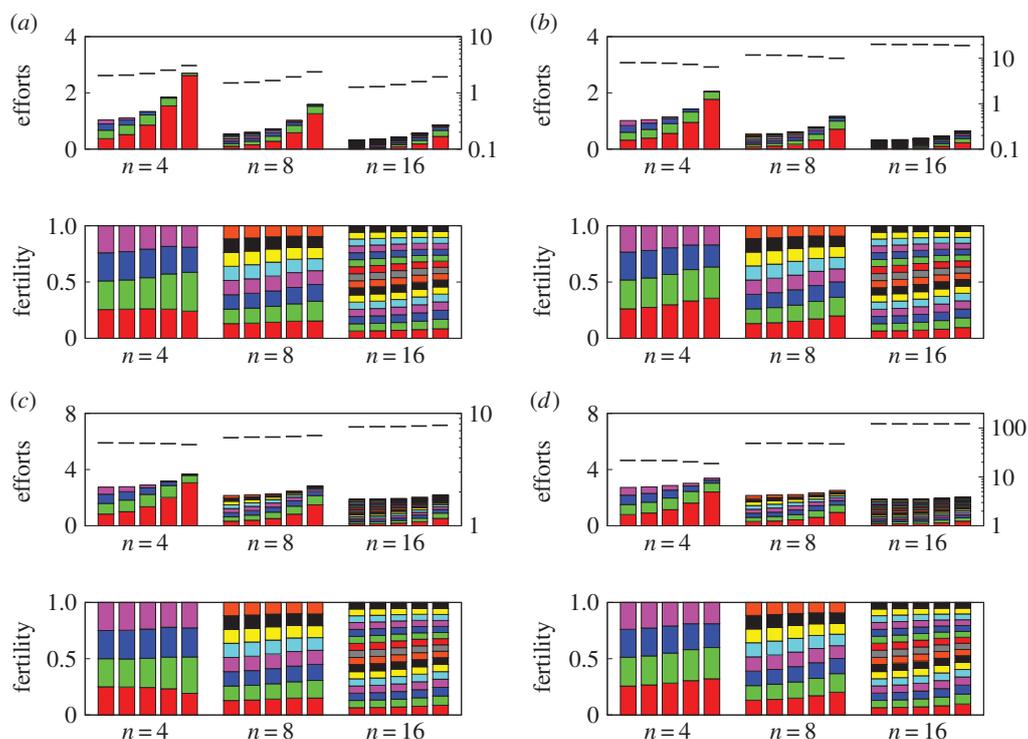
Figure 7. Effects of synergicity in the 'us versus them' game. First column (a,c): $\alpha = 1.5$, second column (b,d): $\alpha = 2$, second column $\alpha = 2.5$. (a,b) No group extinction, (c,d) with group extinction. The dashes show the group effort on the logarithmic scale specified on the right y-axis. (Online version in colour.)

above but individual and group efforts are always higher. In us versus nature games, groups often cooperate only if a corresponding benefit-to-cost ratio exceeds a certain threshold. By contrast, in us versus them games, groups always contribute a non-zero effort. Modelling predictions depend on benefit-to-cost ratios $r_i = b_i/(c_i X_0)$ or $r_i = b_i/(c_i X_0^2)$ in us versus nature games and $r_i = b_i/c_i$ in us versus them games. We can compare these two types of games directly by setting $X_0 = 1$. Then in the basic model, in games against nature collective good is produced if $r_1 > 1$ and the total group effort is $\sqrt{r_1} - 1$. In us versus them games, groups always make an effort equal to r_1. With quadratic costs, the group efforts are a solution of the equation $2X(X+1)^2 = R$ and $\sqrt{R/2}$, respectively, where $R = \sum r_i$. With collaborative ability $\alpha = 2$, the group efforts are $\sqrt{R} - 1$ (which requires $R > 1$) and R, respectively. In all these cases, group efforts in us versus them games are higher than in us versus nature games. I conclude that direct competition with other groups is much more conducive for the evolution of cooperation than collaboration against nature.

(iv) Experimental games

Experimental work on contests including between-group contests was recently reviewed comprehensively by Dechenaux *et al.* [138]. A general conclusion of their analysis is that between-group contests greatly increase individual efforts (up to five times the Nash equilibrium prediction) and mitigate the within-group free-rider problem. A number of experimental studies both in the economics and evolutionary biology literatures have also incorporated group selection in their design by either penalizing groups making the lowest efforts or rewarding groups making the highest efforts [139–143]. These studies show that adding group selection further increases both individual and group efforts.

Most experimental studies assume identical players within each group. One notable exception is Sheremeta

[144], who allowed for within-group variation in valuation. Sheremeta found that with a linear production function, all players expend significantly higher efforts than predicted by theory. In best-shot contests, most of the effort is expended by strong players, whereas weak players free-ride. In weakest-link contests, there is almost no free-riding and all players expend similar positive efforts. Experiments also strongly confirm that individual efforts are higher when members of the group are rewarded proportionally to their efforts rather than equally [127,145,146].

3. Discussion

The ability of groups to be successful in potentially profitable collective actions, aiming to overcome nature challenges or win competition with neighbouring groups of co-specifics, is undermined by a number of factors. One is the possibility of free-riding. If individual efforts are costly and at least some benefits of a collective action can be enjoyed independently of the level of participation, individuals can withdraw their effort to take advantage of this situation or avoid being taken advantage of by others. Another factor is within-group heterogeneity in various characteristics that affect decisions of individuals, such as the valuation or share of the prize, cost of efforts, individual capability, strength and personality. Such heterogeneity, which is ubiquitous both in animal and human groups, augments the conflict between individual interests. There is also a need to be able to efficiently coordinate group activities. Moreover, the success of collective actions is affected by exogenous and/or stochastic factors.

A substantial effort of theoreticians in several disparate research areas has been devoted to understanding the CAP in heterogeneous groups. The existing body of work reviewed above allows one to make certain generalizations about factors affecting individual efforts and group success

in collective actions. Theoretically, individual efforts, the amount of within-group free-riding and the likelihood of the group's success depend on (i) the group size and composition, (ii) how efforts of individuals are converted into fitness costs, (iii) how efforts of individual group members are aggregated into a group effort, (iv) how the latter is translated into the group's success, (v) how success in a collective good production affects the group's survival, and (vi) how members of surviving groups divide the prize if successful. Information on these aspects of collective actions is needed if one is to apply theoretical predictions to specific groups, populations or species.

A very common theoretical conclusion is that the largest beneficiaries of collective goods will make the largest contributions towards their production (but see [73,147]). Some models, e.g. with linear impact and cost functions, predict disproportionately large contributions of the 'great' who are exploited by the 'small' [5]. In these models, there can be one or few contributors per group while the rest free-ride. Other nonlinear models predict that all group members will contribute proportionally to their endowments or the ratio of the valuation of the prize/goods to the cost of individual effort. In humans, high contributors can also increase their reputation which would allow them to get better mates and allies [148].

A paradoxical novel prediction of recent work is that group members who are getting the biggest share of the reward or who value the reward the most can end up with the smaller net pay-offs than the rest of the group ([77] and above). This happens because such individuals make disproportionately high efforts and, as a result, pay very high costs. The possibility of group extinctions augments these effects. Intuitively, for the case of groups with a dominance hierarchy, once such a hierarchy is established and the shares of the reward going to dominant individuals are fixed, they are mostly competing not against their group-mates but against their peers in other groups. This between-peer competition drives the evolution of increasingly large efforts. Under some conditions, high valuators have essentially zero fitness, that is, they effectively sacrifice themselves for the benefit of the group. This self-sacrifice is not opposed by selection because, first, it is expressed conditionally on the rank (which is assigned randomly) and, second, it is not subject to within-group selection (only to between-group selection).

The group effort in a collective action (as well as the degree/probability of its success) increases with the benefit and decreases with the cost parameters. This is intuitive. The effect of the group size on the group effort is complex. Group size can have negative, zero or positive effect on the group production. For example, members of small groups can value the same reward more than members of large groups (because their absolute shares will be larger). This would result in larger efforts of smaller groups. However, if individual costs grow rapidly with their efforts, or if there is a hard limit on individual efforts, or if a goal of a collective action simply cannot be accomplished by a single individual or few individuals, larger groups will be at an advantage (because small individual efforts can be 'compensated' by a large number of contributors). Similarly, the effects of within-group heterogeneity on the group effort vary. They are positive in linear models, absent in some nonlinear models and negative in models with high synergicity or strong nonlinearity in cost functions. Overall, I conclude

that both the first and second Olson's insights require certain qualifications (as was already stressed earlier [8,12]).

The effects of parameters and modelling assumptions in the two types of games considered here are qualitatively similar. However, individual and group efforts are much lower in us versus nature games than in us versus them games. In the former, the success of one group in a collective goods production does not affect that of another group. By contrast, in the latter one group's success means another group's failure. This difference results in stronger natural selection in the us versus them models which in turn produces a larger evolutionary response in individual contributions. In us versus nature games, groups under-contribute, so that the group effort is smaller than what would be an optimum for the group. By contrast, in us versus them games, groups over-contribute as they would be better off if the efforts spent on between-group competition were minimized. Allowing for group extinction greatly increases individual contributions in both types of games.

Most of my discussion focused on within-group differences in cost–benefit ratios, shares of the reward or endowments. However, within-group differences in strengths or capabilities will result in similar effects. That is, stronger or more capable group members are predicted to be the biggest contributors [77,78]. I also assumed that groups had similar size, structure and that they valued the reward equally. The differences in valuation and sizes between groups are converted into the differences in valuation between individuals from different groups; individuals (and groups) with higher valuations will make more effort as discussed above. Another possible extension concerns production function (2.4) and contest success function (2.5) which can be generalized to $P_j = X_j^\beta / (X_j^\beta + X_0^\beta)$ and $P_j = X_j^\beta / \sum X_k^\beta$, respectively, where β is a 'decisiveness' parameter. Large values of β imply that small changes in group efforts can cause significant changes in P_j. Increasing β above one does not change the results qualitatively but increases individual efforts [77,71].

Models show that with certain nonlinear cost and impact functions, efficient within-group collaboration becomes possible. The important factor here is not nonlinearity per se, but the underlying assumptions. For example, with quadratic costs ($\gamma = 2$), small individual efforts are very 'cheap', while large individual efforts are very 'expensive'. Similarly, with large synergicity parameter α, a substantial group effort can emerge from small individual contributions. These are conditions simplifying collective actions with significant participation. Full participation can also be promoted by within-group communication [149] and punishment [150].

Genetic relatedness is a powerful force promoting cooperation [40,86,151]. Some theoretical studies reviewed above have explicitly incorporated genetic relatedness in mathematical models [68,77,85,104]. The results are in line with the expectation that genetic relatedness simplifies collective action. However, assuming realistic population structure and significant dispersal of offspring of one sex leads to relatively low levels of within-group genetic relatedness [77,152] and, correspondingly, low effects on collective actions.

In us versus them games, the group effort X can be viewed as a proxy for intensity of between-group competition. The models thus predict that the latter would increase with larger rewards, smaller costs and higher synergicity of individual efforts. As discussed above, the effects of group size, within-group heterogeneity and the type of costs vary.

(a) Applications to mammals

In mammals, collective actions mostly concern territorial behaviour, hunting and cooperative breeding. CAPs have been identified in lions, wolves, dogs and many primates. For example, capuchines are more likely to run away from territorial intrusions when their group has a numeric advantage; each one-individual increase in relative group size raises the odds of flight by 25% [17]. Individuals also base their decisions on the value of the territory, which is higher for the central parts of the group's range relative to the periphery. In capuchines, the probability that a focal animal fled from a simulated intrusion by a neighbouring group was 91% lower in experiments that occurred in the centre compared with on the edge of its group's range, whereas the odds that it rushed to defend its range were more than sixfold higher. Willems *et al.* [18] argue that CAP affects territorial behaviour of approximately 30% of 135 social primates species in their sample, resulting in a sub-optimal defence of a common range or territory. Further analysis has led Willems & van Schaik [19] to conclude that the only species that do not succumb to the CAP are those that live in relatively small groups with few individuals of the dominant sex, and are characterized by philopatry of this dominant sex or are cooperative breeders.

A number of empirical studies support the prediction of higher effort for high-rank individuals. In chimpanzees, high-rank males travel further into the periphery during border patrols [153] and males with higher mating success are more likely to engage in this activity [154], which is energetically costly [155]. In ring-tail lemurs [14] and blue monkeys [156], high-rank females participate more in the defence of communal feeding territories than low-rank females. In meerkats, dominant males respond more strongly to intruder scent marks [157]. High-rank chacma baboon males are more likely than low-rank males to join inter-group loud call displays [16].

(b) Applications to human origins

Theoretical results have some implications for the origins of successful collective actions in human ancestors. Models show that in games against nature, cooperation becomes successful if the corresponding benefit/cost ratio R is high enough, and that degree of success greatly increases with collaborative ability α. From a modelling perspective, successful large-game hunting may become possible after some technological changes, such as an invention of spears, that would increase the ability to kill large animals (reducing half-success effort X_0) and/or decrease the danger to hunters (reducing cost parameters c_i). In competition against other groups, technological innovations allowing for better defence of a valuable territory and/or resource (increasing B) would cause increasing individual efforts. Direct competition against other groups also strongly promotes within-group collaboration. Moreover, it is more likely to result in group extinction which would augment this effect. Similar effects will follow worsening environmental conditions [158]. All these factors will increase intensity of group selection which in turn would promote collaboration in both types of games. A similar effect will be achieved by an increase in collaborative ability (increasing α) with the emergence of language. (Gavrilets [71] models the evolution of α explicitly). An additional factor could be the appearance of certain behavioural strategies, as a result of technological and/or cultural innovation. For example, raids usually have low individual costs (low c) but large benefit

(large B) [159,160]. Adapting raids as a group strategy would promote more efficient collaboration. Once individuals develop abilities to cooperate effectively in some specific types of activities (like hunting or raiding), their skills can be successfully applied to many other collective actions.

(c) Applications to human psychology

The work reviewed here has a number of implications for behaviour of modern humans. First, it predicts that humans have a genetic predisposition for collaborative group activities. This is in line with a consistent observation that human infants are motivated to collaborate in pursuing a common goal [161] and that cooperative acts result in activation of brain regions involved in reward processing, independently of material gains [162]. People cooperate when groups face failure because of external threats, e.g. harsh environmental conditions or natural disasters [163,164]. However, as predicted by the theory above, cooperation increases dramatically in the presence of direct between-group competition (see experimental economics work discussed above) to a level that 'cues of group competition have an automatic or unconscious effect on human behaviour that can induce increased within-group cooperation' [165]. A number of other observations about human psychology (e.g. in-group/out-group biases, widespread obsession with team sports, and sex differences in the motivation to form, and skill at maintaining, large competitive groups [166]) strongly support the idea about the importance of between-group conflicts in shaping human social instincts.

Existing experimental data on the effects of within-group heterogeneity are also largely in line with theoretical predictions (see above). Additionally, it has been shown that more competitive, individualistic players contribute more to collective goods with group competition [167] and that individuals of high status contribute more towards group goals [168]. Models predict that individuals who find themselves in a leadership position will exhibit more propensity for pro-social and self-sacrificing actions in warfare and other between-group competition scenarios. In line with these expectations in some human groups, the most aggressive warriors have lower reproductive success than other men, as documented for the horticulturalist/forager Waorani of Ecuador [169] and Nyangatom of Ethiopia [170]. The Cheyenne war chiefs were expected to be killed in combat, and leaders in the Nyangatom of Ethiopia, the Kapauka of New Guinea and the Jie of Uganda all take greater risks in combat [171,172]. The data show that the highest mortality in the US Army in the Iraq war was among First and Second Lieutenants, who typically lead combat patrols [173]. In recent public goods experiments [117], actors tacitly coordinated on the strongest group member to punish defectors, even if the strongest individual incurs a net loss from punishment. These experiments showed that an arbitrary assignment of an individual to a focal position in the social hierarchy can trigger changes in his/her behaviour leading to the endogenous emergence of more centralized forms of punishment. Note that models predict higher efforts and costs not only for individuals who actually hold or have been assigned high rank or status, but also for 'potential alphas' who have higher valuation of the prize, lower costs or higher strength. Finally, modelling work suggests that bullish and 'unethical' behaviour by high-rank individuals towards their

group-mates [174] can be accompanied by their higher contributions towards between-group competition.

In a number of models reviewed above, members of hierarchically structured groups align their efforts linearly proportional to their shares of the reward. This suggests that compensation proportional to the effort may be a default human expectation for group members who are unequal in their roles and types of contribution to a group success. Viewed this way, models thus provide a theoretical justification for a major postulate of the classical equity theory [175,176] that employees seek to maintain equity between their input-to-output ratio and that of others, and that any variation in these ratios between group members will be viewed as unfair treatment. (The theory does recognize that the 'input' of workers includes many factors besides working hours, and that their 'output' includes many rewards besides money.)

(d) Final thoughts

Looking at the overall picture emerging from the work reviewed here, to what extent do groups solve the CAP? The answer naturally depends on what one means by 'solving the CAP'. In most cases of us versus nature games with large enough benefit-to-cost ratio and in all cases of us versus them games discussed above, group efforts are positive. Therefore in a weak sense, groups almost always solve the CAP.

However, in almost all cases, some free-riding (i.e. reduced effort of some group members) is present. Therefore in a strong sense, groups almost always succumb to the CAP. Do the 'great' get exploited by the 'small'? The answer is yes in the sense that they usually make a larger effort in collective good production than the 'small'. However, in many cases, the 'great' are well compensated for their effort as their shares of reproduction are higher than those of the 'small'. However, in some situations the 'great' get exploited to the extreme as the logic of evolutionary processes make them effectively sacrifice themselves for the benefit of their group-mates.

Theoretical predictions discussed here are directly applicable only under specific sets of conditions captured by the corresponding models. It is important to check to what extent they hold within other approaches to studying collective actions mentioned at the beginning of this paper.

References

1. Trivers R. 1985 Social evolution. Menlo Park, CA: Benjamin/Cummings.

2. Jens Krause GDR. 2002 Living in groups. Oxford, UK: Oxford University Press.

3. Majolo B, Vizioli ADB, Schino G. 2008 Costs and benefits of group living in primates: group size effects on behaviour and demography. Anim. Behav. 76, 1235–1247. (doi:10.1016/j.anbehav.2008.06.008)

4. Tucker A. 1950 A two-person dilemma. In Readings in games and information (ed. E Rasmussen), pp. 7–8. Oxford, UK: Blackwell, 2011.

5. Olson M. 1965 Logic of collective action: public goods and the theory of groups. Cambridge, MA: Harvard University Press.

6. Hardin G. 1968 Tragedy of commons. Science 162, 1243–1248. (doi:10.1126/science.162.3859.1243)

7. Hardin R. 1982 Collective action. Baltimore, MD: John Hopkins University Press.

8. Sandler T. 1992 Collective action: theory and applications. Ann Arbor, MI: University of Michigan Press.

9. Marwell G, Oliver P. 1993 The critical mass in collective action. Cambridge, UK: Cambridge University Press.

10. Medina LF. 2013 The analytical foundations of collective action theory: a survey of recent developments. Annu. Rev. Polit. Sci. 16, 259–283. (doi:10.1146/annurev-polisci-032311-110742)

11. Ray G. 2013 Foundations of collective action: towards a general theory. In Social capital and rural development in the knowledge society (eds H Westlund, K Kobayashi), pp. 75–109. Google eBook.

12. Pecorino P. 2015 Olson's logic of collective action at fifty. Public Choice 162, 243–262. (doi:10.1007/s11127-014-0186-y)

13. Nunn C. 2000 Collective action, free-riding, and male extra-group conflict. In Primate males (ed. P Kappeler), pp. 192–204. Cambridge, UK: Cambridge University Press.

14. Nunn C, Deaner R. 2004 Patterns of participation and free riding in territorial conflicts among ringtailed lemurs (Lemur catta). Behav. Ecol. Sociobiol. 57, 50–61. (doi:10.1007/s00265-004-0830-5)

15. Nunn C, Lewis R. 2006 Cooperation and collective action in animal behavior. In Economics in nature (eds R Noë, JARAM van Hooff, P Hammerstein), pp. 42–66. Cambridge, UK: Cambridge University Press.

16. Kitchen DM, Beehner JC. 2007 Factors affecting individual participation in group-level aggression among non-human primates. Behaviour 144, 1551–1581. (doi:10.1163/156853907782512074)

17. Crofoot MC, Gilby IC. 2012 Cheating monkeys undermine group strength in enemy territory. Proc. Natl Acad. Sci. USA 109, 501–505. (doi:10.1073/pnas.1115937109)

18. Willems E, Hellriegel B, van Schaik CP. 2013 The collective action problem in primate territory economics. Proc. R. Soc. Lond. B 280, 20130081. (doi:10.1098/rspb.2013.0081)

19. Willems E, van Schaik CP. 2015 Collective action end the intensity of between-group competition in nonhuman primates. Behav. Ecol. 26, 625–631. (doi:10.1093/beheco/arv001)

20. Packer C, Ruttan L. 1988 Evolution of cooperative hunting. Am. Nat. 132, 159–198. (doi:10.1086/284844)

21. Bonanni R, Valsecchi P, Natoli E. 2010 Pattern of individual participation and cheating in conflicts between groups of free-ranging dogs. Anim. Behav. 79, 957–968. (doi:10.1016/j.anbehav.2010.01.016)

22. MacNulty DR, Smith DW, Mech LD, Vucetich JA, Packer C. 2012 Nonlinear effects of group size on the success of wolves hunting elk. Behav. Ecol. 23, 75–82. (doi:10.1093/beheco/arr159)

23. MacNulty DR, Tallian A, Stahler DR, Smith DW. 2014 Influence of group size on the success of wolves hunting bison. PLoS ONE 9, e112884. (doi:10.1371/journal.pone.0112884)

24. Mathew S, Boyd R. 2011 Punishment sustains large-scale cooperation in prestate warfare. Proc. Natl Acad. Sci. USA 108, 11 375–11 380. (doi:10.1073/pnas.1105604108)

25. Glowacki L, Wrangham RW. 2013 The role of rewards in motivating participation in simple warfare. Hum. Nat. 24, 444–460. (doi:10.1007/s12110-013-9178-8)

26. Mathew S, Boyd R. 2014 The cost of cowardice: punitive sentiments towards free riders in Turkana raids. Evol. Hum. Behav. 35, 58–64. (doi:10.1016/j.evolhumbehav.2013.10.001)

27. Hawkes K. 1992 Sharing and collective action. In Evolutionary ecology and human behavior (eds EA Smith, B Winterhalder), pp. 269–300. New York, NY: Aldine de Gruyter.

28. Carballo DM (ed.). 2013 Cooperation and collective action: archaeological perspective. Boulder, CO: University Press of Colorado.

29. Carballo DM, Roscoe P, Feinman GM. 2014 Cooperation and collective action in the cultural

evolution of complex societies. *J. Archaeol. Method Theory* **21**, 98–123. (doi:10.1007/s10816-012-9147-2)

30. Sahlins M. 1972 *Stone age economics*. Chicago, IL: Aldine.

31. Sigmund K. 2010 *The calculus of selfishness*. Princeton, NJ: Princeton University Press.

32. Leininger W. 2003 On evolutionarily stable behavior in contests. *Econ. Gov.* **4**, 177–186. (doi:10.1007/s10101-002-0055-x)

33. Hehenkamp B, Leininger W, Possajennikov A. 2004 Evolutionary rent-seeking. *Eur. J. Polit. Econ.* **20**, 1045–1057. (doi:10.1016/j.ejpoleco.2003.09.002)

34. Crowley P, Baik K. 2010 Variable valuations and voluntarism under group selection: an evolutionary public goods game. *J. Theor. Biol.* **265**, 238–244. (doi:10.1016/j.jtbi.2010.05.005)

35. Bowles S, Gintis H. 2011 *A cooperative species: human reciprocity and its evolution*. Princeton, NJ: Princeton University Press.

36. Darwin C. 1871 *The descent of man, and selection in relation to sex*. London, UK: John Murray.

37. Robinson GE, Fernald RD, Clayton DF. 2008 Genes and social behavior. *Science* **322**, 896–900. (doi:10.1126/science.1159277)

38. Sandholm WH. 2010 *Population games and evolutionary dynamics*. Cambridge, MA: MIT Press.

39. Frank SA. 1995 Mutual policing and repression of competition in the evolution of cooperative groups. *Nature* **377**, 520–522. (doi:10.1038/377520a0)

40. Frank S. 1998 *Foundations of social evolution*. Princeton, NJ: Princeton University Press.

41. Dionisio F, Gordo I. 2006 The tragedy of the commons, the public goods dilemma, and the meaning of rivalry and excludability in evolutionary biology. *Evol. Ecol. Res.* **8**, 321–332.

42. Frank SA. 2010 Demography and the tragedy of the commons. *J. Evol. Biol.* **23**, 32–39. (doi:10.1111/j.1420-9101.2009.01893.x)

43. Killingback T, Doebeli M, Hauert C. 2010 Diversity of cooperation in the tragedy of commons. *Biol. Theory* **5**, 3–6. (doi:10.1162/BIOT_a_00019)

44. Ruttan LM. 2006 Sociocultural heterogeneity and the common. *Curr. Anthropol.* **47**, 843–853. (doi:10.1086/507185)

45. Ruttan LM. 2008 Economic heterogeneity and the commons. *World Dev.* **35**, 969–985. (doi:10.1016/j.worlddev.2007.05.005)

46. McKelvey RD, Palfrey T. 1995 Quantal response equilibria for normal-from games. *Games Econ. Behav.* **10**, 6–38. (doi:10.1006/game.1995.1023)

47. Anderson S, Goeree J, Holt C. 1998 A theoretical analysis of altruism and decision error in public goods games. *J. Public Econ.* **70**, 297–323. (doi:10.1016/S0047-2727(98)00035-8)

48. Anderson S, Goeree J, Holt C. 2002 The logit equilibrium: a perspective on intuitive behavioral anomalies. *South. Econ. J.* **69**, 21–47. (doi:10.2307/1061555)

49. Erev I, Roth A. 1998 Predicting how people play games: reinforcement learning in experimental games with unique, mixed strategy equilibria. *Am. Econ. Rev.* **88**, 848–881.

50. Myatt DP, Wallace C. 2008 An evolutionary analysis of the volunteer's dilemma. *Games Econ. Behav.* **62**, 67–76. (doi:10.1016/j.geb.2007.03.005)

51. Boyd R, Richerson P. 1992 Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethol. Sociobiol.* **13**, 171–195. (doi:10.1016/0162-3095(92)90032-Y)

52. Fowler J. 2005 Altruistic punishment and the origin of cooperation. *Proc. Natl Acad. Sci. USA* **102**, 7047–7049. (doi:10.1073/pnas.0500938102)

53. Janssen MA, Bushman C. 2008 Evolution of cooperation and altruistic punishment when retaliation is possible. *J. Theor. Biol.* **254**, 541–545. (doi:10.1016/j.jtbi.2008.06.017)

54. Boyd R, Gintis H, Bowles S. 2010 Coordinated punishment of defectors sustains cooperation and can proliferate when rare. *Science* **328**, 617–620. (doi:10.1126/science.1183665)

55. Mesterton-Gibbons M, Gavrilets S, Gravner J, Akcay E. 2011 Models of coalition or alliance formation. *J. Theor. Biol.* **274**, 187–204. (doi:10.1016/j.jtbi.2010.12.031)

56. Bissonnette A, Perry S, Barrett L, Mitani J, Flinn M, Gavrilets S, de Waal FBM. 2015 Coalitions in theory and reality: a review of pertinent variables and processes. *Behaviour* **152**, 1–56. (doi:10.1163/1568539X-00003241)

57. Perc M, Gomez-Gardenes J, Szolnoki A, Floria LM, Moreno Y. 2013 Evolutionary dynamics of group interactions on structured populations: a review. *J. R. Soc. Interface* **10**, 20120997. (doi:10.1098/rsif.2012.0997)

58. Granovetter M. 1978 Threshold models of collective behavior. *Am. J. Sociol.* **83**, 1420–1443. (doi:10.1086/226707)

59. Macy MW. 1991 Chains of cooperation: threshold effects in collective action. *Am. Sociol. Rev.* **56**, 730–747. (doi:10.2307/2096252)

60. Oliver PE. 1993 Formal models of collective action. *Annu. Rev. Sociol.* **19**, 271–300. (doi:10.1146/annurev.so.19.080193.001415)

61. Heckathorn DD. 1993 Collective action and group heterogeneity: voluntary provision versus selective incentives. *Am. Sociol. Rev.* **58**, 329–350. (doi:10.2307/2095904)

62. Heckathorn DD. 1996 The dynamics and dilemmas of collective action. *Am. Sociol. Rev.* **61**, 250–277. (doi:10.2307/2096334)

63. Centola DM. 2013 Homophily, networks, and critical mass. *Rationality Soc.* **25**, 3–40. (doi:10.1177/1043463112473734)

64. Centola D. 2013 A simple model of stability in critical mass dynamics. *J. Stat. Phys.* **151**, 238–253. (doi:10.1007/s10955-012-0679-3)

65. Siegel DA. 2009 Social networks and collective action. *Am. J. Polit. Sci.* **53**, 122–138. (doi:10.1111/j.1540-5907.2008.00361.x)

66. Morgenstern AP et al. 2013 Resource letter MPCVW-1: modeling political conflict, violence, and wars: a survey. *Am. J. Phys.* **81**, 805–814. (doi:10.1119/1.4820892)

67. Doebeli M, Hauert C. 2005 Models of cooperation based on Prisoner's Dilemma and the Snowdrift games. *Ecol. Lett.* **8**, 748–766. (doi:10.1111/j.1461-0248.2005.00773.x)

68. Archetti M, Scheuring I. 2012 Game theory of public goods in one-shot social dilemmas without assortment. *J. Theor. Biol.* **299**, 9–20. (doi:10.1016/j.jtbi.2011.06.018)

69. Shutters ST. 2013 Towards a rigorous framework for studying 2-player continuous games. *J. Theor. Biol.* **321**, 40–43. (doi:10.1016/j.jtbi.2012.12.026)

70. Doebeli M, Killingback T, Hauert C. 2013 A comment on 'Toward a rigorous framework for studying 2-player continuous games' by Shade T. Shutters, Journal of Theoretical Biology **321**, 40–43, 2013. *J. Theor. Biol.* **336**, 240–241. (doi:10.1016/j.jtbi.2013.05.035)

71. Gavrilets S. 2015 Collective action and the collaborative brain. *J. R. Soc. Interface* **12**, 20141067. (doi:10.1098/rsif.2014.1067)

72. Diekmann A. 1985 Volunteer's dilemma. *J. Confl. Resolution* **29**, 605–610. (doi:10.1177/0022002785029004003)

73. Diekmann A. 1993 Cooperation in an asymmetric Volunteer's Dilemma game. Theory and experimental evidence. *Int. J. Game Theory* **22**, 75–85. (doi:10.1007/BF01245571)

74. Archetti M. 2009 Cooperation as a volunteer's dilemma and the strategy of conflict in public goods games. *J. Evol. Biol.* **22**, 2192–2200. (doi:10.1111/j.1420-9101.2009.01835.x)

75. Archetti M, Scheuring I. 2010 Coexistence of cooperation and defection in public goods games. *Evolution* **65**, 1140–1148. (doi:10.1111/j.1558-5646.2010.01185.x)

76. Konrad K. 2009 *Strategy and dynamics in contests*. Oxford, UK: Oxford University Press.

77. Gavrilets S, Fortunato L. 2014 Evolution of social instincts in between-group conflict with within-group inequality. *Nat. Commun.* **5**, article 3526. (doi:10.1038/ncomms4526)

78. Kölle F. 2015 Heterogeneity and cooperation: the role of capability and valuation on public goods provision. *J. Econ. Behav. Organ.* **109**, 120–134. (doi:10.1016/j.jebo.2014.11.009)

79. Hirshleifer J. 1983 From weakest-link to best-shot: the voluntary provision of public goods. *Public Choice* **41**, 371–386. (doi:10.1007/BF00141070)

80. Hirshleifer J. 1991 The paradox of power. *Econ. Politics* **3**, 177–200. (doi:10.1111/j.1468-0343.1991.tb00046.x)

81. Helmold RL. 1993 Osipov: the 'Russian Lanchester'. *Eur. J. Oper. Res.* **65**, 278–288. (doi:10.1016/0377-2217(93)90341-J)

82. Lepingwell JWR. 1987 The laws of combat? Lanchester reexamined. *Int. Secur.* **12**, 89–134. (doi:10.2307/2538918)

83. Gavrilets S, Duenez-Guzman EA, Vose MD. 2008 Dynamics of coalition formation and the egalitarian revolution. *PLoS ONE* **3**, e3293. (doi:10.1371/journal.pone.0003293)

84. Gavrilets S. 2012 On the evolutionary origins of the egalitarian syndrome. *Proc. Natl Acad. Sci. USA* **109**, 14 069–14 074. (doi:10.1073/pnas.1201718109)

85. Frank SA. 2010 A general model of the public goods dilemma. *J. Evol. Biol.* **23**, 1245–1250. (doi:10.1111/j.1420-9101.2010.01986.x)

86. Okasha S. 2009 *Evolution and the levels of selection*. Oxford, UK: Oxford University Press.

87. Weesie J, Franzen A. 1998 Cost sharing in a Voluntary's Dilemma. *J. Confl. Resolution* **42**, 600–618. (doi:10.1177/0022002798042005004)

88. Zheng DF, Yin HP, Chan CH, Hui PM. 2007 Cooperative behavior in a model of evolutionary snowdrift games with N-person interactions. *Electrophys. Lett.* **80**, 18002. (doi:10.1209/0295-5075/80/18002)

89. Pacheco JM, Santos FC, Souza MO, Skyrms B. 2009 Evolutionary dynamics of collective action in n-person stag hunt dilemmas. *Proc. R. Soc. B* **276**, 315–321. (doi:10.1098/rspb.2008.1126)

90. Hauert C, Holmes M, Doebeli M. 2006 Evolutionary games and population dynamics: maintenance of cooperation in public goods games. *Proc. R. Soc. B* **273**, 2565–2570. (doi:10.1098/rspb.2006.3600)

91. Pena J. 2011 Group-size diversity in public goods games. *Evolution* **66**, 623–636. (doi:10.1111/j.1558-5646.2011.01504.x)

92. Zhang Y, Wu T, Chen X, Xie G, Wang L. 2013 Mixed strategies under generalized public goods games. *J. Theor. Biol.* **334**, 52–60. (doi:10.1016/j.jtbi.2013.05.011)

93. Zhang Y, Fu F, Wu T, Xie G, Wang L. 2013 A tale of two contributing mechanisms for nonlinear public goods. *Sci. Rep.* **3**, 2021. (doi:10.1038/srep02021)

94. Sefton M, Steinberg R. 1996 Reward structures in public good experiments. *J. Public Econ.* **61**, 263–287. (doi:10.1016/0047-2727(95)01534-5)

95. Laury S, Walker J, Williams A. 1999 The voluntary provision of a pure public good with diminishing marginal returns. *Public Choice* **99**, 139–160. (doi:10.1023/A:1018302432659)

96. Laury S, Holt C. 2008 Voluntary provision of public goods: experimental results with interior Nash equilibria. *Handb. Exp. Econ. Results* **1**, 792–801. (doi:10.1016/S1574-0722(07)00084-4)

97. Doebeli M, Hauert C, Killingback T. 2004 The evolutionary origins of cooperators and defectors. *Science* **306**, 859–862. (doi:10.1126/science.1101456)

98. Geritz SAH, Kisdi E, Meszéna G, Metz JAJ. 1998 Evolutionary singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* **12**, 35–57. (doi:10.1023/A:1006554906681)

99. Bergstrom T, Blume L, Varian H. 1986 On the private provision of public goods. *J. Public Econ.* **29**, 25–49. (doi:10.1016/0047-2727(86)90024-1)

100. Andreoni J. 1988 Privately provided public goods in a large economy: the limits of altruism. *J. Public Econ.* **35**, 57–73. (doi:10.1016/0047-2727(88)90061-8)

101. Kölle F, Sliwka D, Zhou N. 2011 Inequality, inequity aversion, and the provision of public goods. *IZA Discussion Paper 5514*.

102. McGinty M, Milam G. 2013 Public goods provision by asymmetric agents: experimental evidence. *Soc. Choice Welfare* **40**, 1159–1177. (doi:10.1007/s00355-012-0658-2)

103. Weesie J. 1993 Asymmetry and timing in the voluntary's dilemma. *J. Confl. Resolution* **37**, 569–590. (doi:10.1177/0022002793037003008)

104. He J-Z, Wang R-W, Jensen CXJ, Li Y-T. 2012 Cooperation in an asymmetric voluntary's dilemma game with relatedness. *Chin. Sci. Bull.* **57**, 1972–1981. (doi:10.1007/s11434-012-5178-z)

105. He J-Z, Wang R-W, Li Y-T. 2014 Evolutionary stability in the asymmetric Voluntary's Dilemma. *PLoS ONE* **9**, e103931. (doi:10.1371/journal.pone.0103931)

106. Waxman D, Gavrilets S. 2005 Target review: 20 questions on adaptive dynamics. *J. Evol. Biol.* **18**, 1139–1154. (doi:10.1111/j.1420-9101.2005.00948.x)

107. Gavrilets S. 2012 Human origins and the transition from promiscuity to pair-bonding. *Proc. Natl Acad. Sci. USA* **109**, 9923–9928. (doi:10.1073/pnas.1200717109)

108. Chapais B. 2008 *Primeval kinship: how pair-bonding gave birth to human society*. Cambridge, UK: Harvard University Press.

109. Ledyard JO. 1995 Public goods: a survey of experimental research. In *hanbook of experimental economics* (ed. KJ Roth), pp. 111–194. Princeton, NJ: Princeton University Press.

110. Buckley E, Croson R. 2006 Income and wealth heterogeneity in the voluntary provision of linear public goods. *J. Public Econ.* **90**, 935–955. (doi:10.1016/j.jpubeco.2005.06.002)

111. Anderson LR, Mellor JM, Milyo J. 2008 Inequality and public good provision: an experimental analysis. *J. Socio-Econ.* **37**, 1010–1028. (doi:10.1016/j.socec.2006.12.073)

112. Fisher J, Isaac RM, Schatzberg JW, Walker JM. 1995 Heterogeneous demand for public goods: behavior in the voluntary contribution mechanism. *Public Choice* **85**, 249–266. (doi:10.1007/BF01048198)

113. Chan KS, Mestelman S, Moir R, Muller RA. 1996 The voluntary provision of public goods under varying income distribution. *Can. J. Econ.* **29**, 54–69. (doi:10.2307/136151)

114. Reuben E, Riedl A. 2009 Public goods provision and sanctioning in privileged groups. *J. Conflict Resolution* **53**, 72–93. (doi:10.1177/0022002708322361)

115. Secilmis IE, Güran MC. 2012 Income heterogeneity in the voluntary provision of dynamic public goods. *Pac. Econ. Rev.* **17**, 693–707. (doi:10.1111/1468-0106.12006)

116. Przepiorka W, Diekmann A. 2013 Individual heterogeneity and costly punishment: a voluntary's dilemma. *Proc. R. Soc. Lond. B* **280**, 20130247. (doi:10.1098/rspb.2013.0247)

117. Diekmann A, Przepiorka W. 2015 Punitive preferences, monetary incentives and tacit coordination in the punishment of defectors promote cooperation in humans. *Sci. Rep.* **5**, 10321. (doi:10.1038/srep10321)

118. Nious EMS, Tan G. 2005 External threat and collective action. *Econ. Inq.* **43**, 519–530. (doi:10.1093/ei/cbi035)

119. Tullock G. 1980 Efficient rent seeking. In *Toward a theory of the rent-seeking society* (eds JM Buchanan, RD Tollison, G Tullock), pp. 97–112. College Station, TX: Texas A&M University.

120. Münster J. 2009 Group contest success functions. *Econ. Theory* **41**, 345–357. (doi:10.1007/s00199-009-0479-4)

121. Hawkes K, Rogers AR, Charnov EL. 1995 The male's dilemma: increased offspring production is more paternity to steal. *Evol. Ecol.* **9**, 662–677. (doi:10.1007/BF01237661)

122. Kokko H, Morrell LJ. 2005 Mate guarding, male attractiveness, and paternity under social monogamy. *Behav. Ecol.* **16**, 724–731. (doi:10.1093/beheco/ari050)

123. Reeve HK, Hölldobler B. 2007 The emergence of a superorganism through intergroup competition. *Proc. Natl Acad. Sci. USA* **104**, 9736–9740. (doi:10.1073/pnas.0703466104)

124. Katz E, Nitzan S, Rosenberg J. 1990 Rent-seeking for pure public goods. *Public Choice* **65**, 49–60. (doi:10.1007/BF00139290)

125. Cheikbossian G. 2012 Collective action problem: within-group cooperation and between-group competition in a rent-seeking game. *Games Econ. Behav.* **74**, 68–82. (doi:10.1016/j.geb.2011.05.003)

126. Esteban J, Ray D. 2001 Collective action and the group size paradox. *Am. Polit. Sci. Rev.* **95**, 663–672. (doi:10.1017/S0003055401003124)

127. Gunnthorsdottira A, Rapoport A. 2006 Embedding social dilemmas in intergroup competition reduces free-riding. *Organ. Behav. Hum. Decis. Process.* **101**, 184–199. (doi:10.1016/j.obhdp.2005.08.005)

128. Münster J. 2007 Simultaneous inter- and intra-group conflicts. *Econ. Theory* **32**, 333–352. (doi:10.1007/s00199-007-0218-7)

129. Münster J, Staal K. 2011 War with outsiders makes peace inside. *Confl. Manage. Peace Sci.* **28**, 91–110. (doi:10.1177/0738894210396629)

130. Barker JL, Barclay P, Reeve HK. 2012 Within-group competition reduces cooperation and payoffs in human groups. *Behav. Ecol.* **23**, 735–741. (doi:10.1093/beheco/ars020)

131. Baik KH. 2008 Contests with group-specific public-good prizes. *Soc. Choice Welfare* **20**, 103–117.

132. Chowdhury SM, Topolyan I. 2013 The attack and defense group contests. *University of East Anglia AFE Working Paper No. 49*.

133. Epstein GS, Mealem Y. 2009 Group specific public goods, orchestration of interest groups with free riding. *Public Choice* **139**, 357–369. (doi:10.1007/s11127-009-9398-y)

134. Kolmar M, Rommeswinkel H. 2010 Group contests with complementarities in effort. *CESifo Working Paper No. 3136*.

135. Lee D. 2012 Weakest-link contests with group-specific public good prizes. *Eur. J. Polit. Econ.* **28**, 238–248. (doi:10.1016/j.ejpoleco.2011.11.003)

136. Nitzan S, Ueda K. 2014 Intra-group heterogeneity in collective contests. *Soc. Choice Welfare* **43**, 219–238. (doi:10.1007/s00355-013-0762-y)

137. Choi JP, Chowdhury SM, Kim J. 2010 Group contest with internal conflict and power inequality. See http://www.vwl1.ovgu.de/vwl1_media/downloads/yrwocat/Chowdhury_Group_Contest.pdf (accessed 4 November 2010).

138. Dechenaux E, Kovenock D, Sheremeta RM. In press. A survey of experimental research on contests, all-pay auctions and tournaments. *Exp. Econ.* (doi:10.1007/s10683-014-9421-0)

139. Puurtinen M, Mappes T. 2009 Between-group competition and human cooperation. *Proc. R. Soc. B* **276**, 355–360. (doi:10.1098/rspb.2008.1060)

140. Burton-Chellew MN, Ross-Gillespie A, West SA. 2010 Cooperation in humans: competition between groups and proximate emotions. *Evol. Hum. Behav.* **31**, 104–108. (doi:10.1016/j.evolhumbehav.2009.07.005)

141. Reuben E, Tyran J-R. 2010 Everyone is a winner: promoting cooperation through all-can-win intergroup competition. *Eur. J. Polit. Econ.* **26**, 25–35. (doi:10.1016/j.ejpoleco.2009.10.002)

142. Egas M, Kats R, van der Sar X, Reuben E, Sabelis MW. 2013 Human cooperation by lethal group competition. *Sci. Rep.* **3**, 1373. (doi:10.1038/srep01373)

143. Markussen T, Reuben E, Tyran J-R. 2014 Competition, cooperation and collective choice. *Econ. J.* **124**, F163–F195. (doi:10.1111/ecoj.12096)

144. Sheremeta RM. 2011 Perfect-substitutes, best-shot, and weakest-link contests between groups. *Korean Econ. Rev.* **27**, 5–32.

145. Sutter M. 2006 Endogenous versus exogenous allocation of prizes in teams: theory and experimental evidence. *Labour Econ.* **13**, 519–549. (doi:10.1016/j.labeco.2005.03.001)

146. Kugler TAR, Pazy A. 2010 Public good provision in inter-group conflicts: effects of asymmetry and profit-sharing rule. *J. Behav. Decis. Making* **23**, 421–438.

147. Chowdhury S, Sheremeta R, Lee D. 2013 Top guns may not fire: best-shot group contests with group-specific public good prizes. *J. Econ. Behav. Organ.* **92**, 94–103. (doi:10.1016/j.jebo.2013.04.012)

148. von Rueden C, Gurven M, Kaplan H, Stieglitz J. 2012 Leadership in an egalitarian society. *Hum. Nat.* **25**, 538–566. (doi:10.1007/s12110-014-9213-4)

149. Cason T, Sheremeta R, Zhang J. 2012 Communication and efficiency in competitive coordination games. *Games Econ. Behav.* **76**, 26–43. (doi:10.1016/j.geb.2012.05.001)

150. Abbink K, Brandts J, Herrmann B, Orzen H. 2010 Intergroup conflict and intra-group punishment in an experimental contest game. *Am. Econ. Rev.* **100**, 420–447. (doi:10.1257/aer.100.1.420)

151. Hamilton WD. 1964 The genetical evolution of social behaviour I. *J. Theor. Biol.* **7**, 1–16. (doi:10.1016/0022-5193(64)90038-4)

152. Taylor PD, Irwin AJ, Day T. 2000 Inclusive fitness in finite deme-structured and stepping-stone populations. *Selection* **1–3**, 153–163.

153. Wilson ML, Kahlenberg SM, Wells M, Wrangham RW. 2012 Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. *Anim. Behav.* **83**, 277–291. (doi:10.1016/j.anbehav.2011.11.004)

154. Watts DP, Mitani JC. 2001 Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour* **138**, 299–327. (doi:10.1163/15685390152032488)

155. Amsler SJ. 2010 Energetic costs of territorial boundary patrols by wild chimpanzee. *Am. J. Primatol.* **72**, 93–103. (doi:10.1002/ajp.20757)

156. Cords M. 2007 Variable participation in the defense of communal feeding territories by blue monkeys in the Kakamega Forest, Kenya. *Behaviour* **144**, 1537–1550. (doi:10.1163/156853907782512100)

157. Mares R, Young AJ, Levesque DL, Harrison N, Clutton-Brock TH. 2011 Responses to intruder scents in the cooperatively breeding meerkat: sex and social status differences and temporal variation. *Behav. Ecol.* **22**, 594–600. (doi:10.1093/beheco/arr021)

158. Richerson PJ, Bettinger RL, Boyd R. 2005 Evolution on a restless planet: were environmental variability and environmental change major drivers of human evolution? In *Handbook of evolution,* vol. 2. *The evolution of living systems* (eds FM Woketits, FJ Ayala), pp. 223–242. New York, NY: Wiley.

159. Wrangham R, Jones J, Laden G, Pilbeam D, Conklin-Brittain N. 1999 The raw and the stolen. Cooking and the ecology of human origins. *Curr. Anthropol.* **40**, 567–594. (doi:10.1086/300083)

160. Wrangham RW, Glowacki L. 2012 Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers evaluating the chimpanzee model. *Hum. Nat.* **23**, 5–29. (doi:10.1007/s12110-012-9132-1)

161. Moll H, Tomasello M. 2007 Cooperation and human cognition: the Vygotskian intelligence hypothesis. *Phil. Trans. R. Soc. B* **362**, 639–648. (doi:10.1098/rstb.2006.2000)

162. Rilling JK. 2011 The neurobiology of cooperation and altruism. In *Developments in Primatology: Progress and Prospects,* vol. 36. *Origins of altruism and cooperation* (eds RW Sussman, CR Cloninger), pp. 295–306. Berlin, Germany: Springer.

163. Vasi I, Macy M. 2003 The mobilizer's dilemma: crisis, empowerment, and collective action. *Soc. Forces* **81**, 979–998. (doi:10.1353/sof.2003.0047)

164. Milinski M, Sommerfeld RD, Krambeck H-J, Reed FA, Marotzke J. 2008 The collective-risk social dilemma and the prevention of simulated dangerous climate change. *Proc. Natl Acad. Sci. USA* **105**, 2291–2294. (doi:10.1073/pnas.0709546105)

165. Burton-Chellew MN, West SA. 2012 Pseudocompetition among groups increases human cooperation in a public-goods game. *Anim. Behav.* **84**, 947–952. (doi:10.1016/j.anbehav.2012.07.019)

166. Geary DC. 2010 *The origin of mind. Evolution of brain, cognition, and general intelligence.* Washington, DC: American Psychological Association.

167. Probst TM, Carnevale PJ, Triandis HC. 1999 Cultural values in intergroup and single group social dilemmas. *Organ. Behav. Hum. Decis. Process.* **77**, 171–191. (doi:10.1006/obhd.1999.2822)

168. Simpson B, Willer R, Ridgeway CL. 2012 Status hierarchies and the organization of collective action. *Sociol. Theory* **30**, 149–166. (doi:10.1177/0735275112457912)

169. Beckerman S, Erickson PI, Yost J, Regalado J, Sparks C, Iromenga M, Long K. 2009 Long Life histories, blood revenge, and reproductive success among the Waorani of Ecuador. *Proc. Natl Acad. Sci. USA* **106**, 8134–8139. (doi:10.1073/pnas.0901431106)

170. Glowacki L, Wrangham R. 2015 Warfare and reproductive success in a tribal population. *Proc. Natl Acad. Sci. USA* **112**, 348–353. (doi:10.1073/pnas.1412287112)

171. Glowacki L, von Rueden C. 2015 Leadership solves collective action problems in small-scale societies. *Phil. Trans. R. Soc. B* **370**, 20150010. (doi:10.1098/rstb.2015.0010)

172. McAuliffe K, Wrangham R, Glowacki L, Russel AF. 2015 When cooperation begets cooperation: the role of key individuals in galvanizing support. *Phil. Trans. R. Soc. B* **370**, 20150012. (doi:10.1098/rstb.2015.0012)

173. Buzzell E, Preston S. 2007 Mortality in American troops in Iraq war. *Popul. Dev. Rev.* **33**, 555–566. (doi:10.1111/j.1728-4457.2007.00185.x)

174. Piff PK, Stancato DM, Cóte S, Mendoza-Denton R, Keltner D. 2012 Higher social class predicts increased unethical behavior. *Proc. Natl Acad. Sci. USA* **109**, 4086–4091. (doi:10.1073/pnas.1118373109)

175. Adams JS. 1963 Towards an understanding of inequity. *J. Abnormal Soc. Inequality* **67**, 422–436. (doi:10.1037/h0040968)

176. Price ME. 2010 Free riders as a blind spot of equity theory: an evolutionary consideration. In *Managerial ethics: managing the psychology of morality* (ed. M Schminke), pp. 235–256. New York, NY: Routledge.