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GROUP SELECTION: THE QUEST FOR SOCIAL PREFERENCES

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Abstract. This paper surveys the literature on group selection. I describe the early contributions and the *group selection controversy*. I also describe the main approaches to group selection in the recent literature; fixation, assortative group formation, and reproductive externalities.

Keywords: Altruism; spite; externalities; conformity; fixation; signalling

JEL Classification: C70; D03; D62; D64

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1. Introduction

Individual selection has been extremely powerful in explaining both human and animal behavior. However, both empirical and experimental studies have found evidence that humans and animals to some degree have social preferences.[1] Several mechanisms to foster social preferences have been advanced in the literature. Nowak (2006) discusses

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[1]The evidence on social preferences is surveyed in Dawes and Thaler (1988), Ledyard (1995), and Gintis, Bowles, Boyd, and Fehr (2003).

five of them.[2,3] They are kin selection, direct and indirect reciprocity, networks,[4] and group selection. All five mechanisms, at least in their modern forms, are within the selfish paradigm. They all amount to saying that an organism may appear to have social preferences, but that these preferences can be explained by appealing to selfishness.

Kin selection was formally analyzed by Hamilton (1964). The idea, popularized by Dawkins (1976), is that organisms are vehicles for genes to spread. Genes thus have selfish reasons to influence their organism into helping other organisms with the same gene. This implies that it is rational for parents to help their offspring, and for siblings to help each other etc. The principle is illustrated by Haldane's famous quote that he would sacrifice his life for "two brothers or eight cousins".

Direct and indirect reciprocity concern repeated interactions. Direct reciprocity, advanced by Trivers (1971), refers to a situation where these interactions take place between the same individuals. Indirect reciprocity instead refers to situations where the interactions take place between new individuals but where each individual has a reputation acquired through earlier interactions.[5]

Network models build on the idea that if individuals interact within smaller clusters, then this may foster cooperation. Typically, as in Eshel et al (1998), it both reduces the gain from deviating and the cost of cooperating by reducing the number of interactions.[6]

Group selection also involves interactions in smaller clusters, however, there is more to it than just a local interaction. There is also some kind of competition between groups. In this survey I will consider three basic approaches to group selection. The first approach is the fixation approach, where the crucial element is the existence of pure groups. The second approach is the assortative group formation approach, where there is a correlation between being a certain type and being matched with others of that type. The third approach is the reproductive externalities approach, where group competition makes it possible to internalize externalities.[7]

[2]Another recent overview of the evolution of cooperation and altruism is provided by Leimar and Hammerstein (2006).

[3]Regardless of how social preferences have been selected for, it should be noted that they are probably not calibrated for all conceivable situations. Instead, they should rather be suited for situations that are, or have been, common to the organism. In fact, to preserve resources, preferences may not even be perfectly tuned for such situations. It may be more economical to have *rule of thumb preferences*. For example, a predisposition towards cooperation is not always beneficial. However, in most cases it may be. If the predisposition is not sufficiently costly, compared to the resources saved, it may be preserved. Thus, in a broader sense, when resources are taken into account, the preferences may still be optimal.

[4]Nowak uses the term network reciprocity. I will instead only call these models network models, to emphasize that repeated interactions are not needed. These models are also called *spatial* models. Nowak argues that the more general term *network* is better suited.

[5]In game theory direct and indirect reciprocity are often treated as variants of the *Folk theorems,* formally analyzed by Aumann (1959), Friedman (1971), Rubinstein (1979), and Fudenberg and Maskin (1986). The Folk theorems imply that if a Prisoner's Dilemma is repeated indefinitely, and with a sufficiently high discount factor, then there exists several subgame perfect Nash equilibria, some of which consist of cooperation in every period.

[6]Other examples are Ellison (1993) and Ohtsuki and Nowak (2006).

[7]The term externality is widely used in Economics. In Biology the term biproduct is typically used. The terms refer to the effects of an action that were not the reason for that action to be taken. If an externality is internalized, then the initiator of the action is made to take into account these effects.

There is some disagreement in the literature as to what the exact definition of kin selection should be. Lehmann et al (2007) write that "kin selection operates whenever interactions occur among genetic relatives, that is, among individuals who tend to share a more recent common ancestor than individuals sampled randomly from the whole population." This is a very broad definition which implies that all of Nowak's five mechanisms are kin selection as soon as the interaction is "among individuals who tend to share a more recent common ancestor than individuals sampled randomly from the whole population". For example, two siblings engaged in repeated interactions would always fall under kin selection and never under direct reciprocity.[8] This definition thus makes it impossible to disentangle different effects from each other whenever relatives are engaged in an interaction. In the papers treated in this survey this is not an issue. In fact, although the word "offspring" is often used, the possibility that individuals may have the same gene, and may help each other for that reason, is simply neglected. This implies that for all practical purposes the individuals are not related and kin selection is not an issue. This interpretation of kin selection is in line with the definition implied by Nowak (2006): "When evaluating the fitness of the behavior induced by a certain gene, it is important to include the behavior's effect on kin who might carry the same gene."

The term inclusive fitness has come to be more general than kin selection. For example, Ricklefs and Miller (2001) define inclusive fitness as "the fitness of an individual plus the fitness of its relatives, weighted according to the coefficient of relatedness". In addition, Grafen (2007) argues that relatedness should be understood as "genetic similarity, however caused, whether by common ancestry, assortation of genotypes or kin recognition". Thus, according to this definition, two individuals having a larger genetic similarity than the rest of the population, but not sharing the same ancestry in any higher degree than the rest of the population, should fall under inclusive fitness, but not under kin selection. Note that this definition excludes two individuals having a larger phenotypic similarity than the rest of the population, but different relevant genotypes.[9] As with kin selection, also the broader concept of inclusive fitness is irrelevant in the papers treated in this survey. In fact, even in the papers treating assortative group formation inclusive fitness is disregarded, and is thus irrelevant.

The paper is organized as follows. First I discuss two symmetric $2 \times 2-$games - Coordination Games and Prisoner's Dilemma games - where group selection is especially relevant. Group selection may of course also be relevant for more complex games, but these games illustrate neatly the two issues that group selection can address. The first issue is the problem of equilibrium selection: If there are several equilibria, can group selection tell us anything about which equilibrium will be played? The second issue is the problem of social preferences: Can group selection lead to locally altruistic behavior being viable? After going through the games and briefly discussing the main arguments of the various approaches, I go on and describe the early literature on group selection, up to the *group selection controversy.* Then I consider the more recent literature,

[8] In particular, Lehmann et al argue that kin selection and group selection is the same process when groups are rarely reshuffled.

[9] The genotype is the genetic constitution of an organism, whereas the phenotype is the observable characteristic of the organism. Thus, different genotypes may result in the same phenotype.

and consider the three main approaches to group selection that have been formally explored.[10] Finally, I conclude.

2. Preliminaries

To fix ideas, let us consider two symmetric 2×2 games where group selection is of special interest.[11] Originally, the payoffs in these games were considered to be von Neumann-Morgenstern utilities, and still generally are. However, here we interpret the payoffs as fitness, typically the number of offspring.

2.1. Coordination Games. In this class of games there are two Nash equilibria in pure strategies. The game (1) is an example of a Coordination Game.

	A	B
A	$1,1$	$0,0$
B	$0,0$	$2,2$

(1)

One Nash equilibrium is for both players to play A. Then they both get a payoff of 1 each. The other pure equilibrium is for both players to play B. Then they both get a payoff of 2 each.

In evolutionary settings, we often think of a large population. We randomly draw two individuals from the population and let them play the game against each other. The payoffs are then the offspring that the individuals get. Thus, if sufficiently many in the population play A, then individuals playing A will get a higher payoff than individuals playing B. Thus, everybody playing A can be an equilibrium outcome despite the fact that the equilibrium where everybody plays B yields more.

Potentially, a group selection model could eliminate the low-yield equilibrium. A very basic model would be to randomly divide the population into groups, and then randomly draw two individuals from each group and let them play a Coordination Game. The individuals and their offspring are then returned to the group they came from. If the population is large and groups are formed randomly, then some groups will converge to the high-yield equilibrium while others will converge to the low-yield equilibrium. Since individuals in the groups that converge to the high-yield equilibrium earn more, they will outgrow the individuals in the low-yield groups.

This sketchy model is in fact only a network model. There is a group structure, but no group selection. However, if we would dissolve groups at some probability - and let them be replaced by new groups formed by individuals from high yielding groups - then we effectively have a group selection model. Canals and Vega-Redondo (1998) have constructed such a model. They consider a subset of Coordination Games, called Stag Hunt games. The game (2) is an example of a Stag Hunt game.

	A	B
A	$4,4$	$0,3$
B	$3,0$	$3,3$

(2)

[10] I can unfortunately not claim to have covered all papers treating group selection. For other surveys of the vast group selection literature, see Sober and Wilson (1998) and Bergstrom (2002). Dugatkin (2002) and Henrich (2004) also have extensive discussion of the concept.

[11] For a complete categorization of symmetric $2 \times 2-$games, see Weibull (1995).

Again, one of the equilibria, namely when everybody plays A, has a higher payoff. This equilibrium is the Pareto dominant equilibrium. However, the low-yield equilibrium is now a bit different from before. Imagine that player 1 has no idea what player 2 will play, and thus assumes that he will play A or B with equal probability. Then player 1 would achieve a higher expected payoff by playing B. This equilibrium is called the risk dominant equilibrium. Another way of understanding the concept is to say that the risk dominant equilibrium has the largest basin of attraction.

In two very influential papers, Kandori, Mailath, and Rob (1993) and Young (1993) showed that, in a standard one-population setting with mutations, the population would spend most of its time close to the risk dominant equilibrium. The reason is that fewer mutations are needed for a population to shift from the Pareto optimal basin of attraction to the risk dominant basin of attraction than vice versa. As a result, a population process with mutations would spend most of its time close to the risk dominant equilibrium. Since there is no group selection in a network model, this will also be the case in these models, as demonstrated by Ellison (1993). Indeed Ellison showed that convergence to the risk dominant equilibrium will be faster in a network model.

However, in a group selection model, the result may be completely different. Groups in the Pareto optimal equilibrium would spread faster than groups in the risk dominant equilibrium. This may compensate for the fact that mutations are more likely to take the group from the Pareto optimal equilibrium to the risk dominant equilibrium, rather than the other way around. As we will see, Canals and Vega-Redondo (1998) show that this is indeed the case when the mutation rate approaches zero.[12]

2.2. Prisoner's Dilemma games. In this class of games, group selection has been more controversial. The game (3) is a Prisoner's Dilemma game. Here both players will play D in equilibrium, despite the fact that if they could commit to playing C, they would both earn more.

	C	D
C	$4,4$	$2,5$
D	$5,2$	$3,3$

(3)

The strategy C is often referred to as an altruistic strategy. The reason is that by playing C a player confers a benefit on the other player while inflicting harm on himself.

A network model in this context would again be to divide the population into groups. Again high-yield groups, i.e. those with many altruists, should grow faster than low-yield groups. However, now the situation is different compared to the Coordination Games. Within each group the best response is to defect. This means that although groups with many altruists may earn more than other groups, each altruist will earn less than a defector in his group. As a result, in the long run the population should converge to everybody defecting.

A theoretical possibility to avoid such an outcome is if neither migration nor mutations are allowed and all players in at last one group play the pure strategy C. Then

[12] One could also assume that individuals would migrate from low yielding to high yielding groups, which would favor the Pareto optimal equilibrium rather than the risk dominant equilibrium. Oechssler (1997), Ely (2002), and Kuzmics (2003) have shown that this is the case.

that group will grow much faster than the other groups and eventually overtake them. Although such models are really network models, they have historically been called group selection models or Haystack models. To somewhat adhere to this tradition I will call them group selection models based on fixation.

Yet another example of a network model often presented as a group selection model is what I will call group selection models based on assortative group formation. In these models there is again no actual competition between groups, but rather a correlation between playing C and ending up in groups where others also play C.

An easy way to extend a network model into a group selection model is to assume that groups are wiped out - with everybody in the group receiving the payoff 0 - with a probability negatively dependent on the sum of payoffs in the group. For example, consider groups of two players. Suppose that groups with only cooperators never are wiped out, whereas mixed groups are wiped out with the probability 0.5, and defecting groups always are wiped out. Then the expected profit of a cooperator in a pure group is 4, whereas it is 1 in mixed groups. The expected profit of a defector is 2.5 in mixed groups and 0 in pure groups. If we start off with an equal proportion of cooperators and defectors in the population, and group formation is completely random, then a player has an equal probability of ending up in a pure group or a mixed group. As a result, a cooperator's expected payoff is 2.5, while a defector's expected payoff is 1.25. Thus, a cooperator has a higher expected payoff than a defector. Models of this type will be called group selection models based on reproductive externalities.

Before we turn to these three approaches to group selection I will briefly discuss the early group selection literature and the group selection controversy.

3. Early contributions

Fittingly, it was Darwin who made the first allusion to group selection in The Descent of Man and Selection in Relation to Sex.[13] The following sentence is often quoted:

> "There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes, and this would be natural selection." (Darwin (1871), page 166.)

Thus, Darwin saw that social preferences could be developed through natural selection. In addition he seems to have held the view that it was some form of competition between groups that would foster these social preferences.

Carr-Saunders (1922) thought that group selection fostered social evolution only among humans. He argued that it came about in primitive societies. These societies were nominally thought to be nomad societies, but Carr-Saunders argued that they were in fact restricted to a territory, within which they evolved social conventions to optimize the potential for long-term survival. Through abstention, abortion, and infanticide, they restricted their numbers so that an optimum number was reached. At this number

[13] Allee (1943) traces the idea "of natural cooperation" all the way back to the Greek philosopher Empedocles (ca. 490–430 BC).

of individuals, the income per head was maximized. These social conventions served to avoid more Malthusian methods of population control, the objective being to avoid social instability.[14]

Among the early contributions, Wright (1945), was the only one to construct a mathematical model. The aim was to show that a "character of value to the population, but disadvantageous at any given moment to the individual" could survive. He noted that if such a *character* - or *strategy* in game theoretical terminology - completely dominated a group, then that group would grow much faster than other groups. However, if a selfish strategy appeared in the group - either by mutation or migration - it would take over the group and the altruistic strategy would disappear.

Wright thus noted that isolation and fixation of the group was necessary for an altruistic trait to be preserved. His idea seems to be based on several groups that are isolated for long times. He argued that drift - i.e. random occurrences in reproduction - could lead to complete domination of altruists in a group. Once fixation had occurred, there would be no way for the selfish trait to reappear in the group, barring mutations and migration. The group would then reproduce much faster than other groups. Eventually, after a long period of isolation, a migration phase would ensue. The group would then spread over the world and a new phase of isolation would follow. A group would eventually drift into fixation, and the cycle would restart.

By stressing isolation and fixation, and the trade-off between migrating altruists and resident egoists, Wright anticipated the haystack model of Maynard Smith (1964). The main conceptual difference is that, as we will see, Maynard Smith considered group formation to be the phase where the altruists had the largest chance of completely dominating a group.

Wynne-Edwards (1962), somewhat like Carr-Saunders (1922), was concerned with the problem of resource management. In particular he wanted to construct a theory to explain how a species, or a group from a species, managed resources to avoid extinction. He drew the parallel to the North Pacific Sealing Convention of 1911. This treaty was an attempt to curb the overfishing of seal in the North Pacific. It came into place after several years of conflict between fishing vessels from various countries, spurred by the scarcity of seals.

If humans could come up with such a treaty - Wynne-Edwards thought - would not animals also be able to construct similar conventions to avoid excessive consumption of resources?[15] He argued that such conventions could also explain why animals were often not living on subsistence levels. He noted that on the fringes of a species' territory they often did. However, in the centers they were in good health - "and sometimes actually fat".[16] Thus, he wanted to find a theory that did not depend on famine, predators, or diseases, but instead depended on social conventions within a territory, group, or

[14] Williams (1966) discusses the advantage of a low variability in numbers. A high variability implies a higher risk of going extinct.

[15] Although he saw humans as able to form social conventions to manage resources, Wynne-Edwards (1963) argued that modern societies had ceased to manage their own numbers, and in that sense provided "a spectacular exception to the general rule."

[16] This would not surprise present day Economists, who would argue that individuals on the fringe are the *marginal individuals*.

species, that optimized the potential for long-term survival within the territory, or of the group or species.

Interestingly, it seems that he did not think of these conventions as being necessarily upheld by strictly altruistic behavior. Instead, he hypothesized that enforcement of population control would not depend on the parents in each case, but instead on other individuals in the group. By interpreting his theory in this way, group selection would not be needed. Instead it would suffice to say that when resources become scarce, then parents have an interest in killing other parent's offspring, which squares well with individual selection. On the other hand, Wynne-Edwards explicitly states that social conventions are based on group selection. He noted that group selection and individual selection might be in conflict, but then argued that group selection would always prevail. The reason, as he saw it, was that if it did not, then the species would go extinct.

4. The controversy

The *group selection controversy* broke out as a result of Wynne-Edwards (1962). Maynard Smith (1964) commented on a companion paper, Wynne-Edwards (1963), and dismissed Wynne-Edwards' theory. Maynard Smith argued that most of the observations that Wynne-Edwards claimed corroborated his theory in fact could just as easily, if not more easily, be explained by individual selection. However, he also went ahead and constructed a mathematical model as to how group selection could work. This model became known as the *Haystack model*.

The model consists of a field with haystacks. A pregnant mouse is placed under each haystack as it is created. The mice then procreate in the haystacks without any migration between them. In the end of each period the haystacks are collected, and the mice are put into one common population. New haystacks are then constructed and a new pregnant mouse, drawn from the new population, is placed under each. The mice can be of two types; aggressive mice, A, who breeds at the same rate irrespectively of the group size; and timid mice, a, who stop breeding when the group reaches a certain size.

Groups starting off with only aggressive mice will eventually run out of resources and will have a period of starving. However, Maynard Smith excludes the possibility that the mice actually go extinct. In groups with both aggressive and timid mice, both breed at the same rate until the population reaches the timid mice's limit. At this limit, the timid mice stop breeding and the aggressive mice take over the group completely. Since their resource management has been slightly better than the group with only aggressive mice, starving starts later in these groups. Finally, in groups that start off with only timid mice, they breed optimally and avoid starving towards the end of the period.

Thus, the model has some features that stand out. First, as already noted, aggressive mice breed aggressively enough to starve, but not aggressively enough to go extinct, which already Wynne-Edwards' noted in his comment to the paper. Second, in mixed groups the timid mice go completely extinct. This feature may be a shortcut to illustrate that the period under the haystack is very long, or at least sufficiently long for suboptimal strategies to be crowded out.

Thus, since groups of aggressive mice do not go extinct, and since timid mice in mixed groups go extinct, the model is biased against timid mice. Nevertheless, the result is that if only isolation is long enough, then the ratio of timid mice in the population will increase. The reason being that groups with only timid mice will grow very large. However, the general feeling among readers was that these long periods of absolute isolation were unrealistic, at least if this type of group selection should be a feature with wide applicability.

A further blow to the group selection argument was Williams (1966). Williams elaborated on Maynard Smith's argument that most of the phenomena ascribed to group selection could be explained by individual selection. Just like Maynard Smith, Williams did not reject group selection flat out, but insisted that the limited possibility of finding phenomena that group selection, but not individual selection could explain, suggested that it was a very weak force.

Williams argued that natural selection required a certain stability among the entities being selected for. Genes, for example, are fairly stable. There might be mutations, but overall they are fairly rare. Groups, on the other hand, are in constant flux, primarily due to migration. Furthermore, an individuals is fairly short-lived, while groups have longer time-spans. This also limits the possibility of more fit groups to replace less fit ones.

In sum, the papers by Maynard Smith and Williams were very influential. They effectively dismissed group selection in the form advanced by Carr-Saunders and Wynne-Edwards. Maynard Smith's Haystack model also for a long time became the benchmark group selection model.

5. Fixation

The contributions of Wright (1945), and Maynard Smith (1964) stressed the importance of fixation, i.e. pure groups, for group selection to have any effect. The underlying idea is that mixed groups will degenerate over time. Pure groups are thus needed for cooperators to survive and eventually thrive. Wright thought of these pure groups coming into existence through drift, while Maynard Smith thought of them coming into existence when groups were formed.

Eshel (1972) extended the fixation approach to focus on migration. He confirmed Wright's conjecture that altruistic traits will dominate the population if migration is sufficiently low. Eshel also argued that an innovation that increases mobility would lead to less altruism.

Traulsen and Nowak (2006) provide a link between fixation models and the reproductive externality models treated later.[17] They divide a population into groups and let the individuals in each group play an n-person prisoner's dilemma game. A single individual is chosen for reproduction with a probability proportional to its fitness. The offspring is put into the same group. When a group reaches the size n two things can happen: With probability q the group is split into two groups and another group is eliminated. With probability $1 - q$ the group is not split up. Instead a randomly selected individual in the group is eliminated.

[17] That link is not intrinsic. Both Wright (1945) and Maynard Smith (1964) disregard reproductive externalities.

The fact that the group can split in two only after it has reached the size n implies that the model is a reproductive externality model. However, to make it mathematically tractable, Traulsen and Nowak focus on the special case when q is very small, instead stressing the fixation effect. The authors analytically show that the smaller the group size and the more numerous the groups, the higher will the probability be that altruists will dominate the entire population.

Traulsen and Nowak then substantially extend Wright's model. They show that the probability that altruists will dominate the population increases with q. The reason is that as q increases it pays off relatively more to be in a group that has reached the size n, which groups with many altruists reach faster than other groups. In that sense the fixation result is an extreme result, giving a lower bound to the probability of altruists thriving in the population. Traulsen and Nowak also extend the model to include migration and multilevel selection. As in Wright (1945) and Maynard Smith (1964), increased migration makes it more difficult to sustain cooperation.

It is interesting to note that the fixation approach to group selection implies that somewhere in the human species' distant past there was a golden era for the evolution of social preferences. However, as mobility increased the circumstance under which altruism was created ceased to exist. In a somewhat related empirical study, Henrich et al (2001) let subjects from 15 small scale societies play the ultimatum game.[18] They found that the modal offers were between 15 and 50 percent, while it is typically 50 percent in industrialized societies. Mean offers varied between 26 and 58 percent, while it is typically 44 percent in industrialized societies. Thus, Henrich et al's findings do not indicate that industrialized societies have less altruists than other societies. If anything, the results rather suggest the contrary.

6. Assortative group formation

Wilson (1975) was the first to analyze how assortative group formation could lead to altruism being sustainable. While earlier models argued that isolation was a precondition for altruism to thrive, Wilson's model can instead be interpreted as a model were groups are reshuffled in every period. However, for altruists to survive in such a model, being an altruist and being matched with an altruist should be correlated.

Wilson notes that this can be achieved through various venues. Group formation based on kin is one of them, but this is only a special case. In subsequent work, e.g. in Sober and Wilson (1998) and Wilson and Dugatkin (1997), the author has discussed various structures that can result in assortative group formation.

Here we will discuss two mechanisms through which assortative groups may arise. First we will discuss the possibility of there being a conformist bias in imitation. Second we will discuss signalling.

6.1. Conformist bias. Experiments in social psychology has established that there seems to be a tendency for individuals to conform to other individuals' opinions.[19] Such

[18] This is a two player game where one player is given a sum of money and the possibility to divide it with the other player. If the other player rejects the division, then neither player gets anything. If he accepts, then that division is executed.

[19] See Aronson, Wilson, and Akert (2007) and DeLamater and Myers (2007) for textbook treatments of conformity.

conformity can be of two types. It can be an informative influence in the sense that other individuals' opinions may reveal useful information. It can also be a normative influence in the sense that individuals may attach an intrinsic value to conforming.[20]

If the conformist bias is important then it would lead to a fairly strong positive correlation between cooperating and being in groups that cooperate. This would thus lead to these groups performing better than other groups. However, to the extent that it is still better to deviate, or not be a conformist, this behavior would not be evolutionary viable.

Boyd and Richerson (1985) argued that individuals using an imitation rule with a conformist bias will be selected for. They argue that once a majority in the population has adopted a new and better behavior, then it is better to imitate that majority rather than to use an unbiased imitation rule. However, one could argue that when the majority has not yet adopted this new behavior, then it would be better to use an unbiased imitation rule - and even better to use a payoff biased imitation rule.

Henrich and Boyd (1998) considered both individual learning and social learning. They compared an unbiased random rule with a conformist rule in a computer simulation, and found that the conformist rule would survive if the environment did not change too often. Individual learning is in general better than social learning if a new and better technology is only used by a small fraction of the population. However, this is also when a conformist bias would perform badly compared to an unbiased imitation rule. Thus a conformist bias is not really better than no bias per se. It is simply that in situations when no bias are better than conformity, then social learning itself will not be successful.[21]

In essence, a conformist rule is better than an unbiased rule if a majority uses the best strategy. Then individuals using the conformist rule will shift over to the best strategy faster than individuals using an unbiased rule. However, the converse is also true. If the majority uses a bad strategy, then individuals using the conformist rule will shift to the best strategy slower than individuals using an unbiased rule. Eriksson et al (2007) modified Henrich and Boyd's model to prolong the period when a new and better technology is used by a minority. As a result, a conformist bias seems never to be an evolutionary stable strategy - although it seemed to be under some parameter values in Henrich and Boyd's setting.

The idea of a conformist bias being the crucial mechanism to uphold altruism is an interesting one. In particular its proponents have noted that it may serve to favor cooperation also in very large groups. However, it should be noted that although conformism may lead to cooperation, it is also costly for the conformist. Thus, if we invoke exogenous conformity then we somewhat push the problem with defectors outside the model. Henrich and Boyd (2001) have attempted to somewhat address this issue. They consider a Prisoner's dilemma augmented by i stages of punishments. I.e. in the first stage those that did not cooperate in the Prisoner's dilemma are punished. In all

[20] Henrich and Boyd (2001) argues that conformist transmission amounts to "using the popularity of a choice as an indirect measure of its worth". This would thus amount to informative conformism discounted by the risk of the measure being incorrect.

[21] Also see Wakano and Aoki (2007) and Nakahashi (2007) for a fuller treatment of Henrich and Boyd (1998).

stages after that people who did not punish in the previous stage are punished. The payoff difference between a payoff biased rule and a conformity biased rule decreases for every stage. Eventually, in stage i, if everybody has at least some conformity in them, this will outweigh the urge to consider the payoff, and everybody will conform - and punish. Since everybody punishes in stage i, everybody will also punish in stage $i-1$. The backward induction is not perfect though. If there are sufficiently large benefits from defection, then everybody will still defect in the Prisoner's dilemma. Nevertheless, if these gains are not large enough, then cooperation will be sustained. The result is that the game has two Nash equilibria, one with defection and no punishment, and the other with cooperation and punishment to the i^{th} level. Adding group selection to the model, the authors argue that the last equilibrium would be chosen.

Guzmán et al (2007) perform simulations to compare an imitation rule with a payoff bias with an imitation rule with a conformist bias. Individuals are only allowed to imitate other individuals within their own group. This means that the group selection effect disappears completely for payoff imitating individuals, who will never cooperate. Conformity imitating individuals, on the other hand, will sometimes end up in groups with many cooperators, and will then reap the group selection benefits through their imitating rule. The crucial mechanism in Guzmán et al is thus that individuals with a payoff bias will only imitate other group members. Thus, the players in this model seem to have fairly limited cognitive abilities. It would be interesting to let the players mental abilities grow, so that they also can imitate other players outside their own group. It seems likely that then a payoff bias would be favored instead of a conformist bias, suggesting that this type of conformity may have been an advantage early in human development, but since then has become a liability.

Richerson and Boyd (2005) argue that culture would tend to favor a conformist rule. Nevertheless, it seems that a conformist biased rule does not seem to be particularly conducive to technological innovations compared to a payoff biased rule. The incentives to innovate will be lower, as will the possibilities to spread new innovations. It is only after an innovation has been made, and after a majority has accepted it, that a conformist bias will perform as well as a payoff biased imitation rule. Thus, it could indeed be the case that a conformist bias is particularly ill suited for a species where innovations play such an important role as for humans. In addition, to the extent that new and better technologies make groups more successful, it seems that group selection itself would favor a payoff biased rule rather than a conformist biased rule.

6.2. Signalling. Another approach towards assortative group formation is to consider signalling before groups are formed. To my knowledge a formal analysis of such a game has not been made.[22] However, Grégoire and Robson (2003) analyze a somewhat similar game. They add the possibility of sending a costly signal before playing a Prisoner's Dilemma, and then add a group structure to the game.

The problem with signalling before playing a prisoner's dilemma, is of course that individuals will be prone to lie. A signal is not a commitment. Even if it is a costly signal, it will be subgame perfect to deviate from it. To make it possible to avoid being taken advantage off by the defectors, Grégoire and Robson allows for a strategy called

[22] Gintis, Smith, and Bowles (2001) consider a model where providing a public good is a costly signal.

the *secret handshake*. This is a promise to cooperate that is only understood by other secret handshakers. In addition, somebody who plays the secret handshake will indeed cooperate when the game is played. The authors also allow for a strategy that takes advantage of secret handshakers. This strategy is called the *sucker punch*. Somebody who plays the sucker punch sends the secret handshake signal, but then deviates when the game is played.

The authors start off with a one-population game. Each player plays a round robin and gets the average payoff. All players then imitate the strategy that earns the highest payoff. Thus, if the entire population is playing defect without a signal, then the population can be invaded by two secret handshake players. The reason is that the secret handshakers will cooperate when playing with each other, but defect when playing with everybody else. The defectors, on the other hand, will always defect. The secret handshakers will thus earn a higher payoff than the defectors, and take over the population. However, this makes it possible for one sucker punch player to invade the population. Finally, when the population is dominated by sucker punch players, then one non-signaling defector may invade the population. As these defectors take over the population, it again becomes possible for two secret handshake players to invade it. Given that the secret handshake needs two mutations to invade a population, while both the sucker punch and the non-signalling defectors only need one mutation, the population will most of the time consist of defectors.

The authors then add a group structure to the model. Players are first playing within the group. They play against all other players in the group and receive the average payoff. All players in each group then imitate the highest yielding strategy in that group. Players are then playing a second round, again within the group, but now they instead imitate the highest yielding strategy in the entire population. Thus, if at least one group happens to be in a cooperative state, then the entire population will switch to that state. As a result, Grégoire and Robson (2003) show that if there are at least three groups, then all stochastically stable states involve cooperation.

To see this, suppose that the entire population is defecting, without sending any signals. A mutation to two secret handshakers within a group would then transform that group into secret handshakers and then transform the entire population to secret handshakers. To leave this state it is required that each group has a simultaneously mutation to at least one sucker puncher. Naturally, the more groups there are, the less likely is this to happen.

Although the signal is made after groups are formed, it seems that the logic of Grégoire and Robson (2003) would translate also into a setting where individuals first signal, then are put into groups, and finally play a Prisoner's Dilemma. In fact, then it seems it would suffice with two mutations to secret handshakers in the entire population - as opposed to within the same group - to transform first one group and then the entire population into secret handshakers. Such a population would be difficult to invade for sucker punchers though. A sucker puncher would transform his group into sucker punchers, but that group would then be transformed back to secret handshakers in the group stage. Thus, for sucker punchers to take over the population there must first be sufficiently many mutations to sucker punchers, and then at least one would have to end up in each group. To my knowledge such a variant of Grégoire and Robson's model

has not yet been explored formally.

An example of signalling that seems be at work both at the group formation stage and at the strategy selection stage is quorum sensing. This phenomenon has been observed especially in bacteria, but also in some social insects. Bacteria that use quorum sensing secrete a signalling substance as a function of how much of the substance it can sense in its vicinity. This can create a feed-back loop attracting and inducing ever more bacteria to secrete the substance. At a certain threshold, the bacteria can sense that they are in sufficient numbers to achieve a certain effect, e.g. bioluminescence, and can then trigger the necessary behavior to achieve that effect.[23] The phenomenon has been quite thoroughly empirically studied, but it at this point it is not certain whether it is altruistic or if group selection is involved.[24]

7. Reproductive externalities

Many activities create externalities for others. That is, an organism's behavior will affect also other organisms' fitness, without this effect on others affecting the first organism's fitness. In economics this is called an externality. Externalities can be *internalized* through different avenues. In some cases, such as air pollution, extended property rights - i.e. rights to pollute - makes this possible. In other cases, such as defense or public roads, a central authority can at least partially ensure that such public goods are provided. In other cases, although much less explored, competition between companies may lead to higher efficiency within each company.[25] In biology a natural way to internalize externalities is through group selection. Groups that provide the public good will be more successful than others, which will lead to provision of that public good to spread. Weibull and Salomonsson (2006) call externalities relevant for organisms' fitness *reproductive externalities*.[26]

Several group selection papers have implicitly used reproductive externalities. Typically, as in Canals and Vega-Redondo (1998), Vega-Redondo (1996), and Traulsen and Nowak (2006), a group is disbanded at some exogenous probability, and high-yielding groups then have a possibility to colonize the disbanded group's niche or territory. Being a high-yield group is thus a public good. To the extent that they affect the provision of this public good, individual behavior consequently have reproductive externalities - and they can be at least partly internalized through group selection. Other papers, such as Weibull and Salomonsson (2006), and Killingback et al (2006) are more explicitly concerned with externalities and public goods.

Canals and Vega-Redondo (1998) generalize the stochastic evolutionary model of Kandori, Mailath, and Rob (1993) into a group selection model. Individuals are subject both to individual selection and a small mutation rate. The individuals are divided into groups, and these groups are disbanded at some rate and replaced by new groups. The members in the new groups can either imitate strategies that earn the highest average

[23] I am gratful to Olof Leimar for the pointer.

[24] See Joint, Downie, and Williams (2007) for a full issue of Philosphical Transactions B dedicated to quorum sensing.

[25] Examples are Boyer and Orléan (1992), Vega-Redondo (1993), Sjöström and Weitzman (1996) and Weibull (2000).

[26] In biology the term by-product has sometimes been used to describe externalities, see e.g. Connor (1995) and Leimar and Connor (2003).

payoff in the general population, or imitate the strategies in the group with the highest payoff. Any weight on the latter imitation rule is thus a weight on group selection. Canals and Vega-Redondo then look at Coordination Games, in particular Stag Hunt games exemplified in game (2) earlier. As Kandori, Mailath and Rob showed, there will be a mutation force within each group leading to the evolutionary process spending most of its time close to the risk dominant equilibrium. The strength of that mutation force will be very weak if the mutation rate is very small. In Kandori, Mailath and Rob's setting this does not matter. However, with Canals and Vega-Redondo's group structure there is a counter balancing force. Each time a group is disbanded a proportion of the new members will imitate the strategies played in the groups with the highest payoff. Letting the mutation rate go to zero, the authors show that group selection will be a much stronger force, and the system will spend most of its time at the Pareto dominant equilibrium, rather than at the risk dominant equilibrium.

The setup in Vega-Redondo (1996) is similar to Canals and Vega-Redondo (1998),[27] but he only lets new group members imitate strategies from groups with the highest payoff. Furthermore, instead of considering a Coordination Game, a Prisoner's Dilemma is considered. As long as the mutation rate is sufficiently small, Vega-Redondo's model result in a stochastic process spending most of its time with all groups composed of cooperating individuals.

In similar models, Vega-Redondo (1993) and Sjöström and Weitzman (1996) discuss the effect of competition on firms' efficiency. Within companies, employees have an incentive to shirk. However, if they do so, then their companies run a larger risk of going bankrupt, implying unemployment for the staff. Vega-Redondo (1993) considers a stag hunt game, whereas Sjöström and Weitzman (1996) consider a prisoner's dilemma. In both cases the total outcome is that competition between firms hinders shirking within firms. In the setting of Sjöström and Weitzman (1996) a technical issue arises with a finite number of firms. Then it is possible that simultaneous degeneration across all firms lead to a long run degeneration of the entire population. However, they show that with an infinitesimal probability of exogenous mutations in favor of cooperation, this degenerative tendency will lead to the same qualitative results as with an infinite number of firms. Weibull (2000) extends the basic textbook Cournot model to take into account managerial owners' trade-off between profit and effort. The result is that stiffer competition leads to a higher effort from managerial owners, i.e. a higher internal efficiency.

Weibull and Salomonsson (2006) consider both positive and negative reproductive externalities. When externalities are positive, for example when a parent protects the group's young, they foster altruism. When they are negative, for example in competition for mates or food, they foster spite.

The model consists of a finite, but large population. Groups of two players are randomly, and non-assortatively, formed in every period. The group members play the game once and receive the material payoffs in terms of offspring. Survival of the offspring, or effective payoff, depends on a function ϕ that depends on both group

[27] The first version of Canals and Vega-Redondo (1998) was published in 1994 as a Universidad de Alicante working paper.

member's material payoffs. This is thus the group selection element in the model. The group members and their surviving offspring is then returned to the population and a new round starts. The function ϕ can be specified to include both within group competition, fostering spite; and within group cooperation, fostering altruism.

Weibull and Salomonsson first consider symmetric $2 \times 2-$games, and then show that when breeding is cooperative, then some games that are Prisoner's Dilemma games in material payoffs are transformed to either Coordination Games, Hawk-Dove games or Efficient Dominance Solvable games in effective payoffs. As a result, an observer only looking at material payoffs would conclude that the players were altruistic, whereas he would conclude that they were selfish if he looked at effective payoffs. In contrast, when breeding is competitive, then some Coordination Games, some Hawk-Dove games, and some Efficient Dominance Solvable games are instead transformed to Prisoner's Dilemma games.

In a more general formulation, and taking into account both cooperative and competitive breeding, Weibull and Salomonsson derive social preferences reflecting both altruism and spite. The derived preferences qualitatively agree with those discussed in Fehr and Schmidt (1999) and Charness and Rabin (2002). They are, for example, consistent with costly punishment.[28,29] Furthermore, they are also consistent with rejections of "unfair" offers that have been observed in ultimatum game experiments.

Since groups are reshuffled in every period, these social preferences will be robust to migration. In contrast to the fixation approach, the reproductive externalities approach does not hinge on groups being isolated for long periods of time. Nevertheless, Williams (1966) also argued that migration would result in all groups being so similar that selection between them would at best be a very weak force. This argument has been empirically refuted by Bowles (2006) who, based on genetic data from recent hunter-gatherer populations, argues that "genetic differences between early human groups are likely to have been great enough so that lethal intergroup competition could account for the evolution of altruism".

Instead social preferences based on reproductive externalities hinge on the existence of public goods. The existence of such goods have presumably varied extensively during history, but can also be assumed to vary across current societies. Thus, a cultural interpretation of the theory could be used to explain the variability of social preferences between societies, as studied by Henrich et al (2001). Note that, in contrast to the fixation approach, there is nothing in this approach that indicates that social preferences should deteriorate as migration increases. In fact, to the extent that an increase in migration coincides with more public goods, social preferences could in fact become even stronger. Interestingly, in the study by Henrich et al, it was found that in societies where

[28] Also see Herold (2004) for an account of how costly punishment and rewarding may be fostered in a group selection model based on reproductive externalities. Technically, Herold's model is based on reproductive externalities since the players know the composition of their groups. Boyd et al (2003) have looked at a similar model using simulation methods.

[29] There is a fairly large literature on costly, or altruistic, punishment. E.g. Boyd et al (2003) has argued that costly punishment is altruistic since it may serve to uphold cooperation. However, Dreber et al (2008) present experimental evidence suggesting that punishment rather triggers retaliations and that punishers earn less than others.

payoffs to cooperation was high, offers in the ultimatum game were also higher. This result is in line with social preferences being fostered in a cultural model of reproductive externalities.

The ability to internalize reproductive externalities will be smaller in larger groups - and still we can observe that humans are often organized in nations of millions, sometimes billions of people. Despite the fact that humans can be organized in very large groups, sociological studies typically report that humans have remarkably few close friends. McPherson et al (2006) reported that the average American in 2004 only had 2.08 close friends with whom to discuss important matters. Although the number was down from 2.94 in 1985, it is striking that this number is much smaller than the number of acquaintances that our brains are thought to be able to handle. Dunbar (1998) argues that our neocortical processing capacity limits the number of acquaintances we are able to keep track of to 150 individuals. It may be that by allowing for networks and hierarchies it would be possible to reconcile these apparent contradictions.

Killingback et al (2006) allow for different group sizes. They consider a public goods game. Individuals are asked to contribute to a common pool. The contributions are then multiplied by a sufficiently large factor and distributed equally among the individuals. The factor is sufficiently large in the sense that in small populations it makes it a unique evolutionary stable strategy to contribute, while it does not make it an evolutionary stable strategy to contribute in large populations. Instead, in large populations, the evolutionary stable strategy is to not contribute. Killingback et al (2006) simulate the results in a model where group sizes are variable. The fact that the number of small groups is non-zero leads to contributions in the overall population being non-zero.

8. Conclusion

Group selection has typically been used to address two issues: equilibrium selection and altruism. The equilibrium selection issue - illustrated by the Coordination Games - has never really been controversial. The recent literature has instead focused on more complex issues, like whether group selection can lead to the Pareto dominant equilibrium, instead of the risk dominant equilibrium, being stochastically stable. As Canals and Vega-Redondo (1998) have shown, that is indeed the case.

Group selection as an explanation of altruism - illustrated by the Prisoner's Dilemma games - has been more controversial. The first formal models by Wright (1945) and Maynard Smith (1964) argued that group selection could only promote altruism if pure groups of altruists were allowed to be isolated for long periods. However, since then group selection has also been found to work through assortative group formation and reproductive externalities.

Group selection based on assortative group formation begs the question of how assortion comes about. A strand of the literature has focused on a conformity bias in imitation which could create assortion, whereas signalling as a means of obtaining assorted groups seems to have been somewhat neglected. An interesting aspect with signalling is that the interpretation of signals will involve culture. E.g. different cultures may develop different signals for the same behavior.

Group selection based on reproductive externalities has been more successful. Vega-Redondo (1996) has shown that it group selection with reproductive externalities will make altruism viable, whereas Weibull and Salomonsson (2006) have shown that reproductive externalities can result in social preferences discussed by Fehr and Schmidt (1999) and Charness and Rabin (2002). In addition Bowles (2006) have shown empirically that genetic differences between early human groups seems to have been sufficient to foster altruism.

Much empirical work remains to be done. For example, it would be interesting to compare the predictions of the fixation approach to the approach of reproductive externalities. The fixation approach predicts that altruism will increase if migration decreases, while the reproductive externalities approach suggests that altruism will increase if the positive externalities increases - as long as they can be internalized through group selection. It would be interesting to see whether these predictions are borne out, and, if so, which approach has more explanatory value. This may also calm some fears that our societies' increased mobility will lead to less altruism, and thus eventually the demise of civilized society. If the increased mobility also creates more positive externalities that we can try to internalize, then it may in fact lead to more altruism rather than less.

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