

Capturing the superorganism: a formal theory of group adaptation

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Keywords:

formal Darwinism;
group as maximizing agent;
group selection;
inclusive fitness;
individuality;
kin selection;
levels of selection;
major transitions;
natural selection;
Price equation.

Abstract

Adaptation is conventionally regarded as occurring at the level of the individual organism. However, in recent years there has been a revival of interest in the possibility for group adaptations and superorganisms. Here, we provide the first formal theory of group adaptation. In particular: (1) we clarify the distinction between group selection and group adaptation, framing the former in terms of gene frequency change and the latter in terms of optimization; (2) we capture the superorganism in the form of a 'group as maximizing agent' analogy that links an optimization program to a model of a group-structured population; (3) we demonstrate that between-group selection can lead to group adaptation, but only in rather special circumstances; (4) we provide formal support for the view that between-group selection is the best definition for 'group selection'; and (5) we reveal that mechanisms of conflict resolution such as policing cannot be regarded as group adaptations.

I have characterized inclusive fitness as 'that property of an individual organism which will appear to be maximized when what is really being maximized is gene survival'... One might generalize this principle to other 'vehicles'. A group selectionist might define his own version of inclusive fitness as 'that property of a *group* which will appear to be maximized when what is really being maximized is gene survival!' Dawkins (1982, p. 187)

Introduction

Darwinism is a theory of the process and purpose of adaptation. It focuses upon the action of natural selection, which is mediated by changes in gene frequencies due to differences in individual reproductive success (Fisher, 1930). Genes that are associated with greater individual reproductive success are predicted to accumulate in the population through the action of natural selection and Darwin (1859) suggested that this process leads to the evolution of well-adapted individuals that have the appearance of being designed for the purpose of achieving reproductive success. Darwinism is a predictive theory of adaptation, explaining not only the origin of

adaptations, but also who wields them and for what purpose.

This traditional conception of Darwinism struggles to explain many social adaptations. For example, the reproductive altruism of sterile workers in eusocial insect colonies is contrary to the idea that individuals are favoured to maximize their personal reproductive success. Darwin (1859) suggested that heritable tendencies (genes) underlying worker characters could be transmitted to future generations indirectly, through the reproductive success of their fertile relatives: a process that has come to be known as 'kin selection' (Fisher, 1930; Haldane, 1955; Hamilton, 1963, 1964, 1970; Maynard Smith, 1964). As a consequence of kin selection, adaptations are not generally expected to function for the good of the individual, but rather to maximize her 'inclusive fitness', i.e. her impact upon the reproductive success of all her relatives (including herself), weighting according to the genetic relatedness of each (Hamilton, 1964, 1970). The theories of kin selection and inclusive fitness boast firm and formal mathematical foundations (Taylor, 1990, 1996; Frank, 1998; Rousset, 2004; Grafen, 2006a; Gardner *et al.*, 2007a), have gathered much empirical support (Krebs & Davies, 1993; Alcock, 2005) and are now regarded as part of the Darwinian canon.

Recently, Wilson & Wilson (2007) have championed an alternative theory of social evolution. Darwin (1871) suggested that social behaviours might also evolve when

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selection operates at levels of organization higher than the individual organism. A costly behaviour that reduces the relative fitness of an actor within its group can be favoured by group selection provided that it brings a sufficient benefit to the group when it is in competition for space or resources with other groups (Price, 1972a; Hamilton, 1975; Wilson, 1975; Okasha, 2006). Recognition of this multilevel selection process has led many authors to suggest that social adaptations arise for the good of the group, and that groups can be viewed as adaptive individuals in their own right – i.e. ‘superorganisms’ (Wheeler, 1911; Marais, 1925; Wells *et al.*, 1929; Emerson, 1932; Wynne-Edwards, 1962, 1993; Seeley, 1989, 1997; Wilson & Sober, 1989; Hölldobler & Wilson, 1990, 2009; Shapiro & Dworkin, 1997; Shapiro, 1998; Sober & Wilson, 1998; Reeve & Hölldobler, 2007; Wilson & Wilson, 2007).

Wilson & Wilson (2007) have suggested that the theoretical foundations of social evolution should be revised so as to embrace this group-oriented approach. However, group selection has already been incorporated into social evolution theory, and is found to be exactly equivalent to kin selection: the two approaches are simply different ways of describing the same evolutionary process and both lead to the prediction that individuals should maximize their inclusive fitness (reviewed by West *et al.*, 2007). The relative neglect of the group selection approach is due to the difficulty in applying its methodology to the biology of real organisms (reviewed by West *et al.*, 2008). By contrast, a proper treatment of group adaptation and the superorganism is lacking, due to difficulties in articulating exactly what these ideas mean, and because of a general failure to distinguish group adaptation from the quite separate issue of group selection (Lloyd, 1999). The problem is of considerable interest, as it lies at the heart of the research programme on the ‘major transitions’ in evolution, which are usually conceptualized in terms of group adaptation and transitions in individuality from organism to social group (Buss, 1987; Maynard Smith, 1988; Maynard Smith & Szathmáry, 1995; Szathmáry & Maynard Smith, 1995; Queller, 1997, 2000; Stearns, 2007).

In this article, we provide a formal foundation for the group-centred view of social adaptation. Our first aim is to formalize the idea of the superorganism in mathematical terms, and we achieve this by drawing on the concept of maximizing agents from economics theory. In particular, we construct a ‘group as maximizing agent’ (GMA) analogy that conveys in a precise way the idea of the social group as a purposeful unit. Our second aim is to capture the process of group adaptation and we achieve this by establishing links between the mathematics of selection and the mathematics of optimization. In particular, we find that there is a strong mathematical correspondence between the dynamics of gene frequency change and the GMA analogy in scenarios where groups comprise genetically identical individuals or where

within-group competition is repressed. This correspondence reveals that, in such scenarios, natural selection acts to optimize group phenotypes for the purpose of group fitness maximization – i.e. group adaptation.

A biological model

The proper basis of evolutionary theory lies in population genetics and so a formal theory of group adaptation must engage with this discipline. In this section, we develop a population genetic model of a group-structured population, complete with a model of group phenotypes, which will serve to anchor ideas of agency and adaptation to be introduced in later sections. We use Price’s theorem to define natural selection, operating within and between groups, in terms of gene frequency change.

Population genetics

We consider a very large, finite population of individuals with arbitrary (although not mixed) ploidy, organized into M groups of size N within which all social interactions take place. (Mathematical notation used in this article is summarized in Table 1.) We assume discrete, nonoverlapping generations and no class structure at the point of census in every generation. Individuals may separate into distinct classes after the census; so, our model does allow for reproductive specialization and other forms of division of labour. Each social group is arbitrarily assigned a unique index $i \in I = (1, 2, \dots, M)$ and, within every group, each individual is arbitrarily assigned a unique index $j \in J = (1, 2, \dots, N)$. We describe an individual’s additive genetic (breeding) value for any character of interest as a linear weighted sum of genic values, or ‘ p -score’ (Price, 1970; Falconer, 1981; Grafen, 1985). This allows for any number of loci with arbitrary interactions: see Frank (1998) for the distinction between an analysis of additive (average) effects and the assumption of additive gene action. We denote the p -score for the j th individual of the i th group as p_{ij} , and so $p_i = \sum_j p_{ij}/N$ is the average p -score of the i th group and $p = \sum_{i,j} p_{ij}/MN$ is the average p -score of the population.

We incorporate demographic uncertainty in reproductive success by assigning a unique index $\omega \in \Omega$ for every possible reproductive outcome for the population, and by denoting the individual’s reproductive success (number of offspring surviving to next census) under outcome ω as w_{ij}^ω . Thus, the reproductive success of the group can be expressed as $w_i^\omega = \sum_j w_{ij}^\omega/N$ and the average reproductive success taken over all individuals in the population is $w^\omega = \sum_{i,j} w_{ij}^\omega/MN$. Averaging over outcomes, weighting according to their probability of occurrence q_ω , the expected reproductive success of the individual is $w_{ij} = \sum_\omega q_\omega w_{ij}^\omega$, the expected reproductive success of the group is $w_i = \sum_\omega q_\omega w_i^\omega$ and the expected reproductive success of the population is $w = \sum_\omega q_\omega w^\omega$. For simplicity, we will assume that density-dependent regulation

Table 1 A summary of notation for the evolutionary model and optimization program.

| Evolutionary model | | Optimization program | |
|---|-----------------------|-----------------------|--------------------------|
| Meaning | Notation | Notation | Meaning |
| Number of groups | M | M | Number of agents |
| Group size | N | – | – |
| Group index | i | i | Agent index |
| Set of group indices | I | I | Set of agent indices |
| Individual index | j | – | – |
| Set of individual indices | J | – | – |
| p -score of j th individual in i th group | p_{ij} | – | – |
| Average p -score of individuals in i th group | p_i | – | – |
| Average p -score in population | p | – | – |
| Reproductive outcome | ω | – | – |
| Set of reproductive outcomes | Ω | – | – |
| Probability of reproductive outcome ω | q_ω | – | – |
| Reproductive success of j th individual in i th group given ω th outcome | w_{ij}^ω | – | – |
| Expected reproductive success of j th individual in i th group | w_{ij} | – | – |
| Reproductive success of i th group given ω th outcome | w_i^ω | – | – |
| Expected reproductive success of i th group | w_i | – | – |
| Average reproductive success of population | $w^\omega = w$ | – | – |
| Group fitness function | $\mathcal{W}(\pi)$ | $\mathcal{F}(\sigma)$ | Objective function |
| Genotype of j th individual in i th group | g_{ij} | – | – |
| Set of individual genotypes | G | – | – |
| Genotype of i th group | γ_i | – | – |
| Group genotype function (clonal groups model only) | $\mathcal{G}(g)$ | – | – |
| Set of group genotypes | Γ | – | – |
| Phenotype of i th group | π_i | σ_i | Strategy of i th agent |
| Group phenotype function | $\mathcal{P}(\gamma)$ | – | – |
| Optimal group phenotype | π^* | σ^* | Optimal strategy |
| Generic group phenotype | π, ϕ | σ, α | Generic strategy |
| Set of group phenotypes | Π | S | Strategy set |

maintains a constant population size of MN at each census; so, $w^\omega = w = 1$ for all $\omega \in \Omega$.

Group phenotypes

Group adaptations are supposed to manifest in the group's phenotype; so, here we develop an explicit model of group phenotypes and their relation to genotypes and reproductive success. We consider a set of all possible individual genotypes G and we denote the genotype of the j th individual in the i th group as g_{ij} . Next, we describe the genotype of a group as a non-ordered list of the genotypes of its constituent individuals. The set of all possible group genotypes is Γ and the genotype of the i th group is denoted γ_i . We next describe a set of all possible group phenotypes Π and denote the phenotype of the i th group as π_i . We assume that the group's phenotype is fully specified by its genotype; so, we can write $\pi_i = \mathcal{P}(\gamma_i)$, and we refer to \mathcal{P} as the phenotype function. Finally, we assume a simple relationship between the group's phenotype and its expected reproductive success: $w_i = \mathcal{W}(\pi_i)/\bar{W}$, where \mathcal{W} is the

fitness function and the scaling factor $\bar{W} = \sum_I \mathcal{W}(\pi_i)/M$ ensures that population size remains constant. Thus, group reproductive success is unaffected by the phenotype of any other group (consistent with our assumption of no between-group social interaction), except in the density-dependent scaling that is applied equally to all groups in any generation. We will find it useful to denote the maximum value of \mathcal{W} over the set of phenotypes Π as W^* .

Natural selection

Natural selection is formally defined in terms of changes in gene frequencies (Fisher, 1930). Here, we will assume that natural selection due to differential reproductive success of individuals is the only process that is responsible for systematic change in gene frequencies. It is well established that non-Darwinian evolutionary processes tend to erode adaptation (Fisher, 1930; Price, 1972b; Grafen, 2003); so, we exclude these in order to present a 'best case' scenario for adaptation. For example, we eliminate sources of systematic change such as

spontaneous mutation and meiotic drive, but by incorporating uncertainty we do allow for random genetic drift. From Price's (1970) theorem, the change in average p -score under outcome ω is given by:

$$\Delta p^\omega = \text{cov}_{I \times J}(w_{ij}^\omega, p_{ij}), \quad (1)$$

where cov denotes a covariance taken over the indicated set and $I \times J$ is the Cartesian product of sets I and J (i.e. the covariance is taken over all individuals in the population, giving equal weighting to each; see also Robertson, 1968). Averaging over uncertainty eliminates random drift; so, the expected change provides a statement of natural selection and is given by:

$$E_\Omega(\Delta p^\omega) = \text{cov}_{I \times J}(w_{ij}, p_{ij}), \quad (2)$$

where E denotes an expectation, or arithmetic average, taken over the indicated set of individuals. Natural selection is defined according to expected change in gene frequency, and is equal to the covariance of p -score and expected relative reproductive success across all the individuals in the population (Grafen, 1999; and see Grafen, 2000 for more discussion on the development of the Price equation for uncertainty).

Equation 2 summarizes the net effect of selection, operating within and between groups, in the form of a single population statistic. Alternatively, we may apply a 'levels of selection' partition (Price, 1972a), which makes the separate contributions of within-group selection and between-group selection more explicit. Equation 2 can be re-written as:

$$E_\Omega(\Delta p^\omega) = \text{cov}_I(w_i, p_i) + E_I(\text{cov}_J(w_{ij}, p_{ij})), \quad (3)$$

so that the total expected response to selection is the sum of the covariance of expected reproductive success and p -score over groups (first term; 'between-group selection') and the average covariance of expected reproductive success and p -score of individuals within groups (second term; 'within-group selection'). This partition provides the formal basis for the theory of levels of selection (Price, 1972a; Hamilton, 1975; Wade, 1985; Frank, 1998; Keller, 1999; Okasha, 2006). Here, it is averaged over uncertainty for the first time.

Capturing the superorganism

A mechanical population model is sufficient for describing the evolutionary process. Nevertheless, social evolution is often – and usefully – conceptualized in other ways. A popular and powerful approach, employed particularly in the discipline of behavioural ecology, is to view the individual organism as an economic agent that is driven to maximize its inclusive fitness. This 'individual as maximizing agent' (IMA) analogy has been explicitly captured in optimization theoretic terms and formally justified, on the basis that it has strong mathematical links to the dynamics of gene frequency change, by Grafen (1999, 2002, 2006a, 2007). The tantalizing

idea that the social group might also be viewed in this way – i.e. as a purposeful superorganism – can similarly be framed in terms of a GMA analogy. In this section, we introduce the formalism of the optimization program, and we apply this to our biological model in order to develop such a GMA analogy. Our sole aim here is to capture the idea of the superorganism in mathematical terms. Formal justification for applying this idea to social evolution will be sought in the next section of this article.

The optimization program

The optimization program is a mathematical device that is regularly employed in economics theory (see the textbook of Mas-Colell *et al.*, 1995) and control theory (see the textbook of Macki & Strauss, 1982), but it is little used in evolutionary theory. In simple terms, an optimization program describes an objective and the means by which that objective might be pursued. The key elements are: (1) the employed strategy, σ ; (2) the set of all possible strategies, S ; and (3) a real-valued objective function $\mathcal{F}(\sigma)$, defined for all $\sigma \in S$, that describes how well the employed strategy realizes the objective. A better strategy yields a higher value of the objective function and so the optimization program defines a maximization problem where the maximand (quantity to be maximized) is the value of the objective function, i.e.

$$\sigma \max_{\sigma \in S} \mathcal{F}(\sigma). \quad (4)$$

The optimization program provides a mathematical framework for describing goal-oriented phenomena, and so it formally captures the ideas of purpose and function, and it can be interpreted as specifying the agenda of some implicit agent: the strategist. The optimization program also provides a mathematical definition of optimality: an optimal strategy is one that maximizes the objective function within the constraints of the strategy set (it solves the optimization program). Formally, a suboptimal strategy $\sigma \in S$ is defined by the existence of some other strategy $\alpha \in S$ such that $\mathcal{F}(\alpha) > \mathcal{F}(\sigma)$, and an optimal strategy $\sigma^* \in S$ is defined by $\mathcal{F}(\sigma^*) \geq \mathcal{F}(\alpha)$ for all $\alpha \in S$. Note that the optimization program provides an explicit statement of a problem, without the implication that this problem is actually solved. In other words, it establishes the idea of a goal, purpose or function, without implying optimality.

The 'group as maximizing agent' analogy

We have introduced the concept of the optimization program. We now apply this formalism to our biological model, developing a GMA analogy in which the social group is described as a purposeful being with its own agenda. This captures the superorganism concept in explicit, mathematical terms.

The first step is to locate the agent that is implicitly defined by an optimization program as an explicit object in the biological model. As we are forming a GMA analogy, the agent is identified as the social group. More precisely, as there are M social groups in the biological model, we describe M agents, each with its own optimization program. We index agents and their corresponding optimization programs according to the indexing of groups, i.e. $i \in I$. Second, we equip each superorganism with an instrument to be used in the pursuit of its agenda, by identifying the i th social group's phenotype as the i th agent's strategy, i.e. $\pi_i \equiv \sigma_i$. Third, we summarize the constraints faced by the superorganism, by identifying the set of all possible group phenotypes as the strategy set, i.e. $\Pi \equiv S$. These three steps formalize the idea of the group as a purposeful agent – without specifying its agenda – and can be summarized in the form of an optimization program:

$$\pi_i \max_{\pi_i \in \Pi} \mathcal{F}(\pi_i). \tag{5}$$

The fourth, unspecified element of the GMA analogy is the objective function, \mathcal{F} . The idea of the superorganism – i.e. of the group as a purposeful agent – does not in itself commit us to any particular objective function; this decision is largely arbitrary. However, in the spirit of the existing literature on superorganisms (e.g. Wilson & Sober, 1989; Sober & Wilson, 1998), we will proceed on the assumption that the group's objective is to maximize its expected reproductive success, and we write:

$$\pi_i \max_{\pi_i \in \Pi} \mathcal{W}(\pi_i). \tag{6}$$

One benefit deriving from this formal approach is that we can make such a clear distinction between those aspects of the traditional superorganism concept that necessarily follow from the core idea of the group as a maximizing agent, and those aspects that may be adjusted according to our personal tastes. In the Discussion, we revisit the

issue of choice of objective function and suggest that this presents an interesting avenue for future research.

The explicit GMA analogy captured in expression 6 permits us to make formal statements regarding the optimality, or 'aptness', of group phenotypes. This is simply the extent to which the phenotype realizes the superorganism's agenda, and it is given by the fitness function. A suboptimal phenotype $\pi \in \Pi$ is defined by the existence of a variant phenotype $\phi \in \Pi$ such that $\mathcal{W}(\phi) > \mathcal{W}(\pi)$, whereas an optimal phenotype $\pi^* \in \Pi$ is defined as satisfying $\mathcal{W}(\pi^*) \geq \mathcal{W}(\phi)$ for all $\phi \in \Pi$.

The GMA analogy is a statement of an optimization problem, and it does not imply that this problem has been solved. In other words, it captures the agenda of the social group, and the purpose of the group's phenotype, without implying that the group's phenotype is actually optimal. The GMA analogy provides a way of looking at social groups as purposeful, economic agents, but we have not yet provided any justification for this group-oriented view. Formal justification will be sought in the next section of this article, in which we pursue a theory of group adaptation.

A formal theory of group adaptation

Adaptation is the process of optimization of the phenotype under the action of natural selection. A formal theory of adaptation must therefore make explicit links between the mathematics of optimization and the mathematics of selection. Such links have been established for individual-level adaptation, i.e. the theory of inclusive fitness (Table 2; Grafen, 2002, 2006a). They reveal that natural selection acts according to the design principle of inclusive-fitness maximization. In this section, we seek to establish similar links between group optimization (captured by the GMA analogy) and multilevel selection (captured by the Price equation), to provide a formal theory of group adaptation.

Table 2 Adaptation of individuals and groups.

| Correspondence | Description | Group as maximizing agent | | | |
|----------------|---|--------------------------------|---------------|---------------------------|---------------|
| | | Individual as maximizing agent | Clonal groups | Repression of competition | General model |
| I | If all agents are optimal, then there is no scope for selection | Yes | Yes | Yes | No |
| II | If all agents are optimal, then there is no potential for positive selection | Yes | Yes | Yes | No |
| III | If all agents are equally suboptimal, then there is no scope for selection | Yes | Yes | Yes | No |
| IV | If all agents are equally suboptimal, then there is potential for positive selection | Yes | Yes | No | No |
| V | If agents vary in their optimality, then the change in every gene frequency is given by its covariance with the agent's relative maximand value | Yes | Yes | Yes | No |
| VI | If there is no scope for selection and no potential for positive selection, every agent behaves optimally | Yes | Yes | No | No |

The theory of individual-level adaptation (inclusive fitness theory) is formally justified on the basis of six mathematical correspondences between the action of natural selection and the optimization of the individual's phenotype (Grafen, 2002, 2006a). The theory of group-level adaptation and superorganisms is fully justified for clonal groups (six correspondences hold), is partially justified for groups that have complete repression of internal competition (four correspondences hold) and is not justified when group mates are nonclonal and permitted to compete (zero correspondences hold).

Clonal groups

We begin by assuming a special case of our biological model that is expected to be particularly conducive to group adaptation: where social groups comprise genetically identical individuals. In kin selection terms, the coefficient of genetic relatedness between individuals within groups is unity for every trait. Formally, we write $g_{ij} = g_i$ and $p_{ij} = p_i$ for all $i \in I$ and all $j \in J$. This means that the group's genotype and phenotype are both fully specified by the genotype of any individual drawn from that group, i.e. $\gamma_i = \mathcal{G}(g_i)$ and $\pi_i = \mathcal{P}[\mathcal{G}(g_i)]$. This allows us to define a 'group optimal' individual genotype g^* that satisfies $\mathcal{P}[\mathcal{G}(g^*)] = \pi^*$. As genetic variation is a necessary requirement for a response to selection, the assumption of genetic homogeneity within groups abolishes within-group selection. Mathematically, $\text{cov}_j(w_{ij}, p_{ij}) = 0$ for all $i \in I$ and hence, from eqn 3, the action of natural selection is given by:

$$E_{\Omega}(\Delta p^{\omega}) = \text{cov}_I(w_i, p_i). \quad (7)$$

Thus, for the special case of clonal group mates, the evolutionary dynamics of gene frequency change depends only upon between-group selection.

With these assumptions in place, we are able to establish strong mathematical links between the GMA analogy given by expression 6 and the dynamics of gene frequency change described by eqn 7. In particular, we can write the following six correspondences (see Appendix for mathematical details, and Table 2 for a summary):

- I. If all agents behave optimally, then there is no scope for selection (i.e. no expected change in any gene frequency);
- II. If all agents behave optimally, then there is no potential for positive selection (i.e. no introduced genetic variant is favoured when rare);
- III. If all agents behave suboptimally, but equally so, then there is no scope for selection;
- IV. If all agents behave suboptimally, but equally so, then there is potential for positive selection (i.e. at least one introduced genetic variant will be favoured when rare);
- V. If agents vary in their optimality, then there is scope for selection, and the expected change in all gene frequencies and in the additive genetic component of every trait is given by its covariance with the agent's relative maximand value; and
- VI. If there is no scope for selection and no potential for positive selection, then every agent behaves optimally.

Correspondences I–V translate the mathematics of group optimization into the mathematics of selection: they each begin with a scenario within the GMA analogy, and use this to recover the dynamics of gene frequency change. Correspondences I and III collectively provide an equilibrium condition: there is no expected change in any gene frequency if all group phenotypes have the same degree of optimality. Correspondences II

and IV collectively provide a stability condition: the equilibrium is stable against invasion by rare, introduced genetic variants if (and only if) all group phenotypes are currently optimal. Correspondence V describes the out-of-equilibrium dynamics: the expected direction and magnitude of change in all genetic characters is correctly predicted by the optimization view. Finally, correspondence VI translates the mathematics of selection into the mathematics of group optimization, considering a scenario regarding the gene frequency dynamics and using this to recover an optimization interpretation. In particular, if the population is at a stable equilibrium, then all group phenotypes can be said to be optimal.

These six correspondences provide a formal justification for using the GMA analogy as a way of thinking about clonal groups: for this special case of the biological model, group optimization provides a powerful tool for making predictions about the dynamics of gene frequency change under the action of natural selection. It also captures the sense in which, provided the right genetic variation is available, natural selection acts to draw the population away from suboptimal states, and will continue to do so until all group phenotypes are optimal. This process of group optimization – and here we do not imply that optimality is actually obtained (cf. Williams, 1992) – is the process of group adaptation.

Analogous mathematical correspondences between selection and optimization have been derived by Grafen (2002, 2006a) for the IMA analogy, which underlies the theory of individual-level adaptations – i.e. inclusive fitness theory. In fact, we have found (perhaps unsurprisingly) that there is no mathematical difference between an individual organism and a clonal group, in this respect. Thus, to the extent that the above six correspondences between the GMA analogy and the action of natural selection hold, for any given biological model, there is formal justification for the view that the social group is an individual in its own right (superorganism), and that natural selection acts to optimize the group's phenotype (group adaptation).

Repression of competition

We now consider an alternative special case of our biological model, in which we allow for genetic variation within groups, but we now assume that there is no variation in expected reproductive success within groups ('repression of competition'; Frank, 2003). Formally, we can write $w_{ij} = w_i$ for all $i \in I$ and all $j \in J$. This special case is similar to, although more general than, a verbal model described by Wilson & Sober (1989) in which there were no differences in realized reproductive success within groups, and hence reproductive division of labour was not permitted. By contrast, because it is expected (and not realized) reproductive success that is constrained to be equal within groups in our model, we

allow for such complexities as sterile workers. Although there are no differences in expected reproductive success within groups, the expectation of group reproductive success is permitted to vary between groups. Hence, although within-group selection is abolished ($\text{cov}_J(w_{ij}, p_{ij}) = 0$ for all $i \in I$), there is scope for selection to operate between groups and the action of natural selection is again described by eqn 7.

We find that, for this model of competition repression, only four of the previous six correspondences between the GMA analogy and the dynamics of gene frequency change continue to hold (see Appendix for mathematical details and Table 2 for a summary). Because repression of competition abolishes within-group selection, simply by considering fitness effects at the group level, one can correctly predict the scope for (and response to) natural selection (correspondences I, III and V hold). Moreover, because no group can attain higher than average expected reproductive success in an already optimal population, in such a scenario there is no potential for positive selection (no rare genetic variant can invade; correspondence II holds).

However, at a suboptimal selective equilibrium, there is no guarantee of a potential for positive selection (i.e. for some genetic variant to invade from rarity; correspondence IV fails). This is because, although an improved group phenotype is possible, there is no guarantee that corresponding genetic variants will arrange themselves together in groups in such a way as to give rise to the desired group phenotype. No such problem exists for clonal groups, because the genetic composition of the individual determines the group's phenotype; so, introducing the appropriate genetic variant into the population is sufficient to ensure that the desired group phenotype obtains. A consequence of this failure is that, for competitively repressed groups, not all stable equilibria are optimal (correspondence VI fails). Thus, for this special case of the biological model, there is only partial justification for the view that the social group is an individual in its own right and that natural selection acts to optimize the group's phenotype.

General model

We now consider that group mates can vary both genetically and in their expected reproductive success, i.e. the most general form of our biological model. Because selection is free to occur both within and between groups, the dynamics of gene frequency change are described by eqn 3, and not by eqn 7.

We find that, for this general scenario, none of the six correspondences between the GMA analogy and the gene frequency dynamics continue to hold (see Appendix for mathematical details and Table 2 for a summary). Because within-group selection cannot be ruled out, an analysis based solely upon the group's expected reproductive success may fail to correctly

identify selective equilibria (correspondences I and III fail) can misdiagnose stable states (correspondences II and IV fail), and is liable to incorrectly predict the direction and magnitude of genetic change when this does occur (correspondence V fails). As a consequence of these failures, there is no guarantee that a given stable state corresponds to a group optimum (correspondence VI fails). Hence, for this more general version of the biological model, we find no formal justification for the view that the social group is an individual in its own right or that natural selection acts to optimize the group's phenotype.

Discussion

Group adaptationism is the idea that groups of organisms can be viewed as adaptive units in their own right. In contrast to the success of the theory of individual-level adaptation, progress on the issue of group adaptation has been extremely slow. We suggest that this is due to a confusion of 'levels of selection' with 'levels of adaptation' in evolutionary biology, and also due to a difficulty in providing appropriate definitions for terms such as 'group adaptation' and 'superorganism'. In this article, we have developed a formal theory of group adaptation, holding the idea to the high standards set by the theory of individual-level adaptation (inclusive fitness theory; Hamilton, 1964, 1970; Grafen, 2006a). In particular, we have formally separated the issues of levels of selection and levels of adaptation, framing the former in terms of dynamics and the latter in terms of optimization. We have formally captured the function of group adaptation using an analogy between biology and optimization that regards the social group as a purposeful agent (superorganism) that is striving to maximize its reproductive success. Finally, we have established strong links between the mathematics of group optimization and the mathematics of gene frequency change, providing formal justification for group adaptationism, but only for scenarios in which within-group selection has been completely abolished. Importantly, we have failed to find any justification for group adaptationism for scenarios in which within-group selection is permitted.

Our approach to group adaptation has been strongly informed by the theory of individual-level adaptation (inclusive fitness theory; Hamilton, 1964, 1970; Grafen, 2006a). The idea that individual organisms exhibit adaptation does not imply the perfection of organismal design nor even that adaptations are optimal within certain constraints, but rather it is to say that individual organisms appear contrived as if towards some purpose; a quality that is evident only because all the adaptations wielded by the individual appear contrived for the *same* purpose (Paley, 1802; Queller, 2000). The conventional view is that the purpose of individual-level adaptations is to maximize the inclusive fitness of the individual (Hamilton, 1964, 1970, 1996). This idea is formally

captured as an IMA analogy, and is formally justified on the basis of its strong mathematical correspondence with the dynamics of gene frequency change: natural selection acts according to a design principle of inclusive-fitness maximization (Grafen, 2006a). However, the ultimate validation of inclusive fitness theory comes from its overwhelming empirical and experimental support (Krebs & Davies, 1993; Alcock, 2005).

Our analysis makes a crucial distinction between the target of selection and the function of adaptation (Grafen, 2006a). Natural selection favours those individuals with greater personal reproductive success (Darwin, 1859; Fisher, 1930; Price, 1970), but it generates adaptations that function to maximize inclusive fitness (Hamilton, 1964, 1970; Grafen, 2006a). Hence, the function of adaptation (inclusive fitness maximization) is distinct from the target of selection (personal fitness). Unfortunately, previous theory on group adaptation has failed to make this distinction, contributing to a confusion between levels of adaptation and levels of selection. For example, the 'superorganism continuum' (SC) approach to levels of adaptation (Wilson & Sober, 1989; Sober & Wilson, 1998; Reeve & Hölldobler, 2007) conflates the levels of selection partitioned into within-group fitness versus between-group fitness and the function of adaptation at the individual vs. group levels. In a departure from inclusive fitness theory, the SC approach suggests that the function of individual-level adaptation is to maximize the individual's personal fitness relative to her group mates and, observing that between-group selection pushes phenotypic characters away from this 'individual optimum' and towards the group optimum of group fitness maximization, Wilson and colleagues have interpreted a response to between-group selection as defining group adaptation itself. By contrast, we emphasize that the function of individual-level adaptation is to maximize inclusive fitness and that this obtains irrespective of the relative strength of within-group vs. between-group selection. Moreover, if we want the term 'adaptation' to retain its meaning as we move from the individual to the group level, then group adaptation is not simply a response to between-group selection, but instead a rather stronger notion of group optimization – that only obtains if within-group selection is completely abolished.

We have found no formal justification for group adaptationism in any scenario in which within-group selection is permitted. Obviously, no real-world species will perfectly embody the ideal of zero within-group selection. However, we emphasize that this is not sufficient grounds for abandoning the notion of group adaptation in evolutionary biology. The theory of individual-level adaptation is similarly based upon limiting assumptions, such as unbiased genetic transmission, which are not expected to be perfectly realized in any species (Grafen, 2002, 2006a); yet, it enjoys huge experimental and empirical success. A more pragmatic

approach is to employ the theory of individual-level adaptation on the understanding that complications such as Mendelian outlaws are the exception rather than the rule, at least insofar as we are interested in understanding phenotypic evolution. Similarly, we suggest that group adaptationism has validity in scenarios where within-group selection can be considered to have negligible impact upon phenotypic evolution. This may be valid for some species; clearly it is not valid for most species. More generally, the major aim of our study is to highlight the logical error in the view that multilevel selection (including within-group selection) leads to the emergence of group adaptation (e.g. Sober & Wilson, 1998).

We have also made a crucial distinction between group adaptation and group optimality, mirroring the more general idea that adaptation is not synonymous with optimality (Paley, 1802; Williams, 1992). An adaptation is a character that, through the action of natural selection, has become contrived as if for a purpose (Darwin, 1859). A group adaptation, as conceived in our analysis, is a group character that has been selected according to the design principle of group-fitness maximization. A character that has not been selected according to this principle, but which incidentally improves group reproductive success, can be described in terms of 'group optimality', but does not constitute a group adaptation. Conversely, a character that has evolved according to the principle of group optimization, but which does not achieve optimality (for example, owing to insufficient time), is nevertheless a group adaptation. Previous quantitative approaches to group adaptation have often actually provided measures of group optimality. For example, Foster's (2004) approach to group adaptation is to express the fitness of a focal group relative to that of an idealized group that is assumed to have maximal fitness; in terms of our notation, this measure of group optimality is $\mathcal{W}(\pi)/\mathcal{W}(\pi^*)$. We suggest that it will often be useful to measure group optimality, but warn that this is not synonymous with group adaptation. The question of how group adaptation – or indeed, any form of adaptation – is to be measured is one that we leave open for the future.

We have defined a superorganism as a group that wields adaptations in its own right, and have found formal justification for this idea in scenarios where within-group selection is completely abolished. It is unlikely that within-group selection will ever be entirely absent in any real-world species; however, the ideas of superorganism and group adaptation might usefully be employed when thinking about social groups that have mechanisms that abolish almost all within-group conflict for the majority of traits. Certain eusocial insect colonies are obvious candidates. For example, worker policing in honeybee colonies ensures an almost complete repression of competition, so that most traits observable at the group level can be understood in terms of optimization of

group fitness (Seeley, 1989, 1997). Previous theory has emphasized a sterile worker caste as a definitive hallmark of the superorganism (e.g. Wheeler, 1911; Wells *et al.*, 1929; Buss, 1987; Hölldobler & Wilson, 2009). However, our analysis suggests that sterile workers are neither necessary nor sufficient for superorganismality. A clonal group evolves group adaptations and can be considered a superorganism even if none of its members are sterile (sterile caste not necessary), and even sterile workers can be embroiled in conflicts over such group characters as the sex ratio (Trivers & Hare, 1976), which cannot be understood in terms of group optimization (sterile caste not sufficient). Although a sterile caste remains a useful diagnostic for identifying potential superorganisms, we suggest that it is not fundamental. Hence, the evolution of an extreme reproductive division of labour in a mathematical model does not equate to the emergence of a superorganism (e.g. Michod, 2007).

An evolutionary transition in individuality from organism to social group is the basis for several of the 'major transitions' in evolution (Buss, 1987; Maynard Smith, 1988; Maynard Smith & Szathmáry, 1995; Szathmáry & Maynard Smith, 1995; Queller, 1997, 2000; Stearns, 2007). Our analysis of groups as fitness maximizing agents permits a formal definition for when this has happened – insofar as the GMA analogy mathematically corresponds to the dynamics of gene frequencies, a major transition can be said to have occurred – and confirms that the key step is an abolition of selection operating at the lower level, leading to the termination of internal conflicts. The two mechanisms for conflict resolution highlighted in our analysis have long been recognized in the literature on major transitions in individuality. First, clonal relatedness ensures that the interests of social partners exactly coincide, because their ultimate objective (inclusive fitness) is necessarily the same (Hamilton, 1964; Maynard Smith & Szathmáry, 1995). The major transition from protozoan cell to multicellular animal is crucially founded upon a single-cell bottleneck at the initialization of development, which ensures (*de novo* mutation aside) the clonality of the animal's tissues (Maynard Smith & Szathmáry, 1995). Second, a complete repression of within-group competition ensures that the only means by which an individual can maximize its fitness is to pursue the greater good of the social group (Leigh, 1977; Alexander, 1979, 1987; Frank, 2003). Although social partners may differ in their ultimate objectives, here the strategy set is constrained in such a way as to bring them into more proximate agreement for action. Repression of competition is exemplified in the rules of fair meiosis and worker policing in insect societies (Leigh, 1971; Wenseleers *et al.*, 2004a; Wenseleers & Ratnieks, 2006).

We have confirmed the role for mechanisms of conflict resolution in the evolution of higher level individuality. However, the concept of the superorganism cannot itself account for the evolution of such mechanisms – the

superorganism comes into existence after these mechanisms are already established – and hence it provides only limited illumination of the process of such transitions (Maynard Smith & Szathmáry, 1995). In other words, mechanisms of conflict resolution are a cause, rather than a consequence, of group adaptation. This suggests that phenomena, such as punishment, policing and high genetic relatedness, cannot be understood as group adaptations (*contra* Wilson & Sober, 1989; Wilson & Hölldobler, 2005; Wilson & Wilson, 2007). Conversely, insights into the evolution of mechanisms of conflict resolution may be provided by inclusive fitness theory. For example, worker policing in honeybees may be understood in terms of adaptation at the level of the individual worker, motivated by nepotistic interests that need not coincide with the best interests of the colony (Ratnieks, 1988; Ratnieks & Visscher, 1989; Wenseleers & Ratnieks, 2006).

Our analysis of group adaptation offers a potential resolution to the controversy over the correct definition of 'group selection'. Perhaps the most popular approach follows from the levels of selection partition of Price's equation, so that group selection is synonymous with what we have termed 'between-group selection' (Price, 1972a; Hamilton, 1975; Okasha, 2006). However, a potential problem of this definition is that it may diagnose the operation of group selection even in nonsocial contexts; for example, if some groups contain more individuals with better eyesight, then some component of selection operating upon eyesight will be at the between-group level (Hamilton, 1975). It has been argued that this is an undesirable feature for any theory of group selection (Sober & Wilson, 1998; Wilson & Wilson, 2007) and other definitions have been considered. An alternative is the 'contextual analysis' approach of Heisler & Damuth (1987) (see also Damuth & Heisler, 1988; Goodnight *et al.*, 1992), which identifies the impact of group phenotype on an individual's fitness, once all the effects of the individual's phenotype has been stripped away. However, this suffers from problems such as identifying group selection in operation even when all groups have the same fitness (soft selection; reviewed by Okasha, 2006; West *et al.*, 2008). Hence, the proper definition of group selection remains elusive (Wilson & Wilson, 2007). Following Williams (1966) (see also Sober & Wilson, 1998; Wilson & Wilson, 2007), we suggest that a useful approach is to define group selection as that part of gene frequency change that is responsible for group adaptation. Our analysis has identified Price's (1972a) between-group selection as the driver of group adaptation, and hence we suggest that this provides the most useful definition for group selection. In our biological model, it is defined as $cov_I(w_i, p_i)$. We hope that a concrete definition, that demystifies this straightforward evolutionary process by showing that it has no special connection to social behaviour, will allow semantic debate to give way to scientific progress on this topic.

Our intention has not been to develop a general theory of group adaptation, but rather to clarify concepts and to provide an illustration of what a formal theory of group adaptation should look like. Thus, there are several crucial directions in which our basic analysis could be extended. First, our biological model lacks class structure – at the time of census, there is no separation of individuals into male vs. female, or juvenile vs. adult, and mixed ploidy is disallowed. By contrast, the best examples of putative group adaptation and superindividuality come from the eusocial insects (Wheeler, 1911; Marais, 1925; Wells *et al.*, 1929; Emerson, 1932; Wilson & Sober, 1989; Hölldobler & Wilson, 1990, 2009; Sober & Wilson, 1998; Reeve & Hölldobler, 2007; Wilson & Wilson, 2007), which present complexities such as age-structured societies with haploid males and diploid females. In general, class structure has been relatively neglected by group selection theory (West *et al.*, 2008; but see Wenseleers *et al.*, 2003, 2004b), whereas it has been properly integrated into individual selection theory (Fisher, 1930; Hamilton, 1972; Price & Smith, 1972; Taylor, 1990, 1996; Charlesworth, 1994; Grafen, 2006b) and is very amenable to kin selection analysis (Taylor, 1996; Taylor & Frank, 1996; Frank, 1997, 1998; Taylor *et al.*, 2007) – see Gardner *et al.* (2007b) for a recent worked example. Second, because optimization programs are rather alien to biologists, we made expression 6 as simple as possible, focusing on hard-wired phenotypes and disallowing flexible behaviours. However, reaction norms are readily incorporated into this formalism – see Grafen (2002) for further treatment.

Third, in line with the common assumption employed in the literature, we have assumed that the function of group adaptation is to maximize the (expected) reproductive success of the group (e.g. Wilson & Sober, 1989; Sober & Wilson, 1998). This approach to group adaptation is formally justified for groups in which there is no internal conflict, but is not formally justified in any other scenario. However, in forming the GMA analogy, we were free to choose any objective function, and we raise the interesting possibility that some other objective function might support group adaptationism in a wider class of models. By analogy, the discovery that indirect fitness effects could lead to the evolution of altruistic behaviour delivered a devastating blow to the traditional Darwinian view of individuals striving to maximize their reproductive success, yet the theory of individual-level adaptation was salvaged owing to the development of a new objective function – inclusive fitness (Hamilton, 1963, 1964, 1970, 1996). An analogue to inclusive fitness, that similarly rescues group adaptationism from the problems imposed by within-group selection, might await development. The search for such an ‘inclusive fitness for groups’ (Dawkins, 1982) should be at the forefront of the group adaptationist research programme.

Conclusions

We have developed the first formal theory of group adaptation. This has: (1) clarified the distinction between levels of selection and levels of adaptation; (2) formed mathematical links between population genetics theory and optimization theory via a GMA analogy; (3) demonstrated that between-group selection can lead to group adaptation, but only in rather special circumstances; (4) provided formal support for the view that between-group selection is the best definition for ‘group selection’; (5) revealed that mechanisms of conflict resolution such as policing cannot be regarded as group adaptations and (6) pointed out key directions for future group adaptation research. Our emphasis has been on formality and not generality – there is much work to be carried out to establish whether other scenarios will admit a group adaptationist view of social evolution. In the meantime, we suggest that it is safer to view social adaptations as occurring at the level of the individual organism, where they function to maximize inclusive fitness.

Acknowledgments

We thank Nick Barton, Brian Charlesworth, Troy Day, Ford Denison, Kevin Foster, Steve Frank, Alex Kalinka, Laurent Keller, Rolf Kümmerli, Peter Nonacs, David Queller, Thom Scott-Phillips, David Shuker, Joan Strassmann, Peter Taylor, Francisco Úbeda, John Welch, Stu West, Mike Whitlock and two anonymous reviewers for discussion and comments on earlier versions of the manuscript. Andy Gardner was supported by a Junior Research Fellowship from St John’s College, Oxford, and a University Research Fellowship from the Royal Society.

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Appendix

Here, we use the GMA analogy to prove the six mathematical correspondences (I–VI, see Table 2) between the optimization program and the action of natural selection for the clonal groups model. We also note when and why

each correspondence holds or fails for the repression of competition model and the general model.

I. If all agents behave optimally, then there is no scope for selection

All agents solve the optimization program; so, $\mathcal{W}(\pi_i) = \bar{W}$ for all $i \in I$. From eqn 7, the expected change in all gene frequencies is given by $E_{\Omega}(\Delta p^{\omega}) = \text{cov}_I(w_i, p_i)$ and substituting $w_i = \mathcal{W}(\pi_i)/\bar{W} = 1$ for all $i \in I$, this is zero. Thus, there is no expected change in any gene frequency, i.e. no scope for selection.

Correspondence I also holds for the repression of competition model, by noting that eqn 7 also applies when groups are competitively repressed. Correspondence I is not proven for the general model because eqn 7 has not been shown to apply.

II. If all agents behave optimally, then there is no potential for positive selection

We introduce variant individual genotypes into the population at vanishingly low frequency, and assign each individual a special p -score p_{ij}^V to describe whether they are variant ($p_{ij}^V = 1$) or resident ($p_{ij}^V = 0$) genotypes. We denote the set of groups containing at least one variant individual by $H \subset I$, and we denote the number of groups in this set by L . From eqn 7, the expected change in the population frequency of the variant p -score is $E_{\Omega}(\Delta p^{V\omega}) = \text{cov}_I(w_i, p_i^V) = p^V(1 - p^V)(\bar{w}^V - \bar{w}^R)$, where $\bar{w}^V = \bar{W}^V/\bar{W}$ and $\bar{w}^R = \bar{W}^R/\bar{W}$ are the expected reproductive successes obtained by averaging over variant and resident groups respectively, i.e. $\bar{W}^V = \sum_H \mathcal{W}(\pi_h)/L$ and $\bar{W}^R = W^*$. Because $\mathcal{W}(\pi_h) \leq W^*$ for all $\pi_h \in \Pi$, then $\bar{w}^V - \bar{w}^R \leq 0$ and hence $E_{\Omega}(\Delta p^{V\omega}) \leq 0$. Thus, no introduced genetic variant can be favoured when rare, i.e. there is no potential for positive selection.

Correspondence II also holds for the repression of competition model, by noting that eqn 7 also applies when groups are competitively repressed. Correspondence II is not proven for the general model because eqn 7 has not been shown to apply.

III. If all agents behave suboptimally, but equally so, then there is no scope for selection

All agents attain the same maximand value; so, $\mathcal{W}(\pi_i) = \bar{W}$ for all $i \in I$. From eqn 7, the expected change in all gene frequencies is given by $E_{\Omega}(\Delta p^{\omega}) = \text{cov}_I(w_i, p_i)$, and substituting $w_i = \mathcal{W}(\pi_i)/\bar{W} = 1$ for all $i \in I$, this is zero. Thus, there is no expected change in any gene frequency, i.e. no scope for selection.

Correspondence III also holds for the repression of competition model, by noting that eqn 7 also applies when groups are competitively repressed. Correspondence III is not proven for the general model because eqn 7 has not been shown to apply.

IV. If all agents behave suboptimally, but equally so, then there is potential for positive selection

Denote the maximand value corresponding to each resident's suboptimal behaviour $\mathcal{W}(\pi_i) = W^o$ for all $i \in I$. We introduce a variant individual genotype g^* , defined by $\mathcal{P}[\mathcal{G}(g^*)] = \pi^*$ for the clonal groups model, into the population at a vanishingly low frequency, and assign each individual a special p -score p_{ij}^V to describe whether they have variant ($p_{ij}^V = 1$) or resident ($p_{ij}^V = 0$) genotypes. From eqn 7, the expected change in the population frequency of the variant p -score is $E_{\Omega}(\Delta p^{V\omega}) = \text{cov}_I(w_i, p_i^V) = p^V(1 - p^V)(\bar{w}^V - \bar{w}^R)$, where $\bar{w}^V = \bar{W}^V/\bar{W}$ and $\bar{w}^R = \bar{W}^R/\bar{W}$ are the expected reproductive successes obtained by averaging over variant and resident groups, respectively, i.e. $\bar{W}^V = W^*$ and $\bar{W}^R = W^o$. Because $W^* > W^o$ then $\bar{w}^V - \bar{w}^R > 0$ and hence $E_{\Omega}(\Delta p^{V\omega}) > 0$. Thus, at least one introduced genetic variant can be favoured when rare, i.e. there is potential for positive selection.

Correspondence IV is not proven for the repression of competition model, because it has not been demonstrated that any g^* satisfies $\mathcal{P}[\mathcal{G}(g^*)] = \pi^*$. Correspondence IV is not proven for the general model for the same reason, and also because eqn 7 has not been shown to apply.

V. If agents vary in their optimality, then there is scope for selection, and the change in every gene frequency is given by its covariance with the agent's relative maximand value

From eqn 7, the expected change in all gene frequencies is given by $E_{\Omega}(\Delta p^{\omega}) = \text{cov}_I(w_i, p_i)$ and, making the

substitution $w_i = \mathcal{W}(\pi_i)/\bar{W}$, this obtains $E_{\Omega}(\Delta p^{\omega}) = \text{cov}_I(\mathcal{W}(\pi_i)/\bar{W}, p_i)$.

Correspondence V also holds for the repression of competition model, by noting that eqn 7 also applies when groups are competitively repressed. Correspondence V is not proven for the general model because eqn 7 has not been shown to apply.

VI. If there is no scope for selection and no potential for positive selection, then every agent behaves optimally

If agents vary in their optimality, then there is scope for selection (correspondence V). Hence, if there is no scope for selection, agents cannot vary in their optimality – they must all be optimal or else they must all be equally suboptimal. If all agents are equally suboptimal, then there is potential for positive selection (correspondence IV). Hence, if there is no scope for selection and no potential for positive selection, all agents must be optimal.

For correspondence VI to hold, we require that correspondences IV and V both hold. As correspondence IV fails for the repression of competition model and correspondences IV and V fail for the general model, correspondence VI fails for both the repression of competition and general models.

Received 23 October 2008; revised 21 November 2008; accepted 25 November 2008