The Tragedy of the Commons, the Public Goods Dilemma, and the meaning of Rivalry and Excludability in Evolutionary Biology

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ABSTRACT

Problem: In the study of conflicts, both economists and evolutionary biologists use the concepts “tragedy of the commons” and “public goods dilemma". What is the relation between the economist and evolutionist views of these concepts?

Model features: Economics literature defines the tragedy of the commons and the public goods dilemma in terms of rivalry and excludability of the good. On the other hand, evolutionists define these conflicts by fitness functions with two components: individual fitness and group fitness.

Mathematical Method: Evolutionary game theory and calculation of Evolutionarily Stable Strategy trait values by the standard optimization techniques and by replacing slopes of group phenotype on individual genotype by coefficients of relatedness.

Conclusion: There is a direct relationship between rivalry and the individual component of fitness and between excludability and the group component of fitness. Moreover, although the prisoner’s dilemma constitutes a suitable metaphor to analyze both the public goods dilemma and the tragedy of the commons, it gives the false idea that the two conflicts are symmetric since they refer to situations in which individuals consume a common resource – tragedy of the commons - or contribute to a collective action or common good - public goods dilemma. However, the two situations are clearly not symmetric: from the economical point of view, they differ by rivalry, and from the evolutionary biology viewpoint, the two conflicts differ by the significance of the within-group competition in the fitness function.

Keywords: rivalry, excludability, tragedy of the commons, collective action, public goods dilemma, prisoner's dilemma.

INTRODUCTION

Competition and cooperation between humans or other living beings is a major issue in several disciplines, such as evolutionary biology, economy, psychology, or political science. Two types of conflicts often arise in economics and evolutionary biology. In one of these conflicts, there is a resource open to all – the commons - where no one has property rights or control over the resource. Each individual intensifies exploitation because he receives a direct profit from this. Yet, each individual bears only a share of the costs resulting from overexploitation of the common good. However, if an individual restrains from overexploiting the "commons", he is still doomed to pay his share of the costs due to the overexploitation activities of the other members of the group. Therefore, there is no direct advantage in restraining from overexploitation and the best strategy would be to continue overexploitation of the commons. So the resource is fated to be extinct. This is called the "tragedy of the commons" (see (Hardin 1968), but see (Ostrom 1990; Ostrom et al. 1994)) or, more correctly, the tragedy of the unmanaged commons (Hardin 1994). In a second type of conflict – Public Goods Dilemma - each self-interested individual in a group is supposed to act to achieve their common or group interest. If a single individual does not cooperate to the common interest, that interest is most probably accomplished anyway. Therefore, each individual is compelled not to cooperate: he does not pay the individual cost of cooperating but receives his share of the benefit (Hardin 1997; Olson 1965).

In economical sciences, these conflicts are often analyzed by focusing on the properties of the goods for which the individuals compete, namely on the diminishability and excludability of the good (see next section) (Mankiw 2000). Evolutionary biologists, on the other hand, have studied conflicts according to the interactions within and between groups (Brown 1999; Day and Taylor 1998; Frank

1992; Haig and Wilkins 2000). With this method, for example, evolutionists have modeled the evolution of virulence in two different ways resulting in two opposing dependences of virulence on relatedness (Brown 1999; Frank 1992; but see Gardner et al. 2004). In the tragedy of the commons model, the conclusion is that the higher the relatedness of parasites, the lower is virulence, but on the contrary, in the Public Goods model, the higher the relatedness, the higher is the contribution of each parasite to host manipulation. We will show how we can explain this disparity in terms of excludability and diminishability.

A common method to analyze conflicts is game theory in the field of economics or evolutionary game theory in the field of evolutionary biology. In game theory, the advantages and disadvantages (payoffs) in cooperating or competing with other individuals usually is money and the choice of a strategy is supposed to be rational (Davis 1997; Osborne and Rubinstein 1994). In evolutionary game theory, the payoffs represent fitness changes caused by the interaction between individuals and the strategies are hereditary (Maynard Smith 1982; Maynard Smith and Price 1973).

In this paper we want to generalize existing models for the tragedy of the commons and the public goods dilemma after identifying critical concepts in both fields.

The structure of the rest of this paper is the following. First we review the concepts of the tragedy of the commons and public goods dilemma in economical sciences by analyzing the goods according to their excludability and rivalry. Second, we review the same two concepts in evolutionary biology by analyzing the individual and the group components of the fitness. Third, we generalize the evolutionary models to show that, when excludability of a resource is not possible, the best evolutionarily strategy is: (i) to engage in a strategy of high competitiveness when the good is diminishable; or (ii) to lower competitiveness when the good is not diminishable – that is, when there is no rivalry. Fourth, when excludability from a public good is impossible, the best evolutionarily stable strategy is: (i) to cooperate to that common good when the good is not diminishable; or, (ii) not contribute to the public good when the good is diminishable. At the end of the paper we show, with two simple examples, how these concepts can be applied to evolutionary biology.

Tragedy of the Commons and Public Goods Dilemma in Economy

In economical sciences, goods are classified according to two characteristics (Mankiw 2000): (i) is the good excludable? That is, is the exclusion of beneficiaries possible, or is it too costly? (ii) Is the good diminishable? If the good is diminishable, it means that one person's use diminishes its use by others and so there is rivalry between users. When studying conflicts, the most interesting cases arise when the good is non-excludable (irrespectively of whether it is diminishable or not). The reason is that, whenever a good is non-excludable, any individual in a group can profit from it, thus creating the "free-rider problem": all individuals can use the good, even when not contributing to it. Both the tragedy of the commons (Hardin 1968; Ostrom 1990) and the public goods dilemma (Hardin 1997; Olson 1965) describe conflicts in which goods are not excludable, but in the tragedy of the commons goods are diminishable - implying that individuals are rivals, while in the public goods dilemma the individuals are not rivals (Table 1).

Examples of excludable goods are toothbrushes or cable tv. Goods such as toothbrushes are diminishable since, once used by someone, no one else can use it. The cable tv signal is not diminishable. Examples of non-excludable goods are the fish in the sea or national defense: in principle, everyone can fish in the sea and every citizen can profit from national defense (even if not paying taxes). Fish is non-excludable and diminishable, while national defense is non-diminishable (see Table 1).

Tragedy of the commons and Public Goods Dilemma in Evolutionary Biology

In Evolutionary Biology conflicts have been studied by explicitly analyzing interactions within and between groups of individuals, that is, the individual success within a group and group success in competition with other groups (Brown 1999; Brown 2001; Brown and Johnstone 2001; Foster 2004; Frank 1992; Frank 1995; Frank 1996; Gersani et al. 2001; Haig and Wilkins 2000; Wenseleers and Ratnieks 2004).

Tragedy of the commons in Evolutionary Biology

Consider, for example, a bacterial cell infected by several copies of a virus. These viruses face two different selection pressures: (i) viruses compete for resources within the bacterial cell to replicate themselves; the success of this strategy for a given virus is high when its competitiveness is higher than the mean competitiveness of all the viruses infecting that specific bacterial cell. (ii) The second selection pressure is competition among viruses coming out from different bacteria: assuming that viruses with high competitiveness within bacteria kill faster their hosts, the amount of viruses coming out from an infected cell is smaller for higher values of competitiveness. Therefore, within a cell, the best strategy for a virus is to compete for resources as much as possible, but that may result in a fast cell death, hence in a smaller total progeny in comparison with other bacterial cells where the mean competitiveness of infecting viruses was lower. This dilemma is an example for the tragedy of the commons in biology: a certain virus competing more than the others in the same cell increases its direct progeny and the cost is shared by all the co-infecting viruses.

Frank modeled the tragedy of the commons in terms of competition within and between groups as explained above (see (Frank 1998) for a general discussion). He assumed that resources are limiting within groups and that the most competitive individuals gain a disproportionate share of the local resources. If we call z_{ij} the competitiveness of the *j*th individual in a given group *i*, its individual success within the group can be described simply as z_{ij}/z_i, where z_i is the mean value of competitiveness of all individuals in group *i* (see also the ratios appearing in equations 2 to 4 by Haig and Wilkins (2000) or equation 2 by Day and Taylor (1998)).

However, if z_i is very high, the group's overall efficiency in using their local resources is lowered. As a consequence, it lowers the average success of the group members (in competition with other groups). Therefore, Frank assumed that the between-group component of the fitness to be $(1-z_i)$. These two factors (competition within and between groups) determine the fitness of each individual *j* in each *i*th group, ω_{ij}:

$$(1)\quad \omega_{ij} = \frac{z_{ij}}{z_i} \cdot (1 - z_i)$$

This minimal model captures the essential tension between individual and group success, but, of course, more complex mathematical expressions could be used. Later, the same author introduced a cost term associated to each individual due to his investment in the competitive trait. Therefore, equation (1) was modified to include a term expressing the individual cost, *q*, of allocation to competitive traits:

$$(2)\ \omega_{ij} = \frac{z_{ij}}{z_i} \cdot \left(1 - q \cdot z_{ij}\right) \cdot \left(1 - z_i\right)$$

This mathematical expression synthesizes a typical common-pool resource problem, that of the tragedy of the commons, where individual gains lead to group losses.

If we are interested in the total competitiveness of each group, and not only in its mean value, then we may prefer to consider the model:

$$(3)\ \omega_{ij} = \frac{z_{ij}}{z_i} \cdot \left(1 - q \cdot z_{ij}\right) \cdot \left(1 - a.n.z_i\right)$$

where n is the total number of individuals in each group and $n.z_i$ is the total competitiveness of group i. The term $a.n.z_i$ represents the net disadvantage to each ij individual due to competition with the other individuals of the same group, where $a > 0$ is a parameter that describes how this disadvantage affects each individual.

Public Goods Dilemma in Evolutionary Biology

Following the arguments of Brown (1999), let's consider the evolution of host manipulation by parasites. A group of parasites manipulating their host can be viewed as performing a collective action. The between-group fitness component is "an increasing function of total manipulation, reflecting the benefit of manipulation to the parasite group" (Brown 1999). If we call s_{ij} the contribution of the *jth* individual in a given group i, and s_i as the average contribution of the individuals of the *ith* group, then the between-group fitness component can be described simply as $\left(1 + \beta.n.s_i\right)$, where n is the number of individuals in the group i, and β is a positive parameter that describes how the group effort $n.s_i$ is retuned to each individual. Here, the fitness of each individual when there is no collective action is set to unity. As in the previous model, there is also an individual component of the fitness expressing the individual cost in performing the altruistic act, $(1-k\cdot s_{ij})$. Therefore, the fitness of each individual j in a group i is given by:

$$(4)\quad \omega_{ij} = (1-k\cdot s_{ij})\cdot(1+\beta.n.s_i)$$

In this equation (4) it was assumed that the fitness of a non-contributing individual in a group of non-contributing individuals is one. However, in some situations an individual cannot survive if no individual contributes to the public good. In that case, expressions such as $\omega_{ij} = (1-k\cdot s_{ij})\cdot s_i$ or similar should be used (see for example (West and Buckling 2003), where the authors defined individual fitness as $\omega_{ij} = (1-s_{ij})\cdot s_i^{\,b}$, where b is a parameter).

GENERALIZED MODELS

Now, we generalize Frank's and Brown's model and analyze the resulting equations with the notions of rivalry and excludability of goods.

A Common-Pool Resources model

As explained above, users of a common-pool resource often proceed to resource overexploitation when excludability is difficult or impossible and when there is maximal rivalry. Here we proceed with the construction of a model for the consumption of a common-pool resource and then analyze the rivalry and excludability terms to find the situation of a tragedy of the commons.

The expression z_{ij}/z_i that appears in equation (3) *can* be interpreted as a "rivalry" term. The reason is the following. This term means that the success of individual ij is high if the value of its competitiveness, z_{ij}, is higher than the mean competitiveness of group i, z_i. Therefore, if another individual, k, in the same group has its competitiveness increased – hence increasing the mean value of competitiveness in group i, z_i – it has the effect of decreasing the individual component of the fitness of individual ij. In other words, this means that competitiveness is a *diminishable* trait.

One can modulate rivalry by considering the following expression:

$$(1-f)\cdot(1)+(f)\cdot\left(\frac{z_{ij}}{z_i}\right)$$

or simply:

$$1-f+f\cdot\frac{z_{ij}}{z_i}$$

In this model, $0 \le f \le 1$. If $f = 0$, individuals are not rivals (within each group); if $f = 1$, rivalry is maximal. So, a generalized expression for the fitness of each individual in this context is:

$$\omega_{ij} = \left(1-f+f\cdot\frac{z_{ij}}{z_i}\right)\cdot(1-q\cdot z_{ij})(1-z_i)$$

The expression $1-f+f\cdot z_{ij}/z_i$ is but one of the infinitely possible expressions involving one sole parameter (this case, f). Other expressions are also possible (see Appendix A).

In the same way as we modulated rivalry, we can also modulate excludability. We argue that the term $(1-z_i)$ is the maximum state of non-excludability of damage by the group. Group's competitiveness, z_i, is affecting the entire group – that is, all the individuals within a group share the resulting damage. A possible expression modulating excludability is:

$$\left\lfloor 1 - g \cdot z_{ij} - (1-g) \cdot z_i \right\rfloor$$

where $0 \le g \le 1$. Like this, a proportion g of the damage is caused by the individual *ij* himself, and a proportion $(1-g)$ is caused by the average damage of all the members of group i. If $g = 1$, we have total excludability and this expression simplifies to $\left\lfloor 1 - z_{ij} \right\rfloor$ - like this, the decrease in fitness of the individual *ij* is solely caused by the *ij* individual. If $g = 0$, the expression becomes $\left[1 - z_i\right]$ and excludability is minimized.

Putting all these expressions together, the complete expression for studying the common-pool resources problem is:

$$(5)\ \omega_{ij} = \left(1 - f + f \cdot \frac{z_{ij}}{z_i}\right) \cdot \left(1 - q \cdot z_{ij}\right) \cdot \left[1 - g \cdot z_{ij} - (1-g) \cdot z_i\right] \cdot$$

A model of contribution to a Common Good or Collective Action

Contributors to a common good or a collective action may tend to restrain from contributing, but maintain the profit. Like this, each restraining individual does not suffer the respective cost; however, if all the individuals do the same, the common good becomes scarce, and the community falls in a dilemma, the public goods dilemma (Hardin 1997; Olson 1965). This may happen when excludability is difficult (as in the tragedy of the commons) but when there is no rivalry (unlike the tragedy of the commons). Now we proceed with the construction of a model for the contribution to a common good (or collective action) and then analyze the rivalry and excludability terms to find the situation of a public goods dilemma.

According to the arguments previously used to generalize a fitness function for the common-pool resource, let's consider the following function when individuals contribute to a common good or to a collective action:

$$(6)\ \omega_{ij} = \left[1 - \varphi + \varphi.\frac{s_i}{s_{ij}}\right] \cdot \left(1 - k \cdot s_{ij}\right) \cdot \left[1 + \beta.\left(\gamma \cdot s_{ij} + \left(1 - \gamma\right) \cdot n \cdot s_i\right)\right]$$

or many other possibilities (see Appendix A).

The parameter φ appears in this equation - as f in equation (5) – to modulate rivalry. In many biologically relevant situations, $\varphi = 0$, which means that there is no rivalry in altruistic acts. There are contexts, however, in which there is advantage in contributing *less* than the others within the group. For example, we can think that during a fight, and supposing that enough cohorts are contributing to group defense, an individual has an advantage in fighting *less* than the others; then, at the end of this fight, this individual may be in better conditions to reproduce than cohorts.

In equation (6) γ plays a similar role as g in equation (5): modulation of excludability. If there is no excludability, then $\gamma \to 0$ and we obtain the term $[1 + \beta.n.s_i]$; if excludability is maximized, the term becomes $\lfloor 1 + \beta.s_{ij} \rfloor$.

In the model of host manipulation described in equation (4), Brown (1999), assumed that altruistic parasites do not have any competitive disadvantage over non-altruistic group-members other than the individual cost for manipulation (the altruistic act). In other words, if a few parasites do not contribute to the collective effort of host manipulation, that is not disadvantageous for contributors because the host is manipulated anyway. Therefore, the implicit assumption is that this common good (manipulation of the host) is non-diminishable (host manipulation benefits all parasites, including those that do not contribute to manipulation), which implies that φ is close to zero. If, in addition, there is no excludability then γ is close to zero and we get a pure public goods dilemma – so we can obtain equation (4) from (6) in this limit.

The generalized equations (5) and (6) show that we do not need to assume that goods are either excludable or non-excludable; the same applies to rivalry. That is, in addition to extreme cases, we should also consider intermediate ones. For example, there is continuity between congested and uncongested roads; similarly, tolls can be within zero (non-toll roads) and its effective cost (toll roads).

One can find the equilibrium values of equation (5) by maximizing fitness, ω_{ij}, with respect to variants in z_{ij} (Maynard Smith 1982; Taylor and Frank 1996). The "unbeatable" (Hamilton 1967; Verner 1965) or evolutionarily stable strategy (Maynard Smith 1982), z*, can be found by derivation of the model appearing in (5):

$$\left.\frac{d\omega_{ij}}{dz_{ij}}\right|_{z_{ij}=z_i=z^*} = \frac{\partial\omega_{ij}}{\partial z_{ij}} + \frac{\partial\omega_{ij}}{\partial z_i}\frac{dz_i}{dz_{ij}}$$

and making these derivatives equal to zero at $z_{ij} = z_i = z^*$. This is done by taking into account the interactions between kin units (Taylor and Frank 1996): assuming weak selection and additive gene action (additive dependence of phenotype on genotype), the slope of group genotype on individual genotype, $\left(dz_i/dz_{ij}\right)$, can be replaced by the kin selection coefficient, r.

To find the equilibrium value for s (equation (6)), $s*$, we can use the same method. For both equations (5) and (6) there are two equilibrium solutions but only one of them is biologically relevant. Competitiveness, $z*$, decreases with relatedness, while $s*$ increases with relatedness (see Table 2).

In Table 2 we show the expressions of $z*$ and $s*$ corresponding to the extreme situations presented in Table 1. That is Table 2 shows the expressions for competitiveness and levels of cooperation when rivalry is either close to one or close to zero or when excludability is possible (g and γ equal to zero) or not possible (g and γ equal to one). As expected, $z*$ is null when there is no rivalry (f and φ close to zero) and $s*$ is null when rivalry is maximized (f and φ close to zero). Furthermore, it is interesting to see that in the column on the right in Table 2, the two expressions for $s*$ are very similar; the expression for $s*$ on the lower row (when there is no excludability) becomes the expression for $s*$ on the upper row when $r = 1$.

Fig.1 shows the values of z* and of the fitness with different values of rivalry and excludability. Fig. 2 shows the values of s* and of the fitness with the same values of rivalry and excludability used in Fig.1.

Examples of the Tragedy of the Commons and the Public Goods Dilemma in the Evolution of Virulence

Both the evolutionary biology versions of the tragedy of the commons (Frank 1992) and of the public goods dilemma (Brown 1999) emerged in studies to understand the evolution of virulence of parasites towards their hosts. In the tragedy of the commons model, the conclusion is that the higher the relatedness of parasites, the lower is virulence (indeed, we can see that $z* \to 0$ when r is high). On the contrary, in Brown's model, the higher the relatedness, the higher is the contribution of each parasite to host manipulation. By reasoning in terms of rivalry and excludability of goods, we can see why Frank's and Brown's conclusions are different: Frank considered the case in which parasites co-infect a host; the host constitutes a diminishable and non-excludable resource ($f \to 1$ and $g \to 0$, respectively, in equation (5)).

In the logic of collective action, Brown considered the effort made by some parasites to manipulate their hosts (Brown 1999). The author gave the example of quorum sensing in which bacteria can sense their density or number and, if bacterial cells are sufficiently numerous or dense, they can start producing virulence factors together to infect the host (Brown and Johnstone 2001). If the host is a vertebrate, and to escape from the immune system, we may suppose that host invasion will succeed only if many bacterial cells invade host tissues simultaneously. The production of a virulence factor has an individual cost that is going to be reflected in the fitness function. There is, however, no rivalry - $\varphi \to 0$ in equation (6) - because all bacteria gain the same advantage of virulence factor production, irrespectively of having helped with this collective effort or not. If enough parasites contribute to this effort, the other parasites can invade the host without having the cost of host manipulation. So, the good (in this case, the good is the ability in invading host tissues) is non-excludable - and $\gamma \to 0$ in equation (6).

The tragedy of the commons and the public goods dilemma can occur in the same biological system. For example, West and Buckling (2003) have analyzed the virulence of bacteria that need iron to grow (Guerinot 1994; Ratledge and Dover 2000). Bacteria have evolved mechanisms to scavenge iron from their hosts. A common mechanism is the production and uptake of siderophores - iron-binding agents released into the environment in response to iron deficiency. All bacteria within a locality benefit with the presence of siderophores, not only siderophore-producers. Therefore, bacteria not producing siderophores do not pay the cost of their production, yet gains from the presence of siderophores produced and secreted by other local bacteria (Griffin et al. 2004; West and Buckling 2003). This is a public goods dilemma. Siderophores are non-excludable because it is released to the environment and it is available both to producers and non-producers. The relative production of siderophores by a focal bacterial lineage relative to the production by the rest of the bacterial population is not relevant to their bacterial fitness – hence in equation (6), $\varphi = 0$ and there is no rivalry in siderophore production. The second step for bacteria survival is the uptake of iron bound to siderophores. Given that siderophore bound to iron is a diminishable resource, bacteria are rival. On the other hand this resource is non-excludable. In conclusion, this second step constitutes a tragedy of the commons.

CONCLUDING REMARKS

In this paper, we have shown that the economics concepts of rivalry and excludability correspond, respectively, to the evolutionary biology concepts of individual and group component of individual fitness functions. We have constructed two generalized evolutionary models for describing the consumption of a common-pool resource, and for describing the contribution to some common good or to some collective action. In both models, we introduced a parameter modulating rivalry and another parameter modulating excludability, and we have shown how these parameters can be changed to obtain dilemmas such as the tragedy of the commons and the public goods dilemma.

Besides the concepts of excludability and rivalry or the individual component versus group component of individual fitness, other authors commonly use the prisoner's dilemma to analyze the tragedy of the commons or the public goods dilemma (see for example (Ostrom et al. 1994)). Typically, one models these conflicts with this dilemma, in which two individuals have the option of cooperating or not cooperating (defecting). The circumstances are such that it pays more to defect, no matter whether the other cooperates or not, although, together they would be better off if they both cooperated (Brown 2001; Dawes et al. 1986; Hardin 1971). Indeed, the prisoner's dilemma constitutes a suitable metaphor to analyze both the public goods dilemma and the tragedy of the commons: in the public goods dilemma cooperation means to contribute to the public good and defect means not to contribute; in the tragedy of the commons situation, cooperation means to restrain from using too much of a resource and defection means not to restrain. Therefore, and using the language of game theory (Davis 1997; Osborne and Rubinstein 1994), the strategy "defect" is *Pareto inferior* – meaning that there is an outcome (both cooperating) where both players would be better off. However, by comparing both conflict situations with the same game, it is not clear that the tragedy of the commons and the public goods dilemma conflicts refer to different types of non-excludable goods. Moreover, this dilemma gives a false idea that the tragedy of the commons and the public goods dilemma are symmetric situations because they refer to situations in which individuals consume a common resource – tragedy of the commons -, or contribute to a collective action or common good - public goods dilemma. However, the two situations are clearly not symmetric: equations (3) and (4) or (5) and (6) are not symmetric. The same applies to the equations appearing in Table 2.

Cross-pollinating of ideas between Economy and Evolutionary Biology has been extremely useful to both fields and we hope that this paper gives some insights about the meaning of rivalry and excludability in evolutionary biology. To our knowledge, this is the first time that rivalry and excludability of goods are discussed in the context of evolutionary problems.

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APPENDIX A

Both the rivalry and excludability expressions might have other forms. For example, the rivalry term could be:

$$\frac{f + z_{ij}}{f + z_i}$$

In this case, however, f is a real number between zero and infinity, not between zero and one as before.

Moreover, instead of considering ratios such as $(f + z_{ij})/(f + z_i)$, we can write the rivalry term as $(h - z_i)/(h - z_{ij})$, etc.. In the former expression, $f \in [0,+\infty]$ whereas in the latter one, $h \in]0,+\infty[$.

Again, the excludability term could be given by:

$$\left[1 - z_i\left(\frac{g + z_{ij}}{g + z_i}\right)\right]$$

and $g \in [0,+\infty[$, whereas, in equation (5) $g \in [0,1]$.

FIGURE LEGENDS

Figure 1: Evolutionarily stable strategy of competitiveness (left) and fitness of each individual (right) for different rivalry, f, and excludability, g, parameters. The horizontal axes represent relatedness, r, and $q = 0.4$. Top: $g = 0$ and $f = 0.05$ (a), 0.2 (b), 0.5 (c), 0.8 (d) and 1(e). Bottom: $f = 1$ and $g = 0$ (a), 0.2 (b), 0.5 (c), 0.8 (d) and 0.95 (e).

Figure 2: Evolutionarily stable strategy of collective action (left) and fitness of each individual (right) for different rivalry, f, and excludability, g, parameters. The horizontal axes represent relatedness, r. Top: $\gamma = 0$, $B = 0.1$, $k = 0.4$, $\varphi = 0$ (a), 0.2 (b), 0.5 (c), 0.8 (d) and 0.95 (e). Bottom: $\varphi = 0$ and $\gamma = 0$ (a), 0.2 (b), 0.5 (c), 0.8 (d) and 0.95 (e).

Table 1. Types of goods classified according to their excludability and rivalry (adapted from Mankiw 2000).

Excludable? \ Rival?	Yes	No
Yes	-Toothbrush -Congested toll roads	-Cable TV -Uncongested toll roads
No	-Fish in the sea -Congested nontoll roads	-National defense -Uncongested nontoll roads

Table 2: Competitiveness (z^*) and contributions to the group (s^*) in extreme situations of rivalry and excludability.

Excludable? \ **Rival?**	**Yes** ***(f, $\varphi \to$ 1)***	**No** ***(f, $\varphi \to$ 0)***
Yes ***(g, $\gamma \to$ 1)***	$z^* = \frac{(2-r)\cdot(1+q)-\sqrt{(2-r)^2\cdot(1+q)^2-4\cdot(1-r)\cdot(3-r)\cdot q}}{2\cdot q\cdot(3-r)}$ $s^* = 0$	$z^* = 0$ $s^* = \frac{\beta - k}{2\cdot\beta\cdot k}$
No ***(g, $\gamma \to$ 0)***	$z^* = \frac{1+q\cdot(2-r)-\sqrt{(1+q\cdot(2-r))^2-8\cdot q\cdot(1-r)}}{4\cdot q}$ $s^* = 0$	$z^* = 0$ $s^* = \frac{\beta\cdot n\cdot r - k}{\beta\cdot n\cdot k.(1+r)}$

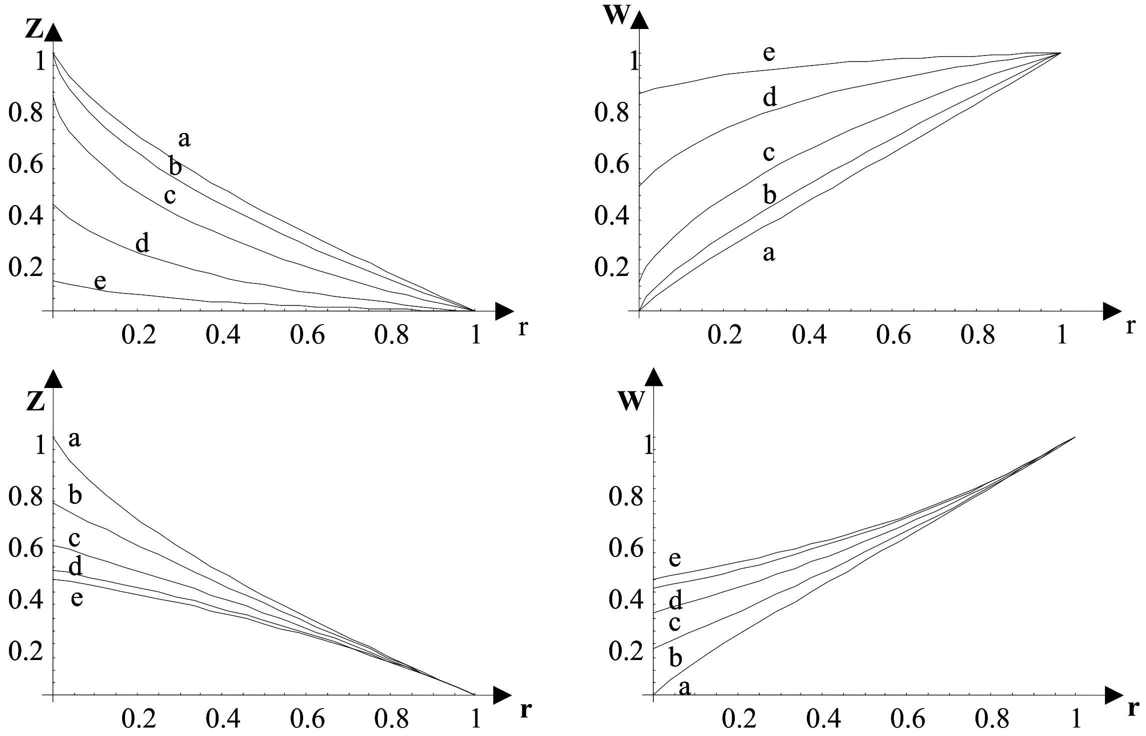
Z
1
0.8
0.6
0.4
0.2
a
b
c
d
e
0.2
0.4
0.6
0.8
1
r
W
1
0.8
0.6
0.4
0.2
e
d
c
b
a
0.2
0.4
0.6
0.8
1
r
Z
1
0.8
0.6
0.4
0.2
a
b
c
d
e
0.2
0.4
0.6
0.8
1
r
W
1
0.8
0.6
0.4
0.2
e
d
c
b
a
0.2
0.4
0.6
0.8
1
r

Figure 1

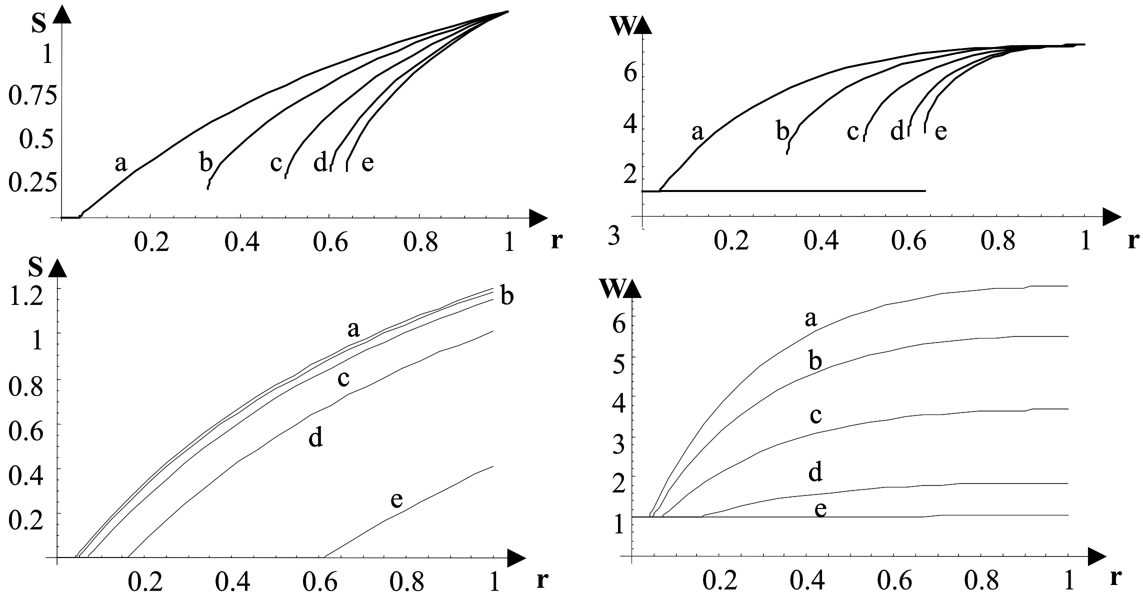

Figure 2