

Controlling excludability in the evolution of cooperation

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ABSTRACT

Background: A tragedy of the commons arises if individuals cannot protect their future use of a depletable resource, and individual fitness increases if individuals exploit the resource at rates beyond sustainability. Natural selection then forces the individuals to diminish, perhaps even to destroy, their resource. One way to protect future use is privatization – that is, locally excluding rivals from the resource. Another is to reduce rivalry among individuals by restricting exploitation rates.

Questions: Under what conditions will natural selection increase excludability? If relatedness among individuals is high, will kin selection be enough to eliminate or weaken the evolution of privatization?

Mathematical method: We use a simple model that captures the tension between individual and group success. Then, we calculate the evolutionarily stable strategy using the standard optimization techniques of evolutionary game theory.

Conclusions: Selection for privatization occurs at low values of relatedness. The conditions for this to occur resemble those previously obtained for the reduction of rivalry because non-excludability of damage, and not rivalry *per se*, is the fundamental cause of the tragedy of the commons.

Keywords: evolution of complexity, excludability, multi-level selection, privatization, rivalry, tragedy of the commons.

INTRODUCTION

Since the beginning of life, there has been a series of significant transitions that have led to a hierarchical organization of the living world: cells, eukaryotes, multicellular organisms, and colonies. This hierarchical structure requires the development of a multi-level selection theory that explains how lower-level units congregate and cooperate to form higher-level units of organization. Moreover, since the interests of a specific individual are not necessarily aligned to that of the group to which it belongs, a multi-level selection theory

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also has to explain how conflicts are avoided or resolved. With this, one can explain how lower levels do not disrupt higher levels (Price, 1972; Hamilton, 1975; Wilson, 1975, 1997; Arnold and Fristrup, 1982; Buss, 1983, 1987; Leigh, 1983, 1991; Wade, 1985; Williams, 1992; Frank, 1995a, 1998, 2003; Szathmary and Smith, 1995; Michod and Roze, 1997; Keller, 1999; Michod, 1999; Sober and Wilson, 1999; Korb and Heinze, 2004).

A common type of conflict is the ‘tragedy of the commons’ (Hardin, 1968) or the ‘tragedy of the unmanaged commons’ (Ostrom, 1990; Hardin, 1994; Ostrom *et al.*, 1994). This type of conflict is frequent, not only among human societies – the subject of economic, political, and sociological researchers – but also among other living organisms and at different levels of selection.

What is the ‘tragedy of the commons’? Consider a pasture open to all – the commons – where no-one has property rights or control over the resource. Each herdsman is expected to intensify exploitation by keeping as many cattle as possible on the commons. Every time a herdsman adds an animal to the commons, he receives a direct profit from this. Yet, he bears only a share of the costs resulting from over-exploitation of the common good. However, if a herdsman refrains from over-exploiting the ‘commons’, he is still doomed to pay his share of the costs due to the over-exploitation activities of the other herdsmen. Therefore, there is no direct advantage in refraining from over-exploitation and the best strategy would be to continue to over-exploit the commons until the cost of doing so equals the advantage or until the resource goes extinct. Hardin (1968) called this conflict the ‘tragedy of the commons’.

In economic sciences, the tragedy of the commons is defined as the conflict that results from the use of a resource that is simultaneously depletable and non-excludable (Ostrom *et al.*, 1994; Mankiw, 2004). A resource is depletable if one person’s use diminishes its use by others, implying rivalry between users. A resource is non-excludable when any individual in a group can profit from its use or when all members of the group share the damage produced by each individual. In evolutionary biology, conflicts have been studied by explicitly analysing interactions within and between groups of individuals – that is, the individual success within a group and group success in competition with other groups (Frank, 1992, 1995b, 1996a; Day and Taylor, 1998; Brown, 1999, 2001; Haig and Wilkins, 2000; Brown and Johnstone, 2001; Gersani *et al.*, 2001; Foster, 2004; Wenseleers and Ratnieks, 2004).

The tragedy of the commons in evolutionary biology

As we will later expand on his analysis, we start by reviewing Frank’s model for the tragedy of the commons (Frank, 1998). Frank 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 .

However, if z_i is very high, the group’s overall efficiency in using its local resources is lowered. As a consequence, the mean success of the group members is lowered (in competition with other groups). Therefore, Frank assumed the between-group component of 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} :

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

This minimal model captures the essential tension between individual and group success, but, of course, more complex mathematical expressions could be used.

We have shown recently how the two terms that appear in equation (1), z_{ij}/z_i and $(1 - z_i)$, correspond to rivalry and (non-)excludability respectively (Dionisio and Gordo, 2006). Because of its importance for an understanding of the present article and for completeness, we will provide a short explanation.

First, why can the expression z_{ij}/z_i be interpreted as a ‘rivalry’ term? 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, competitiveness is a *depletable* trait.

One can modulate rivalry by considering the following expression: $(f) \cdot (1) + (1 - f) \cdot (z_{ij}/z_i)$, or simply $f + (1 - f) \cdot (z_{ij}/z_i)$, with f between zero and one. As f approaches one, the advantage of within-group rivalry decreases; if $f = 0$, rivalry is maximal. The expression $f + (1 - f) \cdot (z_{ij}/z_i)$, of course, is but one of the infinite possible expressions involving one sole parameter (in this case, f).

Now, let us see why the second term in equation (1), $(1 - z_i)$, is the maximum state of non-excludability of damage by the group. The group’s competitiveness, z_i , affects the entire group – that is, all individuals within a group share the resulting damage.

In the same way as we modulated rivalry, we can also modulate excludability. A possible expression modulating excludability is $[1 - g \cdot z_{ij} - (1 - g) \cdot z_i]$, with g between zero and one (Fig. 1). Similarly, 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 other members of group i . As g increases, the ‘commons’ diminishes by a proportion of $(1 - g)$. If $g = 0$, the expression becomes $[1 - z_i]$ and excludability is minimized.

Policing mechanisms

In the context of rivalry and excludability, the tragedy of the commons can be solved in at least two ways: controlling rivalry and controlling excludability. For example, consider

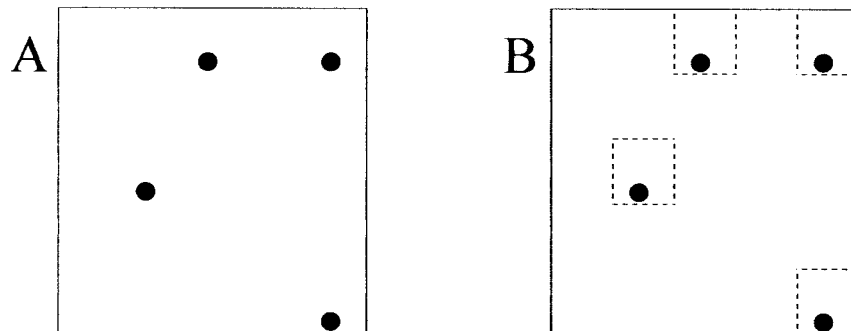


Fig. 1. Modulation of excludability. In this example a group has four elements. (A) Here $g = 0$, which means that there is no privatization. Therefore, all individuals have access to the entire commons and all damage is shared by all elements of the group. (B) Here $g > 0$, which means that part of the commons was privatized and the rest is still available to all individuals in the group.

again the pasture with cows belonging to different herdsmen. A way to control rivalry would be to establish an agreement between herdsmen such that each has a maximum number of cows. To control excludability (i.e. to increase excludability), the herdsmen could divide part of the pasture among themselves, but leaving the remainder as a ‘commons’ (see Fig. 1B). Then, each herdsman can graze as many cattle as he wants on his own fraction. In this case, only abusers suffer from the cost of overgrazing. In this paper, we examine the conditions for policing mechanisms to ensure such levels of excludability do not arise. We find that the conditions for the evolution of such policing mechanisms are the same as those for rivalry control (Frank, 1996b), namely that low relatedness is more conducive to excludability control than high relatedness (in which case, kin selection is sufficient for the evolution of cooperation).

RESULTS

The control of rivalry

Frank (1996b) has studied the control of rivalry in the context of evolutionary biology. He asked under which conditions a rivalry-repressing mechanism would be selected when individuals face the tragedy of the commons. We now solve the tragedy of the commons by increasing excludability instead of repressing rivalry. Before explaining our model, however, we review Frank’s repression mechanism. This is also useful because he never referred to this rivalry–excludability dichotomy in his models. He considered the following model (Frank, 1996b):

$$\omega_{ij} = \left[a_i + (1 - a_i) \cdot \frac{z_{ij}}{z_i} \right] \cdot (1 - c \cdot a_{ij}) \cdot [1 - (1 - a_i) \cdot z_i]$$

↑

Modulation of rivalry

↑

Reduction of damage
to local resources

(2)

In equation (2), trait a determines each individual’s contribution to a mechanism that reduces competition among all members of the local group (mutual policing), and a_{ij} is an individual’s contribution to mutual policing, which has a cost to the individual given by $c \cdot a_{ij}$ (Frank, 1995b, 1996b). The average amount of policing in the local group is a_i and each potentially competitive interaction is reduced in both opportunity for gain by the vector, $(1 - a_i) \cdot z_{ij}/z_i$, and damage to local resources, $(1 - a_i) \cdot z_i$ (Frank, 1995b). With this model, Frank varied rivalry as a rationale to diminish the amount of damage to local resources.

The control of excludability

We now show how one can solve the tragedy of the commons by increasing the level of excludability. Suppose that a trait b now determines each individual’s contribution to a mechanism that increases excludability. In other words, the second term of equation (1), $(1 - z_i)$, becomes $[1 - (b_i \cdot z_{ij} + (1 - b_i) \cdot z_i)]$. This has four important consequences. First, the fitness of each individual is decreased, partly due to its own competitiveness and partly due to the competitiveness of the group; that is, it assigns more damage to the author of the damage itself than in the model of equation (1). Second, this reduces the opportunity for this

competitiveness to manifest the proportion of only $(1 - b_i)$. Third, as a consequence of the previous point, the impact of rivalry is reduced from z_{ij}/z_i to $z_{ij}/(b_i \cdot z_{ij} + (1 - b_i) \cdot z_i)$. Finally, this last point implies that there is less opportunity for damage to the resource. Therefore, the complete excludability term becomes $(1 - b_i) \cdot (b_i \cdot z_{ij} + (1 - b_i) \cdot z_i)$ and the complete model is:

$$\omega_{ij} = \left[\frac{z_{ij}}{b_i \cdot z_{ij} + (1 - b_i) \cdot z_i} \right] \cdot (1 - c \cdot b_{ij}) \cdot [1 - (1 - b_i) \cdot (b_i \cdot z_{ij} + (1 - b_i) \cdot z_i)] \quad (3)$$

Reduction of damage
to local resources

↓

↑ ↑

Modulation of excludability

We now ask what conditions are required for this policing mechanism to invade (Verner, 1965; Hamilton, 1967; Maynard Smith, 1982; Frank, 1995b, 1996b, 1998; Taylor and Frank, 1996). Consider a population in which there is no policing. Then, equation (1) holds and the equilibrium level of competitiveness is $z^* = 1 - r$ (Frank, 1992), where $r = dz_i/dz_j$ (Taylor and Frank, 1996). Therefore, in equilibrium and before policing appears, the fitness of each individual is $\omega^* = r$. Suppose now that a mutant invests $b_{ij} = \delta$ in policing when relatedness is r , where δ is small. In the mutant's group, the mutant's neighbours have a probability r of sharing the policing allele. Therefore, the average level of policing in the mutant's group is $b_i = r\delta$. With these values of b_{ij} and b_i , the fitness of the mutant is:

$$\omega_\delta = \left[\frac{z^*}{r\delta \cdot z^* + (1 - r\delta) \cdot z^*} \right] \cdot (1 - c\delta) \cdot [1 - (1 - r\delta) \cdot (r\delta \cdot z^* + (1 - r\delta) \cdot z^*)]$$

or

$$\omega_\delta = [1] \cdot (1 - c \cdot \delta) \cdot [1 - (1 - r\delta) \cdot z^*]$$

Given that $z^* = 1 - r$ when policing rises in the population, the fitness of the mutant is:

$$\omega_\delta = (1 - c \cdot \delta) \cdot [1 - (1 - r\delta) \cdot (1 - r)]$$

The necessary condition for such a mutant to increase in the population is $\omega_\delta > \omega^*$. That is, $(1 - c \cdot \delta) \cdot [1 - (1 - r\delta) \cdot (1 - r)] > r$ or, ignoring terms of order δ^2 or higher, the condition simplifies to:

$$r < 1 - c \quad (4)$$

That is, these policing mutants are selected when relatedness is low and/or the cost of the policing mechanism, c , is low. Condition (4) is the same as that previously obtained when policing mechanisms repress rivalry (Frank, 1995b). When relatedness is higher than $1 - c$, policing is not selected and kin selection is enough to keep competitiveness at low values.

Biologically, one can see why equation (4) is the same as that obtained by Frank (1995b) for when policing controls rivalry. Non-excludability (of damage) is the fundamental cause of the tragedy of the commons (second term of equation 1). Therefore, the objective of

Frank's and our mechanisms is to decrease the common damage. This goal can be achieved by reducing the opportunity for gain by the victor (Frank, 1995b), or by decreasing the opportunity for selfishness to occur and conferring more damage to the author of the damage itself (this study). Moreover, the initial selection of the policing mechanism occurs when the system is in the evolutionarily stable strategy of the model described by equation (1). Therefore, and given that in an evolutionarily stable strategy all individuals adopt the same strategy, z^* , the effect of policing on each individual is the same as the effect on the mean value of z among a group. In other words, in our model, with the policing mechanism conferring more damage to its producer, the damage is partially 'transferred' from the group i to the individual ij . So, when policing is still rising from low values in the population, the total damage is the same, z^* , and the excludability term changes from $(1 - z^*)$ to $[1 - (1 - r\delta) \cdot z^*]$ because now less damage is subtracted from the commons.

DISCUSSION

The tragedy of the commons can disappear if rivalry is decreased (Frank, 1995b) or if excludability is increased (this study). In this paper, we have shown that control mechanisms that increase excludability are selected for low relatedness (equation 4). This condition is the same as that previously obtained when considering the control of rivalry (Frank, 1995b).

That the tragedy of the commons occurs when there is both rivalry between individuals and non-excludability of damage created by rivalry has long been recognized in economics and recently stressed in evolutionary biology (Dionisio and Gordo, 2006). It is noteworthy, however, that a control mechanism that results from individual effort (with a cost c for each individual performing this control), and that confers an advantage that is shared by all the members, is selected for low values of kin selection relatedness, not high values. This can be understood from the fact that, for high values of relatedness, kin selection reduces competitiveness (Frank, 1995b, 1996b). Therefore, at high relatedness, not only is the advantage of policing lower, but self-restraint is enough to prevent extreme competition.

While constructing the model, we did not specify any level of organization. Therefore, in principle, *privatization* may be relevant in the resolution of conflicts at any level. For example, at the cell level, compartments may be used to solve conflicts between cells or between groups of cells (see below). However, what happens if a species cannot find a way of forming compartments when needed? The cost of their absence seems to be very high, at least in the case of the amoeba *Dictyostelium discoideum*. Under starvation conditions, these free-living cells aggregate to form a motile, multicellular slug that moves towards heat and light (Bonner, 2000). A slug may be clonal or chimeric (Strassmann *et al.*, 2000). Chimeric slugs experience a reduction in fitness compared with clonal slugs of the same size (Foster *et al.*, 2002; Castillo *et al.*, 2005). Given this fitness reduction, one would expect the evolution of a mechanism to exclude unrelated cells to join in the aggregate. However, because larger slugs move further than small slugs, perhaps this size benefit outweighs the cost of chimerism observed in slugs of the same size (Foster *et al.*, 2002). If this size advantage did not exist, one would have expected the evolution of an excludability system in *D. discoideum*.

There is another interesting stage of the life cycle of *D. discoideum* that is relevant in the context of this paper. The slug, after reaching its destination, differentiates into a fruiting body whose spores become dispersed, which then develop into single amoebae. The fate of stalk cells, on the other hand, is death. Therefore, if a fruiting body contains different genotypes, one of them may try 'to cheat' on the others – that is, increase in frequency

relative to genotypes that contribute relatively more to the stalk (Strassmann *et al.*, 2000). This threat of being invaded by ‘cheater’ cells is avoided, at least in part, by the *csA* gene (Queller *et al.*, 2003). Wild-type cells are more likely to form stalk cells (that is, are more altruistic) than *csA*-knockout cells. However, cheating by *csA*-knockout cells is prevented because wild-type cells preferentially recognize and allow wild-type cells (rather than *csA*-knockout cells) to form spore cells. In other words, this gene helps altruists to choose their partners – a ‘green beard’ effect (Hamilton, 1964, 1970; Dawkins, 1976; Haig, 1997). On the other hand, this is a suitable system of altruist cells to exclude non-altruist cells from the group, hence attributing more damage to their authors – the *csA*-knockout mutants. It is a policing mechanism in the excludability term, which then reduces the impact of rivalry because the group becomes more homogeneous upon exclusion. This is, however, a side-effect of the exclusion of cheater cells (Hurst, 1994).

Compartments can be ‘defined’, not only by competing individuals themselves, but also by other entities. Consider the example of rhizobia that expend resources on fixing nitrogen for the benefit of their host plant. The paradox here is why should an organism (rhizobia) perform a costly behaviour that provides a benefit for an individual of a different species (host plant), hence indirectly benefiting rhizobial competitors that share the same plant? West *et al.* (2002) have recently suggested that nitrogen fixing may be favoured when plants preferentially supply more resources to – or are less likely to senesce – nodules that are fixing more nitrogen. Again, this has the consequence that it reduces the chance for egoism to be manifest. It could be argued that each nodule is a compartment. We note, instead, that if this ‘sanction’ (Denison, 2000) from the plant was absent, any nodule in the same plant would be naturally associated through the plant tissues. It is the sanction, however, that *distinguishes* the nodules – that is, that establishes variance in fitness among nodules by providing advantages to the nodules that deserve it.

In conclusion, there are at least two potential solutions for resolving the tragedy of the commons. Evolution can proceed towards repression of internal competition (Frank, 1995b, 2003) and/or proceed towards privatization. These latter mechanisms, which attribute more damage to the author of the damage itself, are selected when the kin-selection relatedness coefficient is low. As we have illustrated above, examples of such mechanisms have previously been described precisely for situations in which relatedness is low. However, to our knowledge, this is the first study to show that such a policing mechanism is selected when relatedness is low, and that the higher its cost, the more stringent are the conditions for its selection.

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