

Evolutionary stable investment in products that confer both an individual benefit and a public good

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TABLE OF CONTENTS

1. Abstract
2. Introduction
3. Basic model
4. Game theoretical solutions
 - 4.1. Well-mixed population
 - 4.2. Spatially-structured population with global competition
 - 4.3. Spatially-structured population with local competition
5. Relationship to classical discrete games
6. Perspective
7. Acknowledgements
8. References

1. ABSTRACT

Why should a microbe manufacture extracellular enzymes if its competitors can free-ride on these enzymes? Similarly, why should an animal place seeds into storage when others can exploit this stored resource? A solution to this general class of problems becomes apparent if one assumes that investors directly benefit from a proportion of the investments they make. Thus, when individuals benefit from a proportion p of their investments, but share the rest with other individuals in the system, then an evolutionarily stable level of investment can evolve which is higher the higher the value of p . These evolutionarily stable investment points mark the junction at which several classical games meet, so that changes in investment can move interactions from one game type to another. Non-zero optimal levels of investment also arise under conditions when investments are only shared locally, and even when producers lose more product to competitors than they save for themselves. Overall, this “personal gain” approach offers a simple yet robust explanation for why individuals engage in activities which may concomitantly benefit others.

2. INTRODUCTION

Microorganisms are known to invest in a wide range of compounds that are released and/or leaked into their local environment. These extra-cellular compounds typically confer a direct benefit to the individuals that produce them. To the extent that these compounds also provide a benefit to other, often nearby, cells, then extra-cellular compounds may be considered to be “public goods”. As with all public goods, those that invest in their production may potentially be undermined by cheats, individuals that reap the benefit of the good itself but contribute nothing to its production. The fact that the production of public goods is often energetically expensive makes the persistence of the phenomenon difficult to understand in evolutionary terms: why should an individual invest time and energy in the production of a compound that may benefit conspecifics who do not themselves engage in its production?

Evidence that microbial public goods systems can be undermined by cheats on evolutionary time scales has been experimentally demonstrated in a number of cases

including biofilm formation (1), the degradation of penicillin by β -lactamase (2), the production of iron-scavenging siderophores (3), bacteria-killing compounds such as colicins (4), and extracellular enzyme production in yeasts (5). Yet examples of potential public goods in the microbial world abound, many of which have been summarized by West *et al* (6). Additional examples not included in their tally are the production of the precursors of dimethyl sulfide by marine plankton, which some workers have argued may incidentally benefit the population as a whole (7), and the formation of nitrogen-fixing heterocysts in cyanobacteria (8).

Analogous social dilemmas are also known in metazoans, and it is especially evident in the act of food storage by birds and mammals. For instance, acorn woodpeckers drill acorns into oak trees for future consumption, but why is this strategy not undermined by “freeloaders” who put less effort into storing food themselves and simply exploit the actions of others (9, 10)? The well-known producer-scrummer (11, 12) and more general snowdrift games (13, 14) capture the essence of interactions in which individuals face the temptation to sit back and let others do the work. Such temptations are familiar to us in the human world, forming the basis of moralistic folk tales such as the ‘Little Red Hen’ and the Aesop fable “The Ant and the Grasshopper”.

A solution to this diverse set of problems becomes apparent when one recognizes that: (i) a proportion of any given investment in food resource gathering or storage directly benefits the investor, a scenario termed “weak altruism” by Wilson (15; see also 16, 17), and (ii) the returns from any investment are rarely shared out equally among all individuals in a population. In this way, it may pay an individual to incur a cost to gather resources simply because, while conspecifics may incidentally benefit from the behavior, the individual stands to gain even more.

Several mechanisms may facilitate an unequal sharing of investment returns. For example, the importance of spatial asymmetry for the production of extracellular enzymes was recently recognized by Allison (18) who noted that lower rates of enzyme diffusion tended to favor microbes that produced these enzymes compared to cheats that did not. Similarly, Anderson & Krebs (19) proposed that for hoarders to persist, a necessary (but not sufficient) condition is that a hoarder has a greater probability of recovering its own stored items (through territory use or memory) than another member of the group.

The usual practice in modeling social dilemmas is to assume the existence of distinct strategies. Thus Allison’s (18) detailed model assumed the discrete strategies of “produce” or “cheat”, the food-hoarding models of Anderson & Krebs (19) and Smulders (9) considered “hoarders” and “non-hoarders”, and Barnard & Sibly (11) considered “producers and scroungers”. Here we take a more general approach by allowing individuals to vary continuously in the amount of investments they make in obtaining/storing food resources (20). These

investments might be thought of as the quantity of extracellular enzymes, or the energy required to procure and to store seeds, both of which are liable to vary continuously. It is important to develop models in this way not only because it improves their realism, but also because it allows for quantitative (21-23). The models presented here are therefore designed to understand the optimal level of investment, rather than the equilibrium proportion of extreme strategies such as “cheat” and “cooperate”.

As our main motivation is to understand investment in public goods from a microbial perspective, our approach considers large populations of potential contributors. However, we allow such populations to be well mixed or spatially structured. We identify analytical solutions using mathematically convenient functions, but we also explore general properties of more realistic relationships using numerical simulations. In what follows, we introduce the basic model and its derivatives. We then highlight a general feature of these systems, showing that they can reflect a range of different game-theoretical structures and that their solution arises where classical game structures meet.

3. BASIC MODEL

As we are attempting to represent a variety of systems, our model is of general form. In a recent paper, Doebeli *et al.* (24) developed and explored a continuous investment game in which the payoff $P(x, y)$ to an individual investing x interacting with an individual (or group of individuals) investing y could be represented:

$$P(x, y) = B(x + y) - C(x) \quad (1)$$

where $B(x + y)$ represents the benefit function to the recipient for the combined investment $x + y$ and C is the cost function to the x strategist for its own investment. The authors concluded that the evolutionary dynamics of investment levels in this system would often lead to a surprising outcome in which some individuals invest nothing, while others make significant investments.

To allow for the very real possibility of asymmetries in the proportion of benefits each individual receives from a given investment, one can modify the above formulation. Thus, let only a proportion p of the investments of an individual be available to provide a direct return to that individual. In the simplest case, let us assume that a fixed proportion $(1-p)$ of investments that are not directly available to an individual, are shared equally between all other individuals in the system. The payoff to a rare mutant individual which invests y when interacting with members of a large population which each invest x then becomes:

$$P(y, x) = B(y p + x (1-p)) - C(y) \quad (2)$$

while

$$P(x, x) = B(x) - C(x) \quad (3)$$

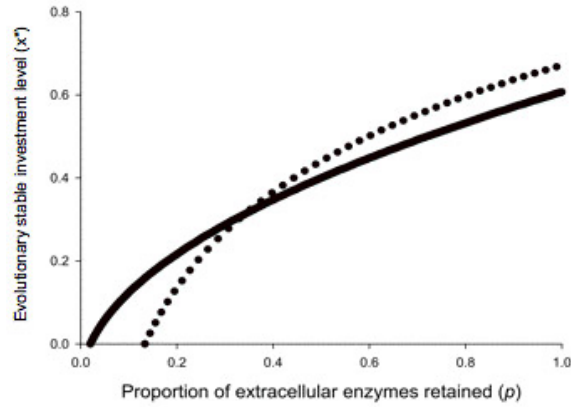


Figure 1. Investment level as a function of the fraction of enzymes retained by the producer. As the proportion of enzymes (p) that are retained by the producer cell increases, then so too does the predicted ESS investment level. Solid line: benefit function 1, $k_1 = 5$, $k_2 = 0.1$, $k_3 = 1$. Dotted line: benefit function 2, $k_1 = 5$, $k_2 = 3$, $k_3 = 2$.

The invasion fitness $f_x(y)$ of the rare mutant with investment level y in a resident population of conspecifics that each invest x is given by:

$$f_x(y) = P(y, x) - P(x, x) \quad (4)$$

which in effect measures the relative success of the rare mutant compared to a random member of the population.

We now introduce specific forms of the cost and benefit functions, which assume in the first instance that the benefits of investment increase non-linearly with the amount of investment, but that the costs increase linearly. The benefit to any given individual from a combined available investment z (which equates to $y + x(1-p)$ in the case of a rare mutant that invests y , and x in the case of an individual that invests the population standard x) was either assumed to be:

$$B(z) = k_1 z / (k_2 + z) \quad [\text{function 1}](5)$$

or

$$B(z) = k_1 \{1 - \exp(-k_2 z)\} \quad [\text{function 2}](6)$$

while the cost of investing q was assumed, in the first instance, to be a simple linear function:

$$C(q) = k_3 q \quad (7)$$

where k_1 , k_2 , k_3 and k_4 are positive constants. The asymptotic benefit function simply reflects diminishing returns in which higher investments do not necessarily bring about greater rewards. By contrast, the cost function reflects a situation in which overall costs increase at a fixed rate with investment size (this restrictive assumption is later relaxed).

4. GAME THEORETICAL SOLUTIONS

4.1. Well-mixed population

How would investment levels tend to evolve from a given starting point in the above model? We can apply standard methodologies from the framework of adaptive dynamics (24-26) to derive analytical insights into the underlying properties of the above model. Singular points (whether they be branching points, or evolutionary stable strategies) are given by solutions to $\delta f_x(y)/\delta y|_{y=x} = 0$.

Using function 1, a singular point occurs at the investment level x^* where:

$$x^* = (1/k_3) \{ (p k_1 k_2 k_3)^{1/2} - k_3 k_2 \} \quad (8)$$

Since $\delta^2 f_x^* / \delta y^2|_{y=x^*} = -2 p k_3^2 (p k_1 k_2 k_3)^{1/2}$ which is negative for all positive values of $\{k_1, k_2, k_3\}$, then this investment level x^* represents a local maximum and therefore an evolutionary stable strategy (ESS). Using Function 2, a singular point occurs at the investment level x^* where

$$x^* = [\ln(p k_1 k_2) - \ln(k_3)] / k_2 \quad (9)$$

Note that $\delta^2 f_x^* / \delta y^2|_{y=x^*} = -p k_2 k_3$, which is less than 0, such that x^* again marks an ESS.

Thus, with both function 1 and function 2, the ESS investment level increases as the proportion of investments that are available to the producer increases (Figure 1). Note that when $p = 1$ then this represents the solution to the single individual optimal investment in which payoffs are individually maximized; conversely, when p approaches zero then the optimal level of investment will be zero for all positive solutions of x^* .

When the costs of investment increase exponentially with investment level such that:

$$C(q) = k_3 \exp(k_4 q) \quad (10)$$

then simulation-based solutions to the evolutionary optimal investment levels confirm that the same general relationships hold. For example, Figure 2 shows the predicted evolutionarily stable investment level when benefit function 1 and exponentially increasing costs are assumed.

4.2. Spatially-structured population with global competition

The assumption that the proportion $(1-p)$ of investment products of an individual are shared out equally amongst all others is a rather extreme scenario. Instead, one might envisage a situation in which individuals share their investments locally, such as with their nearest neighbors (be they cells in close proximity, or territory owners). We begin by assuming that a producer shares its investments between itself (fraction p) and its 2 nearest neighbors in a large linear array, each obtaining fraction $(1$

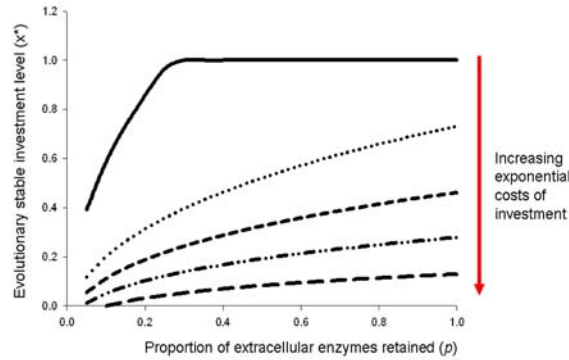


Figure 2. Effect of exponentially increasing costs on investment in extracellular enzyme production. The predicted ESS investment level rises with the proportion of enzymes (p) retained by a producer even when the costs of investment increase exponentially with investment size. Here benefit function 1 is assumed with $k_1 = 5$, $k_2 = 0.1$, while exponential costs (equation 10) are assumed with $k_3 = 1$ and $k_4 = 0.1, 0.5, 1, 2$ or 5 . Solutions were derived numerical simulation, with maximum and minimum investments of 1 and 0 respectively. As the exponential coefficient increases then the evolutionarily stable investment level in enzymes decreases.

$p/2$ of this investment. Let us assume in the first instance that the processes of competition and invasion that give rise to population replacement continue to take place between randomly chosen pairs of individuals in the system. The payoff to a rare mutant individual which invests y interacting with members of a large population which each invest x then becomes:

$$P(y, x) = B(y p + 2 [x (1-p)]/2) - C(y) \quad (11)$$

which reduces to (2), while $P(x, x)$ remains the same, such that the ESS for function 1 and function 2 are precisely those as given by equations (8) and (9). Clearly, the result is extendable to any number of neighbors (hence a two or three dimensional grid), whenever the fraction of total investment $(1-p)$ that is available to neighbors is shared out equally among them. Therefore, so long as there is global competition our original predictions for the ESS investment level remain valid.

4.3. Spatially-structured population with local competition

When there is spatial structure in the way investments are leaked and in the way competition takes place, then the analysis is more complicated because one must separately consider the conditions for invasion from extreme rarity, and spread from this initial seed. For example, it is possible that a lone mutant can have a higher fitness than its nearest neighbor and thereby invade it, but once there are two such mutant strategies adjoining one another, then these two individuals have a lower fitness than their neighbors (we have invasion without spread). Likewise, a particular mutant form may be unable to spread from extreme rarity, but should a cluster of mutants happen by chance to arise together (for example, a second high-

investment mutation arises in the neighbour, before the lone mutant is out-competed), then it may nevertheless spread.

Here we identify the conditions for initial invasion and subsequent spread in a linear array of investors, but the same principles are readily applied to systems with more than 2 nearest neighbors, such as grid systems with 8 nearest neighbors (Figure 3a,b). In both cases it is readily shown that non-zero levels of investment can evolve, with higher mean investments the higher p .

Any lone mutant individual investing y in a linear array of individuals that invest x will spread so long as:

$$B(p y + x (1-p)) - C(y) > B(p x + \{y (1-p)/2\} + \{x (1-p)/2\}) - C(x) \quad (12)$$

Assuming benefit function 1 and linear costs, and solving (12), it is possible to show that a lone mutant investing slightly more than the population ($y > x$) will spread so long as $x < (1/2 k_3) \{ [2 k_1 k_2 k_3 (3p - 1)]^{1/2} - 2 k_3 k_2 \}$ [threshold 1], indicating evolutionary selection away from non-zero investment. Conversely, a lone mutant investing slightly less than the population ($y < x$) will invade whenever the population level of investment x is greater than this threshold.

Nevertheless, despite passing the criterion for invasion, such mutants will only spread in a linear array so long as a cluster (in this case 2 or more mutants in a row with an y - x interface), can invade, namely:

$$B(p y + \{y (1-p)/2\} + \{x (1-p)/2\}) - C(y) > B(p x + \{y (1-p)/2\} + \{x (1-p)/2\}) - C(x) \quad (13)$$

Assuming benefit function 1 and linear costs, and solving (13) we note that inequality (13) is satisfied for y slightly larger than x , so long as $x < (1/k_3) \{ (p k_1 k_2 k_3)^{1/2} - k_3 k_2 \}$ [threshold 2]. Conversely, a cluster of mutants investing slightly less than the population ($y < x$) will invade whenever x is greater than this threshold.

When all individuals invest less than thresholds 1 and 2, then any individual investing slightly higher than the population level will not only invade, it will also subsequently spread. Likewise, when all individuals invest more than threshold 1 and 2, then any individual investing less than this population level will not only invade, it will also spread. The evolution of investments between these thresholds is the outcome of a more complex dynamic in which any clusters of high investors that happen by chance to form can spread, but once widespread, they will be undermined by the establishment of single mutants with lower investment which can invade their nearest neighbor, but then fall victim to their own limited success. Simulations confirm this precise result (Figure 3a). Analogous arguments about the ability to invade and spread apply to the two dimensional case (Figure 3b), and again confirm that if investment products are shared out locally, and competition is local, then non-zero investment levels readily evolve. Indeed, the greater the extent of local

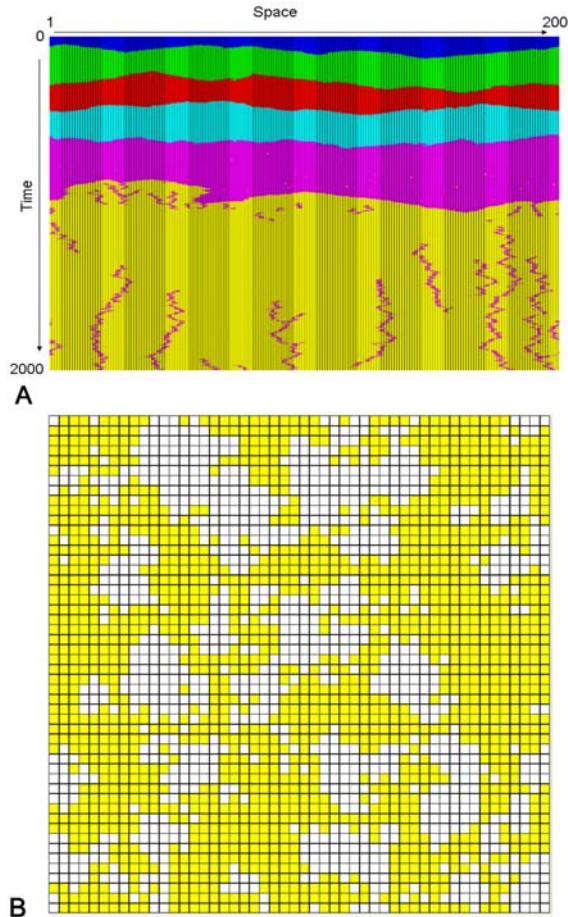


Figure 3. Spatial simulation results. Results of a simulations over 2000 generations involving a linear array (A), and two dimensional array (B), of n individuals which each invest in extracellular products that can leak locally to their two nearest neighbors (linear array) or eight nearest neighbors (two dimensional array). Terminal cells were assumed to wrap around. Initial investments of individuals were selected from a normal distribution with mean 0.02, standard deviation 0.02. Each generation n randomly chosen pairs of neighbors were repeatedly chosen and the individuals with the highest payoffs invade their neighbor. There was also a small probability of a mutation (0.005 per individual per generation), following which the investment in the cell was incremented by a normally distributed value with mean 0 and standard deviation 0.01. Benefit function 1 was assumed, with $p = 0.7$, $k_1 = 5$, $k_2 = 0.1$, $k_3 = 1$. Under these conditions, threshold 1 is 0.424 and threshold 2 is 0.492 for the linear case (see text). Each cell is colored according to the investment (x) of the individual it contains. Color codes: blue $x < 0.1$, green $0.1 \leq x < 0.2$, red $0.2 \leq x < 0.3$, cyan $0.3 \leq x < 0.4$, magenta $0.4 \leq x < 0.45$, yellow $0.45 \leq x < 0.5$, white $0.5 \leq x < 0.52$ (A) In the linear case ($n = 200$), individuals evolve investments towards the threshold 2, but the evolved solution is continually undermined by individuals investing slightly less. (B) In the two dimensional case ($n = 50 \times 50$), individuals evolve investments even closer to the predicted ESS for global competition (0.492), although temporary clusters of investors investing slightly higher can temporarily succeed.

sharing the closer the mean level of investment matches the ESS for the global competition.

5. RELATIONSHIP TO CLASSICAL DISCRETE GAMES

Although the model analysis outlined in section 4.1 is couched purely in terms of investment levels, we can gain qualitative insight into the evolutionary stable strategies that evolve by comparing the tensions involved to those in classical games. Thus, one might define mutual cooperation as an act in which both interacting parties (the mutant and the resident) give the higher of two possible investments x and y , and mutual defection as an act in which both partners give the lower of these two investments. If we cast the model in this way, then with $y > x$ and a large well mixed population, the payoffs to a rare mutant become:

		Action of other individuals	
Action of mutant	C [= y]	C [= y]	D [= x]
	D [= x]	$B(y) - C(y)$	$B(py + (1-p)x) - C(y)$
		$B(px + (1-p)y) - C(x)$	$B(x) - C(x)$

The game is effectively a Prisoner's Dilemma (PD) if the payoffs from adopting particular actions are such that $DC > CC > DD > CD$. However, it is a chicken (= snowdrift) game if $DC > CC > CD > DD$, a deadlock game if $DC > DD > CC > CD$ and a simple cooperative game if $CC > CD > DC > DD$ ("Mutual 1") or $CC > DC > CD > DD$ ("Mutual 2") - see Poundstone (14). From these inequalities, it is clear that changes in game type will occur when $CC = DC$ and $DC = DD$. Solving $CC = DC$ for non trivial solutions of x with function 1 and substituting this expression into $DC = DD$, generates precisely the same solution for x^* as (8). A similar result applies to function 2. Thus the points at which evolutionary-stable investment levels occur (as given by (8) and (9) in this instance) consistently mark the point at which several game structures meet (Figure 4a,b).

The evolutionary dynamic giving rise to the ESS is now easier to see. It is clear that the simple payoff schemes in equation (2) and (3) represent several different games dependent on investment levels, rather than any one single type of game. At low investment levels cooperative games are played and higher investment is favored, whereas at high investment levels, more exploitative games are being played and lower investment is favored. An equilibrium is reached at the juncture between games that favor increased investment and games that favor reduced investment.

6. PERSPECTIVE

The model we have explored here treats the degree of investment in extracellular enzyme production as a continuous rather than an all-or-nothing discrete strategy. Overall, we feel that such an approach is more realistic (see for example 22, 23, 27, 28). Indeed, as Greig & Travisano

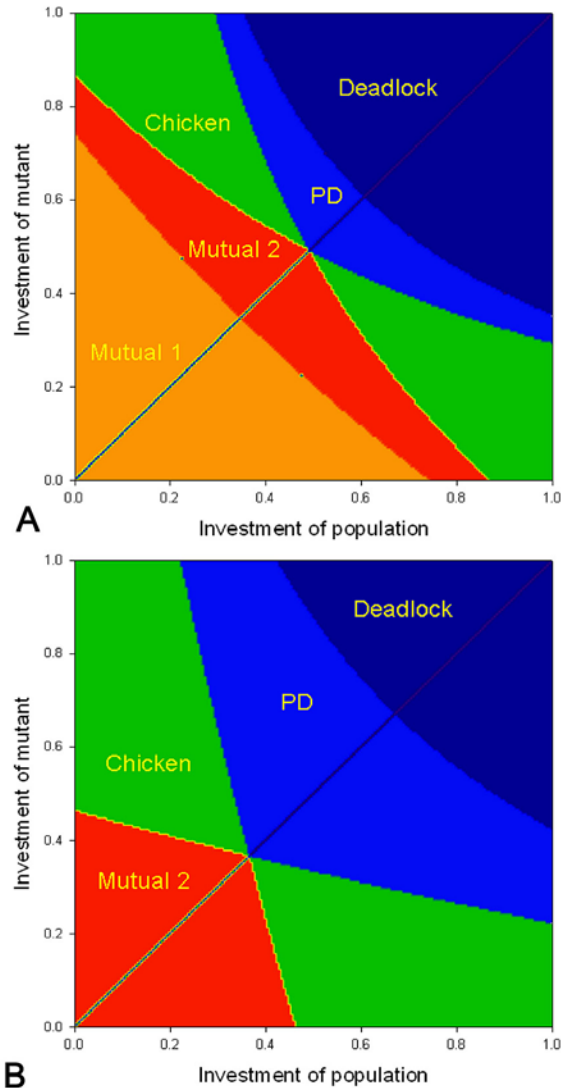


Figure 4. The type of game played varies as a function of investment level. The types of game played between mutants and members of the rest of the population when mutual cooperation corresponds to each player investing the higher of two investments and mutual defection is each player investing the lower of two investments. The evolutionary stable points mark investment levels at which games promoting cooperation and games promoting defection meet. (A) Benefit function 1, $k_1=5$, $k_2=0.1$, $p=0.7$, cost equation (7) with $k_3=1$ (B) Benefit function 2, $k_1=5$, $k_2=3$, $p=0.4$, cost equation (7) with $k_3=2$.

(5) note, “continuously variable heritable levels of enzyme production may be envisaged in real life”. Our approach also allows one to identify solutions, such as the optimal level of investment, which is simply not possible with a discrete formulation involving investors and cheats. Our model clearly shows that it frequently pays individuals to invest in extracellular enzyme production, even if other individuals may also incidentally benefit (29). The same type of approach might equally apply to producer-scrummer systems. Thus, the observation of investment in

processes that also incidentally confer benefits to conspecifics is not such a difficult phenomenon to explain.

Note that our approach differs fundamentally from many other continuous games of cooperation in recognizing that a proportion (p) of an individual’s investments can bring a direct return to the producer. For example Killingback *et al.* (30) explored a continuous game of cooperation in a spatial lattice in which *all* the benefits of an individual’s investment were enjoyed by neighbors, and the producer received no direct return at all from its investment. Introducing the possibility of a direct return to the individual not only makes the system more realistic, but clearly facilitates greater investment. Do such behaviors constitute cooperation? A proportion of the investment ($1-p$) of an individual clearly benefits other individuals, but it is not selected for because of its beneficial effect on the recipient, and would therefore not constitute cooperation, as defined by recent commentators (31).

In the simplest model structure, in which a proportion of investments are shared globally, a single evolutionarily stable level of investment was identified and characterized. We find that the higher the proportion of investments that an individual is able to retain, the higher its optimal level of investment, all else being equal. This hypothesis could, in principle, be tested experimentally by following the level of investment that evolves in genotypes that differ in the fraction of product they retain for themselves, as in Dugatkin *et al.*’s (2) experiments employing *E. coli* strains that shared β -lactamase to different extents.

Note that positive investment solutions are possible even for $p < 0.5$, so that even if the majority of an individual’s investment is “squandered” on the population as a whole then investment can still be profitable. Interestingly, many bacteria appear to have adaptations that help keep the enzymes used in extracellular digestion in very close proximity to the cell membranes (32), thereby keeping p high. Many extracellular proteins produced by Gram-negative bacteria are, for example, secreted into the periplasmic space between the cytoplasmic membrane and the outer membrane, and only secondarily leak passively across the outer membrane into the environment (33), suggesting that the outer membrane may have evolved in part as an adaptation for retaining investment products. It has also been suggested that phagocytosis in eukaryotes may also have evolved as a way around problems with extra cellular digestion (34). At an extreme, one might think that an individual should have some physical means of bringing back all of the products of their investment so as to prevent them from being shared, a form of ‘tethering’. Indeed, many bacteria do have tethering mechanisms in the form of specific uptake systems embedded in the outer membrane designed to take up key resources such as iron (35). However, bacteria also produce iron-binding molecules such as siderophores and hemophores that are released freely into the environment. Why should they maintain both systems when the production of siderophores and hemophores could be so readily undermined by cheats?

An interesting avenue for future research would therefore be to identify conditions that promote or prevent the evolution of tethering.

In adopting a continuous model, our approach has been rather different than traditional approaches which adopt a frame structure such as Prisoner's Dilemma model and identify strategies that would do well. By contrast our approach, like Doebeli *et al.*'s (22), has been based on generalized payoff functions. Our analysis has revealed how simple payoff functions can generate a variety of games dependent on investment levels. The fact that stable solutions occur at positions where game structures meet can be readily understood on the basis of games favoring increasing investment adjoining games favoring reduced investment.

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