



# Siderophore production and the evolution of investment in a public good: An adaptive dynamics approach to kin selection



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## HIGHLIGHTS

- We use a mechanistic description of the biology of siderophore producing bacteria, and the laboratory protocols under which they are grown, to derive fitness measures.
- We provide an adaptive dynamics based approach for kin selection and derive conditions for evolutionary stability.
- We found that selection can lead to an intermediate strategy which is always evolutionarily stable, but that highly cooperative strains can invade the ESS.

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## ABSTRACT

Like many other bacteria, *Pseudomonas aeruginosa* sequesters iron from the environment through the secretion, and subsequent uptake, of iron-binding molecules. As these molecules can be taken up by other bacteria in the population than those who secreted them, this is a form of cooperation through a public good. Traditionally, this problem has been studied by comparing the relative fitnesses of siderophore-producing and non-producing strains, but this gives no information about the fate of strains that do produce intermediate amounts of siderophores. Here, we investigate theoretically how the amount invested in this form of cooperation evolves. We use a mechanistic description of the laboratory protocols used in experimental evolution studies to describe the competition and cooperation of the bacteria. From this dynamical model we derive the fitness following the adaptive dynamics method. The results show how selection is driven by local siderophore production and local competition. Because siderophore production reduces the growth rate, local competition decreases with the degree of relatedness (which is a dynamical variable in our model).

Our model is not restricted to the analysis of small phenotypic differences and allows for theoretical exploration of the effects of large phenotypic differences between cooperators and cheats. We predict that an intermediate ESS level of cooperation (molecule production) should exist. The adaptive dynamics approach allows us to assess evolutionary stability, which is often not possible in other kin-selection models. We found that selection can lead to an intermediate strategy which in our model is always evolutionarily stable, yet can allow invasion of strategies that are much more cooperative. Our model describes the evolution of a public good in the context of the ecology of the microorganism, which allows us to relate the extent of production of the public good to the details of the interactions.

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## 1. Introduction

Cooperation can take several forms. Individuals can help each other directly in pairwise interactions, but also indirectly, for

instance, by investing in traits that improve the environment so as to increase population growth. If such a modification of the environment benefits all members of a population, it is referred to in the biological literature as a public good (Rankin et al., 2007).

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It is well-known that public good production can evolve despite the possibility of cheaters or free-loaders, if there is spatial structure or some other form of assortment (Lion and van Baalen, 2008; Fletcher and Doebeli, 2009). However, it is not always clear how to relate these quite general models to specific cases, in particular when aspects such as relatedness are not constants but depend on the local and global dynamics. Here, we will explore how cooperation via a public good can evolve in the specific instance of siderophore production in parasitic bacteria.

Virtually all bacteria need iron for various metabolic functions (Andrews et al., 2003). Parasitic bacteria, in particular, live inside host organisms where free iron is scarce but also many other bacterial habitats have little free iron available. In order to take up iron many bacteria excrete siderophores, which are molecules that bind to iron with high affinity. A siderophore–iron complex, once formed, can be taken up by any cell with appropriate siderophore receptors (Ratledge and Dover, 2000; Griffin et al., 2004; Wandersman and Delepelaire, 2004). This system has been particularly well studied for the bacterium *Pseudomonas aeruginosa*, an opportunistic pathogen which produces the siderophore pyoverdine. Experimental work has shown that when iron is limiting, pyoverdine producing strains reach higher densities than strains which do not produce pyoverdine, yet when put in competition the pyoverdine producers are outcompeted, which shows that there is a cost associated with siderophore production (Griffin et al., 2004; Ross-Gillespie et al., 2007). Thus, because the production of these siderophores is costly, strains that produce less, or altogether no siderophores should be advantaged when competing against high siderophore producers, and cooperation should not evolve if selection is dominated by local competition (West and Buckling, 2002; Kümmerli et al., 2009, 2010).

The evolution of siderophore use depends on how strains interact, both locally and globally. Bacterial populations that produce more siderophores reach higher densities and thus contribute more to the next generation. But these strains are vulnerable to cheater strains that are better local competitors (as these do not pay the cost yet benefit from siderophores). Bacterial strains that produce siderophores thus face a trade off between their ability to compete locally (siderophore production reduces growth rate), and productivity (siderophores allow higher densities). The balance between these two forces has been shown to affect the evolution of siderophore production (Griffin et al., 2004; Kümmerli et al., 2009, 2010).

There has been considerable debate whether siderophore production can invariably be seen as a public good (Zhang and Rainey, 2013; Kümmerli and Ross-Gillespie, 2014; Ghoul et al., 2014). Zhang and Rainey (2013) argued, on the basis of an experimental approach, that under some conditions siderophore production can be outright counterselected, in which case non-producers cannot be considered to be ‘cheats.’ Whether siderophores are a common good thus depends on the conditions. This debate shows that fitness functions should be *derived* from the full underlying dynamics and for arbitrary trait complexes (siderophore production and use) (see also Alizon, 2013).

This argument extends to evolution in general, but in particular to the evolution of pathogens. Pathogen evolution, for instance in the development of resistance, depends on the epidemiological interaction between host and bacterium, bacterial genetics as well and the molecular mechanisms of antibiotic action. To predict and understand such evolutionary processes we need models that integrate all these aspects (MacLean et al., 2010a,b; Metcalf et al., 2015). Here we show that it is possible, and practically feasible, to derive fitness expressions from models that include a detailed description of the dynamics. This allows us to apply an inclusive fitness perspective to evolutionary problems using an adaptive dynamics approach. Although this paper focuses on siderophore

production, the approach can, and should, be used for a much wider class of evolutionary problems.

Evolutionary models for siderophore production have tended to focus on scenarios in which the local and global interactions are described in a highly stylised form, either based on the model framework developed by Frank (1998) (e.g., West and Buckling, 2002; Brown et al., 2009) or models based on *a priori* chosen, stylised fitness functions (Ross-Gillespie et al., 2009, 2007; Cornforth et al., 2012). The construction of such models appears to be based on simply filling in the components of Hamilton's Rule by choosing plausible functions. This may give insight in the potential for kin selection, but this methodology can easily miss essential feedback mechanisms. This is particularly relevant if one goes beyond marginal fitness considerations and one needs to know the fitness to a higher degree of approximation than a first degree. This is important if larger mutational steps are studied and if one wants to know where the long-term evolutionary process will end (i.e. if the endpoint is evolutionarily stable or whether branching will occur). As we wish to develop an understanding of how ecological and evolutionary processes interact in shaping the evolution of common goods, we here derive the fitness from a model based on simple but plausible assumptions about experimental protocol and the local bacterial ecology. Because we base our model on explicit mechanisms, we can assess how the relevant costs and benefits (as well as the relatedness parameter) depend on the ecological details, instead of having to assume that they are constants, as it is usually done. In doing so we go beyond agent-based simulation models in which such realism is included, but for which it is normally not possible to interpret the results in terms of inclusive fitness theory, or to identify cost and benefits. Without identifying costs and benefits it is hard to generalise the results from models and to form an integrative understanding of the evolutionary process.

To analyse our model we have applied a separation of time-scales. This is based on the observation that while bacteria grow fast, competition between strains (in a local population) is much slower. This analysis allows us to easily identify fitness costs and benefits. Furthermore, this approach enables us to assess how the degree of assortment in a metapopulation, as measured by relatedness, depends on local and global processes. We will study how this feedback affects the evolutionary end result using an adaptive dynamics approach (Metz et al., 1992). This not only allows us to work out the optimum compromise between cooperation and cheating, but also to assess whether this optimum is an evolutionarily stable strategy, that is, whether natural selection will favour a monomorphic population with a unique strategy or whether it will favour a heterogeneous population with divergent strategies (Geritz et al., 1998). Such approaches have been developed and are frequently used in ecologically inspired models of evolution, but have rarely been applied to the evolution of social interactions (but see Ohtsuki, 2010).

In previous work we have shown that social interactions can lead to the emergence of a diversity of competing types of cooperators and cheaters (Lee et al., 2012). For this work we assumed that all cooperators (and all cheaters) have the same level of siderophore production, and hence, a strain can be characterised by the type of siderophore it produces, and its strategy (cooperate or cheat). However, there exists a high diversity of siderophore production rate between different strains (Jiricny et al., 2010). Here, we focus on the evolution of production rate of a single siderophore type. We assume that all strains produce the same type of siderophore, but each strain is now characterised by its rate of production. Similar to Lee et al. (2012), we determine if social interactions can lead to the emergence of a diversity of different coexisting strains. We do this by formulating and analyzing a model for the evolution of siderophore production that takes into

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