

Invited reply

Assortment is a more fundamental explanation for the evolution of altruism than inclusive fitness or multilevel selection: reply to Bijma and Aanen

Broadly speaking, altruistic traits can be thought of in two categories: those where the benefits of a helpful behaviour go only to others (excluding the actor), and those where these benefits go towards some common good, a portion of which feed back to the actor. In both cases the actor alone bears the cost involved in exhibiting the behaviour. Pepper (2000) refers to these as ‘other-only’ and ‘whole-group’ traits, respectively, and provides many empirical examples of each.

In accordance with the usual formulation of the public goods game, in our paper (Fletcher & Doebeli 2009, hereafter FD09) we chose to model a whole-group trait. Specifically, we defined the benefit and cost parameters b and c in terms of the direct consequences of a cooperative behaviour, where b is a measure of how much fitness benefit the behaviour contributes to the public good and c is the direct fitness cost to the actor for exhibiting the cooperative behaviour. (Imagine for example a cooperative hunter who shares any spoils with its interaction group; a hunter loses c calories in the act of hunting but provides b calories to the group in the form of food, so that both of these parameters have a straightforward biological interpretation.) The goal of our paper was to present a simple framework that highlights the role of genotype–phenotype assortment in the evolution of cooperation. This framework is based on interaction environments, and on the distinction between payoffs due to self and payoffs due to others.

In their comment, Bijma & Aanen (2010, hereafter BA09) are suggesting that we should do something different: we should analyse our whole-group public goods model as if it were a model of an other-only trait instead. To make their point, BA09 present a simple re-parametrization of the public goods game discussed in FD09, and acknowledge that their re-parametrization is mathematically equivalent to our original formulation. The re-parametrization consists of including the benefit that a cooperating individual provides to itself in the cost of cooperation (by subtracting the benefit to self from that cost), and to adjust benefits to the public good by the same amount (by again subtracting the benefit to self from the benefit accruing to the group). In other words, BA09 re-parametrized the public goods game so that it looks like an other-only model. BA09 claim that their re-formulation lends itself more easily to comparisons with kin and group selection, but in fact

our approach better matches work in these theories where they apply to whole-group traits. For example, the ‘coefficient of relatedness’ r for whole-group traits that we defined in FD09 connects easily to multilevel selection theory, because it can be interpreted as the portion of the total variance in a trait that is due to variance among groups (Breden 1990). (See Pepper (2000) for a review of both whole-group and other-only inclusive fitness models, and the relationship between them.)

When the condition for the evolution of cooperation in the public goods game is formulated as a Hamilton’s rule, the other-only version BA09 prefer generates a relatedness r that has a value of zero for random interactions in infinite populations, rather than the $1/N$ value that one obtains for the whole-group version of r (Pepper 2000). BA09 claim that their model is biologically more meaningful, because the coefficient of relatedness, measured as a regression coefficient, is zero in infinite populations with random interactions. However, this amounts essentially to a tautology, because in infinite populations with random interactions this regression is expected to be zero only in others-only models of cooperation. (Note that even in these models the regression coefficient would not be zero for random interactions in finite populations.)

There are many mathematically equivalent ways to write Hamilton’s rule, depending on what values and meanings one assigns to the ‘cost’, ‘benefit’, and ‘relatedness’ variables. This has allowed Hamilton’s rule to be applied to not only inclusive fitness models, but many others, including multilevel selection models (Wade 1980; Wilson 1980; Frank 1998) and reciprocal altruism models (Queller 1985; Frank 1994; Fletcher & Zwick 2006). In particular, in our formulation of FD09, the value of $r = 1/N$ for random interactions simply reflects the fact that a cooperator’s relatedness to itself is always 1 in any given public goods interaction group of size N . Essentially, BA09 argue that we should interpret the variables in Hamilton’s rule as Hamilton (1964, 1971, 1975) did originally, but this is not necessary or desirable, especially given that we are modelling a whole-group public goods game, whereas Hamilton’s empirical examples were other-only traits (Pepper 2000). In addition, by focusing on Hamilton’s view, BA09 return to a purely genetic (relatedness) interpretation of assortment: ‘The correlation coefficient of the gene in the partners on the gene in the focal individual’ (BA09, p. 674). On the other hand, in FD09 we emphasize a more general genotype–phenotype view of assortment

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(Eshel & Cavalli-Sforza 1982; Queller 1985; Fletcher & Zwick 2006), an interpretation BA09 support in the first part of their comment: 'Genetic relatedness is merely one of the possible mechanisms that can create the required assortment' (BA09, p. 673). Most notably, the purely genetic interpretation falls short in the case of interspecific altruism (i.e. mutualism), in which the basic requirement of assortment between altruistic genotype and helping behaviour of others (in this case, individuals in the other species) remains exactly the same, but relatedness is out of the picture.

It is generally good practice to question the choices made in constructing scientific models (including evolutionary models), and we commend BA09 for raising this issue. While there is nothing wrong with their reformulation, BA09 seem to see our framework only through the lens of more familiar treatments. However, one of the main points of our paper was to present a more fundamental way of understanding the evolution of cooperation. Our framework does not depend on the concepts of kinship, inclusive fitness, or selection among groups, but instead focuses on genotype-phenotype assortment and comparing the direct benefits different types receive from their average interaction environments.

We think our original whole-group formulation of the public goods game nicely reveals this very general perspective. In particular, our approach using the whole-group benefit b highlights the payoffs accruing to individuals from their average interaction environment in a biologically meaningful way. For example, if one wants to measure the benefits that accrue to a population of bacteria due to secretion of enzymes by individual bacterial cells, it would seem to be much easier to measure the quantity b used in our formulation, i.e. the benefit that accrues to the whole population (e.g. in terms of growth rate), than to measure the others-only benefit of BA09, i.e. the benefit to the group minus the benefit to the individual producing the enzyme. In general, translations between methods of analysis may be useful in demonstrating mathematical equivalence, but can also be confusing when one moves away from the empirical motivation behind a model. As we acknowledge in FD09, different perspectives can of course be applied to our model. Our goal in FD09 was to offer an alternative to these traditional perspectives, which are embroiled in historical and semantic controversies (West *et al.* 2007, 2008; Wilson & Wilson 2007; Wilson 2008), and call attention to the central importance of genotype-phenotype assortment, and to the fact that assortment can, in principle, be easily assessed using the concept of interaction environments.

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