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A simple model of group selection that cannot be analyzed with inclusive fitness



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HIGHLIGHTS

- We formulate a simple set of group selection models.
- For some of those, inclusive fitness gets the direction of selection wrong.
- Inclusive fitness also does not offer a way to find the model solution.
- One needs to have the solution already in order to even compute inclusive fitness.

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ABSTRACT

A widespread claim in evolutionary theory is that every group selection model can be recast in terms of inclusive fitness. Although there are interesting classes of group selection models for which this is possible, we show that it is not true in general. With a simple set of group selection models, we show two distinct limitations that prevent recasting in terms of inclusive fitness. The first is a limitation across models. We show that if inclusive fitness is to always give the correct prediction, the definition of relatedness needs to change, continuously, along with changes in the parameters of the model. This results in infinitely many different definitions of relatedness – one for every parameter value – which strips relatedness of its meaning. The second limitation is across time. We show that one can find the trajectory for the group selection model by solving a partial differential equation, and that it is mathematically impossible to do this using inclusive fitness.

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1. Introduction

Group selection has always been a controversial issue. It is both advocated as an essential ingredient of human evolution (Sober and Wilson, 1998; Wilson and Wilson, 2007), and described as a superfluous concept, that does not explain any phenomenon we do not already understand with other models (Williams, 1966; Dawkins, 1989; Pinker, 2012). While there is disagreement concerning the relevance, both sides of the debate have come to agree that group selection models can always be reformulated in terms of inclusive fitness (Queller, 1992a,b; Lehmann et al., 2007; Holldobler and Wilson, 2009; Wild et al., 2009; Wade et al., 2010; Lion et al., 2011; Marshall, 2011a; Gardner et al., 2011).

The agreement on the equivalence still leaves room to disagree which one of the two is more valuable for understanding how group selection works. One position is that, since both are equivalent, there is no reason to look at group selection models other than through the lens of inclusive fitness (Dawkins, 1989; Lehmann et al., 2007; West et al., 2007,2008; Wild et al., 2009; Lion et al., 2011; Marshall, 2011a; Gardner et al., 2011). Another position is that, even though the two are equivalent, there is value in the alternative way of looking at models, that stresses a balance of within-group selection and between-group selection (Sober and Wilson, 1998; Wilson and Wilson, 2007; Wilson, 2008; Holldobler and Wilson, 2009; Wade et al., 2010).

Because the “mathematical equivalence” is such a central point of consensus, one would expect it to be a well-defined mathematical statement with a mathematical proof. There is, however, no such theorem in the literature (see also Queller, 1992a; van Veelen et al., 2012). As a consequence it remains unclear what “mathematical equivalence” means here, and whether or not the claim is

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correct. In this paper, we will present a class of group selection models that allows us to explore what it could mean for group selection models and inclusive fitness to be equivalent.

It also uncovers two different kinds of limitations. The limitations imply that group selection and inclusive fitness are not equivalent in general, even though they can be under certain assumptions.

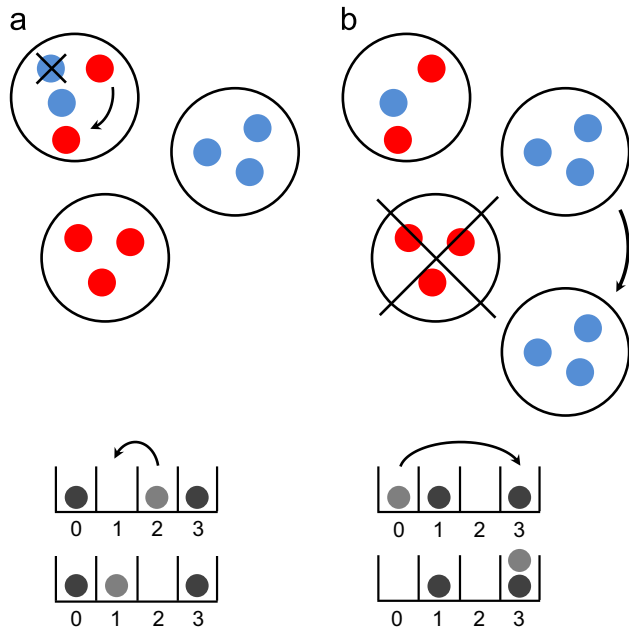


Fig. 1. Panel (a) depicts an individual level event, panel (b) a group level event. Cooperators (blue) reproduce individually at intensity 1, defectors (red) at intensity $1+s$. When an individual reproduces, a random individual is chosen to die. Groups reproduce at intensity $1+u(i/n)^\alpha$, where i is the number of cooperators in a group, and n the group size. When a group reproduces, a random group is chosen to die. The effect of the events on the composition of the population is visualized below each panel; they change how many groups there are with 0, 1, 2 and 3 cooperators. In the limit of the group size going to infinity, groups are characterized by the fraction x of cooperators, and as the number of groups goes to infinity, the population state becomes a density over $(0, 1)$, that describes how many groups there are for different cooperator frequencies x . (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

2. The model

The model is a generalization of Luo (2014). Individuals find themselves in groups of equal size, and can be one of the two types: defectors and cooperators. Individual reproduction happens at different rates: cooperators reproduce at rate 1, defectors reproduce at rate $1+s$. Every individual reproduction event induces a death event; if one individual reproduces, one random individual from the same group is chosen for elimination, thereby keeping group sizes constant. Entire groups also reproduce, and when they do, they produce a daughter group with the exact same proportion of cooperator and defectors. The rate at which this occurs depends on the fraction of cooperators in the group; a group of size n with i cooperators in it reproduces at rate $1+u(i/n)^\alpha$. That implies that all-defector groups reproduce at rate 1, and all-cooperator groups reproduce at rate $1+u$. Every group reproduction event induces a group death event; if a group reproduces, a random group is chosen for elimination (see Fig. 1).

Being a cooperator therefore comes at a cost – it reduces the reproduction rate of the individual by s – but it has a benefit for all group members, including itself, through an increase in the rate at which the group as a whole reproduces. The baseline reproductive rates for individuals and groups are set to unity for simplicity, but Appendix E also covers the more general case where the baseline reproduction rates of individuals and groups are allowed to differ. A setup that allows for groups of different sizes and a variety of group level events is also possible (Simon, 2010; Simon et al., 2012, 2013). Several other models (for example Kimura, 1983; Gardner and West, 2006; Traulsen and Nowak, 2006) are based on group level dynamics with a similar flavor, although the analysis we carry out on the dynamics of the distribution of the population is distinct from these previous approaches.

If we take a limit, where group size and number of groups go to infinity, then the dynamics simplify to a partial differential

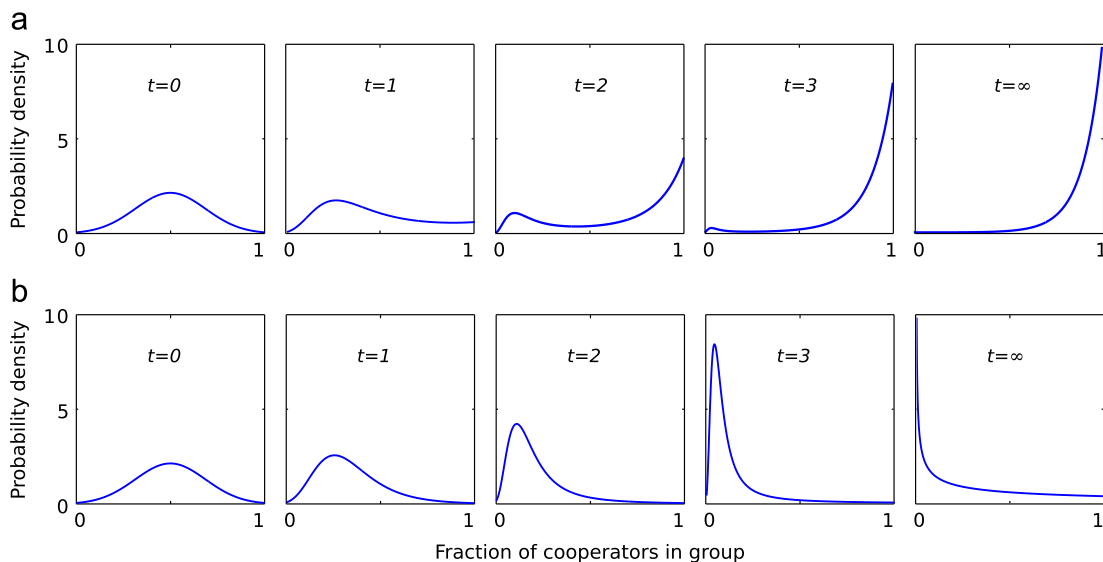


Fig. 2. A density describes the relative frequencies of groups with different fractions x of cooperators, where x varies between 0 and 1. The PDE describes how these densities change over time. The changes are caused by two effects. The first is that individual reproduction makes all groups to become less cooperative – which makes the “humps” in the distributions move to the left in both examples. The second is that cooperative groups as a whole reproduce faster – which results in the right end of the distributions being lifted up. As time elapses, the densities change, until the two effects balance at a stable steady state, described by the equilibrium distribution. The upper series (a) has $\alpha = 3$, $s = 1$ and $u = 4$, the lower series (b) has $\alpha = 1$, $s = 1$ and $u = 1.5$. For both the initial distribution is proportional to a truncated normal distribution with mean 0.5 and variance 0.035. In both cases the densities converge to a steady state density in which all group types are represented, but in the first case there are more cooperators than defectors, overall, and in the second there are more defectors than cooperators.

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