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Group selection and inclusive fitness are *not* equivalent; the Price equation vs. models and statistics

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ABSTRACT

It is often suggested that any group selection model can be recast in terms of inclusive fitness. A standard reference to support that claim is "'Quantitative genetics, inclusive fitness, and group selection" by Queller (1992) in the American Naturalist 139 (3), 540-558. In that paper the Price equation is used for the derivation of this claim. Instead of a general derivation, we try out a simple model. For this simple example, we find that the result does not hold. The non-equivalence of group selection and kin selection is therefore not only an important finding in itself, but also a case where the use of the Price equation leads to a claim that is not correct.

If results that are arrived at with the Price equation are not correct, they can typically be repaired by adding extra assumptions, or explicitly stating implicit ones. We give examples with relatively mild and with less mild extra assumptions. We also discuss why the Price equation is often referred to as dynamically insufficient, and we try to find out what Price's theorem could be.

The Dude: This is a very complicated case, Maude. You know, a lotta ins, lotta outs, lotta what-have-yous. A lotta strands to keep in my head, man. Lotta strands in old Duder's head.

The Big Lebowski

1. Introduction

George R. Price produced two of the most influential papers about the evolution of cooperation in the last 50 years. One of them, written together with Maynard Smith (Maynard Smith and Price, 1973) is about why conflicts between animals do typically not escalate. In order to be able to predict which strategies for conflict will evolve, it introduces the notion of an evolutionarily stable strategy (ESS). This has become the central concept in evolutionary game theory, together with the replicator dynamics that was introduced by Taylor and Jonker (1978). There is no doubt that evolutionary game theory in general and the idea of an ESS in particular has been essential for understanding the evolution of cooperation. In models with mutation and selection, the ESS is the most natural refinement of a Nash equilibrium, and to formulate a model and look for evolutionarily stable strategies has become a standard approach.

The other paper—this one single authored—introduces what is now known as the Price equation (Price, 1970). This paper has also been very influential, and the equation is regularly described as giving a simple, but very deep insight into the fundamentals of population genetics (see for instance Frank, 1995; Grafen, 2002; Gardner, 2008). Countless papers have been written using the Price equation, and its fame as the equation that describes the evolution of altruism has given $\overline{w}\Delta z = cov(w,z)$ in biology something of the appeal that $E = mc^2$ has in physics. This appeal is enhanced by Price's remarkable life story, and his equation has therefore become the nucleus of the biography by Harman (2010), where scientific thinking about the evolution of selflessness in general, all the way from Fisher, Haldane and Wright to Maynard Smith and Hamilton, culminates in the discovery of Price's equation.

There is a difference, though. While the ESS is undisputed as a tool for modelling, the Price equation is not, and nor are the results that are arrived at with it. Especially in the debate about the value of inclusive fitness (Nowak et al., 2010; Gardner et al., 2011) and the relation between group selection and inclusive fitness (Queller, 1992; Sober and Wilson, 1998; Wilson and Wilson, 2007; Traulsen and Nowak, 2006; Lehmann et al., 2007; Killingback et al., 2006; Grafen, 2007a; Van Veelen, 2009, 2011a,b; Wild et al., 2009; Wade et al., 2010; Marshall, 2011a,b) results that are derived with the Price equation are contested. In Van Veelen et al. (2010) we claim that the disagreement about these results is partly caused by the use of the Price equation. If we ignore the abuse of the word covariance, then the Price equation is an identity, and can therefore not be wrong. Its typical use

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however confuses probability theory and statistics, as well as identity and causality.

If the Price equation indeed is not a proper tool for doing statistics, nor for making models or deriving predictions, as claimed in Van Veelen (2005), then there are a lot of questions that arise concerning the large literature in which the Price equation is used. Has using the Price equation ever lead to incorrect claims? If the Price equation is bad statistics, then what would good statistics be? Does that imply that these results are all wrong? Is there such a thing as Price's theorem? And why is it called dynamically insufficient? In this paper we will try to address these issues. The different sections in this paper are therefore somewhat loosely connected, as they answer different questions concerning the Price equation and the literature using it. The central part however concerns the question whether or not using the Price equation has ever lead to incorrect results.

Queller (1992) is regularly referred to as support for the widely held belief that models of group selection and inclusive fitness are equivalent (see for instance Okasha, 2010). The paper uses the Price equation to show that both group selection models and inclusive fitness work for the same reasons if they do, and fail for the same reasons if they do not. In Section 3 we will go through all steps of the argument, not with the Price equation, but with an extremely simple example. It turns out that none of the steps of the argument is correct already for a very simple set of models. If the claim is not correct for one example, then it surely cannot be correct in general. This particular result, arrived at with the Price equation, therefore, turns out to be wrong.

Section 4 describes the relation between the Price equation and the statistics literature.

Section 5 looks at the issue of dynamic sufficiency. We argue that the fact that the Price equation is regularly described as limited by dynamic insufficiency is really a symptom of the real problem with the Price equation. An identity itself cannot be dynamically sufficient or insufficient. Models can. We claim that the lack of rigour concerning what the numbers are that go into the Price equation can induce people using it to make implicit assumptions that amount to dynamically insufficient models.

The literature mentions not only the Price equation, but also Price's theorem and Price's rule. While the Price equation can be traced back to Price's work (1970, 1972), this is not true for Price's theorem or Price's rule. Section 6 discusses what Price's theorem could be.

Of course not all results arrived at with the Price equation are wrong—even if the Price equation does not provide a proper proof. In Section 7 we therefore look at the scope for repair of results "derived" with the Price equation. For some results one can simply write down a proper proof without the Price equation. For other results it turns out that we need to make some extra assumptions to repair the result. This indicates that using the Price equation induces assumptions being swept under the carpet. Rederiving results without the Price equation then forces one to get them back from under there.

2. The Price equation

What can go wrong when the Price equation is used for the derivation of a theoretical result can best be explained with the words of a famous Dutch football player. When he was once asked what you should do in order to win a game, Johan Cruijff replied that you should score [at least] one more goal that your opponent. This of course is a funny reply (although it is not sure if it was actually meant as such) because it is both indisputably correct as well as completely useless. It is quite possible that it was Cruijff's way of saying that the question was rather unspecific and broad, but then again, it is equally possible that Cruijff himself actually thought that he had stumbled upon a deep truth. It is also possible that what he really meant to say is "don't play too defensive; you can concede a goal and still win the game". What is important for the analogy with the Price equation is that it is certainly not an answer to the question as the journalist meant it; he or she expected an answer like "play 4-3-3" or "train less" or "don't play too defensive", preferably with an explanation of why that would be the key to winning a game. Johan Cruijff's answer just rephrased what it is to win, and did not suggest how to do it. Still it was correct as any answer can be. But it is not an answer that is of too much use.

Price formulated his equation well before Cruijff formulated this particular footballogism. But even though he cannot possibly be inspired by Cruijff, Price's famous equation and Cruijff's (locally) famous answer share the same basic logic, although with the Price equation this is much harder to see. The Price equation does not concern what happens in a football game, but it is about what happens between two subsequent generations. The numbers that it uses are the genetic compositions of the two generations. Van Veelen (2005) goes into more detail here, but what is most important is that we realize that the numerical input of the Price equation is a list of numbers. It is a list that concerns two generations, and which tracks who is whose offspring. But whatever it reflects, it is crucial to realize that the point of departure is nothing but a list of numbers. This list of numbers is used twice. First we use it to compute the frequencies of the gene under consideration in generations 1 and 2, respectively, and subtract the latter from the former. This amounts to the change in gene frequency. Then we use the same list to compute a few other, slightly more complex quantities. The essence of the Price equation is that these quantities also add up to the change in gene frequency. One way of computing the change in frequency therefore can be rewritten as the other and vice versa. What they are, therefore, is nothing but two equivalent ways to compute the change in gene frequency, given a list of numbers concerning genes in two subsequent generations (see Fig. 1).

What is important to realize, is that this equivalence is tautological. Therefore it is true whatever the numbers are that are on the list. Whether this particular second generation is likely to follow the first or not, the two ways of computing the change in frequency return the same number. Had the list of numbers been

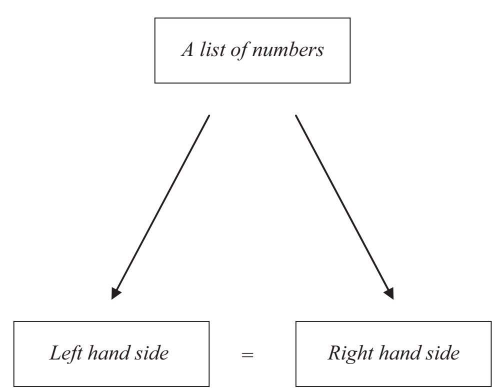

Fig. 1. In its most simple form, the list contains (1) per individual in the parent population the dose of a gene, (2) the same for individuals in the offspring generation, and (3) who in the offspring population got which gene from which parent. The simple way to compute the change in gene frequency (left hand side) is just to calculate the gene frequency in the parent population, calculate the gene frequency in the offspring population, and subtract the latter from the former. The right hand side is much more complex, but nonetheless it is the same change in gene frequency that follows from the list of numbers being what it is; see Box 1, Van Veelen (2005) and www.evolutionandgames.com/price for details. Less simple forms of the Price equation exist, but they are not fundamentally different.