



Q2 Hamilton's Rule in finite populations with synergistic interactions

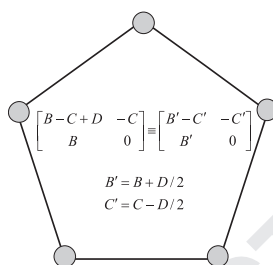
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HIGHLIGHTS

- Q5 • I review a number of recent results from synergistic games on evolutionary graphs.
- In general, higher-order coefficients of relatedness are needed for the inclusive fitness effect.
- However when genetic variance is maintained by rare mutation, standard (linear) coefficients will suffice.
- In this case, a synergistic game has an equivalent additive game.

GRAPHICAL ABSTRACT



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ABSTRACT

Much debate has appeared in the literature over the generality of the inclusive fitness approach in the modeling of evolutionary behavior. Here I focus on the capacity of the inclusive fitness approach to effectively handle non-additive or synergistic interactions. I work with a binary interaction with the matrix game $\begin{bmatrix} a & b \\ c & d \end{bmatrix}$ and I restrict attention to transitive (homogeneous) populations with weak selective effects. First of all I observe that the construction of “higher-order” relatedness coefficients permits these synergistic interactions to be analyzed with an inclusive fitness analysis. These coefficients are an immediate generalization of Hamilton's original coefficient and can be calculated with exactly the same type of recursive equations. Secondly I observe that for models in which the population is not too large and local genetic renewal is rare (e.g. rare mutation), these higher order coefficients are not needed even with non-additive interactions; in fact the synergistic interaction is entirely equivalent to a closely-related additive one. The overall conclusion is that in the study of synergistic binary social interactions (2-player games) in a finite homogeneous population with weak selection and rare genetic renewal, a standard inclusive-fitness analysis is able to predict the direction of allele-frequency change. I apply this result to analyze a recent model of Allen and Nowak (2015).

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1. Introduction

The study of the evolution of social behavior has been hugely enriched by Hamilton's (1964) construction of inclusive fitness and the wealth of literature which has developed and extended its ideas over the past half century. Much recent controversy (Nowak et al., 2010; Abbot et al., 2011; Bourke, 2011; Herre and Wcislo,

2011; Nowak et al., 2011; Allen et al., 2013; Liao et al., 2015; Queller et al., 2015) has arisen over the significance and centrality of the inclusive-fitness approach. The resulting debate, which typically identifies apparent misunderstandings, has certainly led to a clarification and sharpening of our understanding of the inclusive fitness method. One of the most significant issues in this debate concerns the capacity of the inclusive-fitness approach to handle non-additive or “synergistic” fitness effects and this question is close to my own recent interests. I believe that a synergistic inclusive fitness theory is now firmly in place and that has

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prompted me to reply to a recent paper of [Allen and Nowak \(2015\)](#) where it is asserted that “inclusive fitness can only be formulated if each individual’s genotype contributes a separate, well-defined amount to each other individual’s fitness.” In my response below I first observe that a natural generalization of the standard notion of relatedness can give us an inclusive-fitness analysis of non-linear (quadratic) fitness effects. Secondly I point out that there are some quite standard population models for which the classical “additive” inclusive-fitness analysis is already able to handle synergistic fitness effects. Those are the ones in which the process through which new genetic material enters a neighborhood, for example, mutation, is rare.

At the core of an inclusive-fitness analysis is the inclusive-fitness effect

$$W_{IF} = \sum_k a_{ik} R_{i-k} \quad (1.1)$$

of a single focal actor i whose behavior generates a fitness change a_{ik} in a number of recipients k ([Hamilton, 1964](#)). Here W_{IF} is a linear combination of the effects a_{ik} each weighted by the focal relatedness R_{i-k} to the individual k , this being a measure of the extent of common genetic ancestry between i and k ([Michod and Hamilton, 1980](#)). It has been shown many times in different ways ([Hamilton, 1964](#); [Charlesworth, 1980](#); [Queller, 1992a](#); [Taylor 1996](#), and many more recent papers cited below) that under a suite of simple assumptions, particularly weak selection and additive gene action, the sign of W_{IF} will tell us whether the selective effects of the action of an allele will cause its frequency to increase or decrease.

To be more precise about the assumption of additivity, it requires that the fitness effect a_{ik} of the action of i on individual k depends only on the genotype of i and is independent of all other genotypes, particularly that of k . This is, I believe, the condition that [Allen and Nowak \(2015\)](#) had in mind with the stipulation that “each individual’s genotype contributes a separate, well-defined amount to each other individual’s fitness.”

An enormous body of work generated over the past 50 years has produced many versions and extensions of the fundamental Eq. (1.1). Much of the recent work in social evolution looks at binary matrix games in which the selective effects of the behavior are directly coded by genetic alleles, and in that domain it appears to be the case that a linear combination of fitness effects such as is found in Eq. (1.1) will do the job only under particular “additive” conditions, often referred to as “equal gains from switching.” [Queller \(1985, 1992b\)](#) was the first to discuss these non-additive or “synergistic” effects and he observed that they would require an extension of the standard approach.

One such extension is based on the use of a multilinear regression analysis ([Queller, 1992a, 1992b](#); [Gardner et al., 2011](#)). This approach retains the mathematical form of the inclusive fitness effect (1.1) but the fitness effects a_{ik} are no longer constructed mechanistically directly from the entries of the payoff matrix (e.g. by following the effects of a fecundity benefit through the pattern of offspring dispersal), rather they are replaced by more general coefficients of linear regression. Effectively this approach is says that for the purpose of measuring allele frequency change, the fitness-determining interactions behave as if they combine additively. However in forming this linear combination, the biologically meaningful parameters such as the entries of the payoff matrix and offspring dispersal probabilities are often replaced by more abstract entities and one loses the direct intuition of the formulation.

Here I will work with another type of extension, one that preserves the meaning of the fitness effects a_{ik} , but extends the summation found in (1.1) to incorporate quadratic fitness effects a_{ijk} and corresponding relatedness coefficients R_{ij-k} . In this extension, individuals i and j are in a sense joint actors in that the fitness effect a_{ijk} on k depends not simply on the genotype of the

focal actor i , but on the product $x_i x_j$ of the genotypes of i and j , and the coefficients of relatedness R_{ij-k} depend on the various probabilities of genetic identity among all three individuals.

Finally and unexpectedly, I will observe that in the case in which local genetic renewal (mutation or migration) is rare, and the population size is not too large, these generalized relatedness coefficients R_{ij-k} are not actually needed; rather the quadratic synergistic effects referred to above can be handled with the standard coefficients R_{i-k} . To be more explicit, I will show (Eq. (2.6) below) that in this case, the inclusive-fitness effect can be given an “additive” formulation in which every individual’s genotype does indeed contribute a separate, well-defined amount to each other individual’s fitness. In the [Appendix I](#) provide a simple worked example of this. I end with an inclusive fitness analysis of the two examples discussed by [Allen and Nowak \(2015\)](#).

2. Inclusive fitness with pairwise interactions

2.1. Population structure

I begin with a finite population represented as an evolutionary graph, a set of nodes, indexed by i and j , etc., each occupied by a single asexual haploid breeder. The structure of the population is a specification of fitness interactions among the nodes as well as node succession, the probability that in each time step, breeder i is replaced by breeder j or by its offspring. An evolutionary graph has a homogeneous or *transitive* structure ([Taylor et al., 2007b](#)) if for any given pair i, j of nodes there is an *isomorphism* of the node set mapping i to j , that is, a bijection which preserves all components of the structure: interaction and node replacement. Roughly speaking, the structure “looks the same” from every node, that is, if an inhabitant of any node was blindfolded and removed and then put back on a node at random, it would be unable to tell whether it had been moved. When transitivity fails, the orbits of the set of all isomorphisms partition the node set into reproductive classes and individuals in different classes might have different reproductive values which typically need to be accounted for. To keep the analysis simple I will assume the population has a transitive structure.

There are many ways to model birth and death and here I allow either a Moran process in which in any time-step there is a single birth and death, or a Wright-Fisher process in which generations are non-overlapping and in each time-step all individuals bear offspring and die and the offspring repopulate the nodes.

I suppose that there are two alternative alleles A and B in the population determining behavior and I let the genotypic value x_i of the breeder on node i be the frequency of A in its genotype. To maintain local genetic variability, we need a source of new genetic material and I assume that this comes through “long-range” migration or mutation or both.

2.2. Matrix games

In each generation an individual has a number of pairwise interactions, each playing the game with payoff matrix $\begin{bmatrix} a & b \\ c & d \end{bmatrix}$ ([Maynard Smith, 1982](#); [Queller, 1985](#); [Nowak and May, 1992](#); [Nowak et al., 2004](#)) where the first row gives the payoffs to an A-player (with an A or B partner) and the second row belongs similarly to B. I assume that the payoffs represent small increments in fitness, small enough that we can ignore second-order effects. For each offspring, the average payoff is added to the baseline fitness of 1. Here we take individual fitness to measure genetic contribution to the next generation.

In inclusive-fitness studies, a normalized version of the matrix is often used. If we subtract d from each entry so that the payoff

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