Available online at www.sciencedirect.com
ScienceDirect
Journal of Theoretical Biology 247 (2007) 382–390
Journal of Theoretical Biology
www.elsevier.com/locate/yjtbi

The different limits of weak selection and the evolutionary dynamics of finite populations ☆

Geoff Wild[a], Arne Traulsen[b,*]

[a]Department of Applied Mathematics, The University of Western Ontario, London, Ont., Canada N6A 5B7
[b]Program for Evolutionary Dynamics, Harvard University, Cambridge, MA 02138, USA

Received 10 January 2007; received in revised form 13 March 2007; accepted 13 March 2007
Available online 18 March 2007

Abstract

Evolutionary theory often resorts to weak selection, where different individuals have very similar fitness. Here, we relate two ways to introduce weak selection. The first considers evolutionary games described by payoff matrices with similar entries. This approach has recently attracted a lot of interest in the context of evolutionary game dynamics in finite populations. The second way to introduce weak selection is based on small distances in phenotype space and is a standard approach in kin-selection theory. Whereas both frameworks are interchangeable for constant fitness, frequency-dependent selection shows significant differences between them. We point out the difference between both limits of weak selection and discuss the condition under which the differences vanish. It turns out that this condition is fulfilled by the popular parametrization of the prisoner's dilemma in benefits and costs. However, for general payoff matrices differences between the two frameworks prevail.

Keywords: Evolutionary game theory; Finite population; Fixation probability; Kin selection; Moran model; Weak selection

1. Introduction

The evolutionary dynamics of finite populations has recently generated a tremendous amount of interest (Nowak et al., 2004; Taylor et al., 2004; Wild and Taylor, 2004; Traulsen et al., 2005; Imhof et al., 2005; Imhof and Nowak, 2006; Antal and Scheuring, 2006). The majority of this work studies evolution under the so-called Moran process (Moran, 1958, 1962), or variations thereof. In the Moran process a population, consisting of a finite number of "mutant" and "wild-type" individuals, is repeatedly updated by paired birth and death events. The pairing of births and deaths ensures that population size stays constant. Updating continues until only one type (mutant or wild type) remains.

Fixation in a Moran process is inevitable, and so the probability that one type or the other becomes fixed is of much interest. Naturally, the fixation probability of a given type depends, in part, on the rate at which that type is able to reproduce. In the absence of fitness differences different types in the population reproduce at the same rate, and fixation probabilities are the initial fractions of the types in the population. However, the general expressions for fixation probabilities are complicated making mathematical study difficult.

When faced with a complicated expression for fixation probability, the standard procedure has been to analyze the weak selection approximation of the expression. In this case, one assumes that different types in the population have reproductive rates that are very "close" to one another. Interestingly, the definition of "close" may or may not have important implications for how we interpret the results of our analysis.

Reproductive rates may be "close" because the difference between mutant and wild-type phenotypes (which may be quite large) plays only a very small role in the overall determination of reproductive rate. This is the

---

☆Both authors contributed equally to this work. Order of authorship was determined by reproductive fitness.

*Corresponding author. Tel.: +1 617 496 5564.

E-mail addresses: gwild@uwo.ca (G. Wild), traulsen@fas.harvard.edu (A. Traulsen).

0022-5193/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jtbi.2007.03.015

standard notion of "closeness" found in most evolutionary game theory (Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998; Nowak et al., 2004).

Reproductive rates might also be "close" because the difference between the mutant and wild-type phenotypes is only very slight. This alternative definition of "closeness" arises whenever we have a way to measure distance in the set of phenotypes, and is usually applied in kin-selection models of evolution (Grafen, 1985; Taylor, 1989; Eshel, 1983; Christiansen, 1991).

The goal of this paper is to describe the conditions under which both definitions of weak selection yield the same conclusions about evolution under the standard Moran model and its generalization to populations with hierarchical structure, i.e. multilevel selection. We restrict our comments to symmetric two-player games. So far, the consequences of these different concepts have not been explored. Here, we relate two different approaches to weak selection and show under which conditions the same results can be expected.

In Section 2 we recall the Moran model and we discuss analyses under different forms of weak selection. In Section 3, the different fixation probabilities are discussed and viewed from a kin-selection perspective. In Section 4, we compare both approaches and discuss the condition under which both forms of weak selection are equivalent, both for mixed populations and a hierarchical generalization with two different levels of selection.

2. Reproductive rates and two kinds of weak selection

2.1. A 2×2 matrix game

We assume a single, well-mixed population of constant size N, and we suppose the population is, at least temporarily, dimorphic. We consider two types of individuals, "mutant" and "wild type". We suppose that the rate at which a given individual reproduces is determined by the outcome of some game. In the game, mutants use one strategy (i.e. phenotype), and wild types use a different one. The game itself is played by two individuals (players). In any round of the game a player opts for one of the two pure strategies A and B with probabilities according to its phenotype. The payoffs of the game can be summarized in a simple matrix form as

$$\boldsymbol{M} = \begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array}. \tag{1}$$

The entries of $\boldsymbol{M}$ are payoffs given to the row strategy when paired against a particular column strategy.

Since mutant and wild-type individuals can use different strategies, reproductive rates will, in general, depend on the numbers of each type in the population. If i is the number of mutant individuals in the population, then $N-i$ is the number of wild-type individuals. We use $f_m(i)$ to denote the reproductive rate of the mutant, and $f_{wt}(i)$ to denote the reproductive rate of the wild type. During a short time interval of length h, $f_m(i)h$ is the probability that a single mutant individual produces identical offspring. Similarly, $f_{wt}(i)h$ is the probability that a single wild-type individual reproduces.

2.2. Small fitness contribution from the game: w-weak selection

As mentioned in the previous section, two kinds of weak selection are considered in this setting. The first we call "w-weak selection". Under w-weak selection, reproductive rates are calculated as a convex combination (i.e. weighted average) of the background fitness, which we set to one, and the expected payoff from the game. The relative weight given to the payoff in this calculation is denoted by w. "Weak selection" is $w \ll 1$. In other words, weak selection means that the payoff from the game has only a marginal influence on $f_m(i)$ and $f_{wt}(i)$ while the phenotypes may differ substantially.

For w-weak selection, we restrict ourselves to pure strategies. The mutant always uses strategy A, whereas the wild type always uses strategy B. If an individual cannot play the game against itself, we obtain

$$f_m(i) = 1 - w + w\left(\frac{i-1}{N-1}a + \frac{N-i}{N-1}b\right), \tag{2}$$

$$f_{wt}(i) = 1 - w + w\left(\frac{i}{N-1}c + \frac{N-i-1}{N-1}d\right). \tag{3}$$

If $w=0$, then $f_m(i) = f_{wt}(i) = 1$ for all states i and we recover the case of neutral selection mentioned above.

2.3. Small distance in phenotype space: δ-weak selection

The second kind of weak selection we call "δ-weak selection". δ-weak selection assumes that the game means much to the determination of reproductive success, but that selection is weak because mutant and wild-type strategies are very similar.

Under δ-weak selection, mutants and wild types use mixed strategies. Suppose wild-type individuals choose strategy A with probability p and strategy B with probability $1-p$, and suppose mutants choose A with probability $q = p + \delta$ and B with probability $1 - q = 1 - p - \delta$. Weak selection in this framework corresponds to small (and positive) δ, i.e. the two mixed strategies are very similar to each other.

It is convenient to define the vectors $\boldsymbol{p} = (p, 1-p)^{\mathrm{T}}$ and $\boldsymbol{\delta} = (\delta, -\delta)^{\mathrm{T}}$. This allows us to write the reproductive rates as

$$f'_m(i) = 1 + \frac{i-1}{N-1}(\boldsymbol{p}+\boldsymbol{\delta})^{\mathrm{T}}\boldsymbol{M}(\boldsymbol{p}+\boldsymbol{\delta}) + \frac{N-i}{N-1}(\boldsymbol{p}+\boldsymbol{\delta})^{\mathrm{T}}\boldsymbol{M}\boldsymbol{p}, \tag{4}$$