Fitness and evolutionary stability in game theoretic models of finite populations

Geoff Wild[*] and Peter D. Taylor

Department of Mathematics and Statistics, Queen's University, Kingston, Ontario K7L 3N6, Canada

We investigate two methods of measuring fitness in evolutionary games played among members of a finite population. Classical notions of stability account for the action of selection only, and use immediate reproductive gains as a measure of fitness. This classical interpretation of fitness is what we call reproductive fitness (RF), and is found in the early studies of evolutionary stability in finite populations. More recent work has incorporated the influence of random genetic drift by applying fixation probability (FP) as a measure of fitness. When defined in this way, fitness represents a measure of ultimate evolutionary success. Our main result describes an equivalence between candidate evolutionarily stable strategies under both the RF and FP interpretations of fitness. We apply this result to matrix games in which the use of mixed strategies is permitted, and find here an equivalence between the RF and FP conditions for evolutionary stability.

Keywords: finite population; evolutionary stability; genetic drift; fixation probability; matrix game

1. INTRODUCTION

The theory of games (e.g. Maynard Smith 1982) is now standard fare in evolutionary biology. Game theoretic models of evolution describe the fitness of a mutant who competes in a social group, composed mainly of normal (wild-type) individuals. From the description of fitness, certain strategies are identified as being 'evolutionarily stable'. Such strategies are typically regarded as the end result of evolution (Hammerstein 1996).

Evolutionary game theory is well developed for infinite populations. That is to say, there are accepted ways to define 'fitness' (Metz *et al.* 1992), and there are several meaningful concepts of evolutionary stability (Maynard Smith & Price 1973; Eshel 1983; Taylor 1989; Christiansen 1991; Abrams *et al.* 1993; Apaloo 1997). However, the same cannot be said for finite populations.

There are, typically, two approaches to defining fitness in a finite population. The first approach considers only immediate gains, for example, the payoff in a two-player contest (Vickery 1987; Maynard Smith 1988; Schaffer 1988; Neill 2004), and is usually employed when modelling a large population. With the assumption that immediate gains are translated into offspring, we refer to this approach as reproductive fitness (RF). The second approach incorporates the possibility that any strategy with non-zero RF can persist over evolutionary time by genetic drift. Fitness in this second sense is described by the probability that a mutant strategy (or allele) becomes fixed in the population (e.g. Proulx & Day 2001, and references therein; Rousset 2003). This approach, which we refer to as fixation probability (FP), is especially appropriate in smaller finite populations. Understandably, with various definitions of fitness come various interpretations of stability concepts (cf. Schaffer 1988; Neill 2004; Nowak *et al.* 2004).

We consider evolutionary games in which strategies are chosen from a continuum of possibilities. We derive fitness functions using both RF and FP approaches. We then define three concepts of evolutionary stability that can be applied during the analysis of these fitness functions. Our main result states that, under certain conditions, RF and FP result in equivalent conclusions about candidate evolutionarily stable strategies. The main result is elaborated for the case of matrix games with so-called 'mixed strategies'.

2. FITNESS FUNCTIONS

We consider a population of haploid, asexual organisms that is of constant size $N > 2$. We posit a normal or 'wild-type' behaviour that is subject to recurrent mutation; however we assume that the mutation rate is low enough that we can disregard the possibility that two different types of mutant coexist. With this assumption we define the state i of the population to be the number of mutant individuals present ($i = 0, 1, \ldots, N$). Let q and p denote the strategies used by the mutant and wild type, respectively, in the evolutionary game ($0 \leqslant q, p \leqslant 1$) thought of as the probability of a certain type of behaviour.

We work with an overlapping generation model in which each individual, mutant and normal, independently of the others, reproduces in any small time-interval according to an exponential distribution with rate parameters f_i and g_i. More precisely, at any time, a mutant individual has probability $f_i \mathrm{d}t$ of having a single offspring within a differential time interval of length $\mathrm{d}t$, and the corresponding probability for a normal individual is $g_i \mathrm{d}t$. The rates f_i and g_i depend on the population state i, but they also depend on the mutant and normal strategies. Thus $f_i = f_i(q, p)$ and $g_i = g_i(q, p)$. To maintain a constant population size, each time a birth occurs we replace a random individual with the newborn offspring.

(a) *The RF interpretation*

The RF approach to mutant fitness works with the relative reproductive rate:

$$W_i^{\mathrm{RF}}(q, p) = f_i(q, p)/g_i(q, p). \tag{2.1}$$

[*]Author for correspondence (gwild@mast.queensu.ca).

When the mutant behaves normally, f_i and g_i are the same; hence

$$W_i^{\mathrm{RF}}(p,p) = 1. \tag{2.2}$$

We will assume that W_i^{RF} is sufficiently 'well behaved', mathematically.

(b) The FP interpretation

The model we consider here is based on the so-called Moran model from population genetics (Moran 1958, 1962), which belongs to a class of stochastic processes known as continuous time Markov chains.

When the population is in state i $(1 \leqslant i \leqslant N-1)$ we let $\lambda_i \mathrm{d}t$ (resp. $\mu_i \mathrm{d}t$) denote the probability that the population will move to state $i+1$ (resp. $i-1$) within a differential time-interval of length $\mathrm{d}t$. It follows from this that in state i, the time until the process moves to state $i+1$ is exponentially distributed with mean $1/\lambda_i$ and is independent of the time until the process moves to state $i-1$, which itself is exponentially distributed with mean $1/\mu_i$.

From our definition of f_i and g_i, it follows that

$$\lambda_i = i f_i(q,p)\left[\frac{N-i}{N}\right], \tag{2.3}$$

$$\mu_i = (N-i) g_i(q,p)\left[\frac{i}{N}\right]. \tag{2.4}$$

Given that the population is currently in state i, we know that with probability one it will end up in either state 0 or state N; that is, either the mutant becomes fixed or it does not. The measure of fitness we use here is the probability that, beginning in state i, the population ends up in state N. This is the mutant fixation probability, and a standard conditional probability argument (e.g. Ross 2000; Nowak *et al.* 2004; Appendix A) yields

$$W_i^{\mathrm{FP}}(q,p) = W_1^{\mathrm{FP}}(q,p)\left(1 + \sum_{k=1}^{i-1}\prod_{j=1}^{k}\frac{g_j(q,p)}{f_j(q,p)}\right), \tag{2.5}$$

where

$$W_1^{\mathrm{FP}}(q,p) = \left(1 + \sum_{k=1}^{N-1}\prod_{j=1}^{k}\frac{g_j(q,p)}{f_j(q,p)}\right)^{-1}. \tag{2.6}$$

Note that $W_i^{\mathrm{FP}}(p,p) = i/N$; that is, the probability that a neutral mutant is the sole founder of a future population is equal to its initial frequency in the population. As before, we assume that $W_i^{\mathrm{FP}}(q,p)$ is sufficiently 'well behaved'.

3. STABILITY CONCEPTS

We will use the term evolutionary stability, broadly, to describe a behaviour or trait that (i) is favoured by selection to be the outcome of the evolutionary process, and (ii) once attained is favoured by selection to persist over time. More precise notions of stability are outlined below. Each definition refers to a function W_i, and either W_i^{RF} or W_i^{FP} can be substituted in its place.

Definition 1: A strategy, p^*, is said to be a Nash equilibrium (NE) provided

$$W_i(q,p^*) \leqslant W_i(p^*,p^*) \tag{3.1}$$

for all q and for all $i = 1, \ldots, N-1$. If the inequality in equa-

tion (3.1) is strict for all $q \neq p^*$ and for all $i = 1, \ldots, N-1$, we call p^* a *strict* NE.

If the strategy p^* is a mixed NE, meaning $0 < p^* < 1$, the equilibrium condition

$$\left.\frac{\partial W_i}{\partial q}\right|_{q=p=p^*} = 0 \quad \text{for all } i = 1, \ldots, N-1 \tag{3.2}$$

must hold. A standard local second derivative condition, which guarantees a local (q close to p^*) strict NE is

$$\left.\frac{\partial^2 W_i}{\partial q^2}\right|_{q=p=p^*} < 0 \quad \text{for all } i = 1, \ldots, N-1. \tag{3.3}$$

Definition 2: If p^* is a NE, then it is said to be convergence stable (CS) provided that for all $p \neq p^*$ but sufficiently 'close' to p^*, and for any $q \neq p$ but sufficiently 'close' to p we can say

$$W_i(q,p) > W_i(p,p) \text{ if and only if } |q - p^*| < |p - p^*| \tag{3.4}$$

for all $i = 1, \ldots, N-1$.

This definition of stability is 'local' in the sense that only arbitrarily small variations in CS strategies are considered. A strategy p^* is CS when selection, in populations fixed for a 'nearby' strategy p, favours only those mutants q that more closely resemble p^* itself. This concept of stability is presented in Taylor (1989) and Christiansen (1991), and a similar one is presented in Eshel (1983), who demonstrates that p^* is CS if

$$\left.\frac{\partial^2 W_i}{\partial q^2} + \frac{\partial^2 W_i}{\partial q \partial p}\right|_{q=p=p^*} < 0 \text{ for all } i = 1, \ldots N-1. \tag{3.5}$$

Definition 3: The NE p^* is said to be a neighbourhood invader strategy (NIS) if, for all $p \neq p^*$ but sufficiently close to p^*,

$$W_i(p,p) < W_i(p^*,p) \text{ for all } i = 1, \ldots, N-1. \tag{3.6}$$

The NIS was introduced by Apaloo (1997). A strategy is NIS when selection favours it to replace other strategies. If equations (2.2) and (3.2) hold, Courteau & Lessard (2000) show that $\partial W_i/\partial p|_{q=p=p^*} = 0$; so that a sufficient condition for an NIS is

$$\left.\frac{\partial^2 W_i}{\partial p^2}\right|_{q=p=p^*} > 0 \quad \text{for all } i = 1, \ldots, N-1. \tag{3.7}$$

In general, the strict NE, CS and NIS are not equivalent. The reader is referred to examples of this non-equivalence in the game theoretic literature for infinite populations (e.g. Christiansen 1991; Abrams *et al.* 1993; Apaloo 1997). These examples extend, *mutatis mutandis*, to the case of finite populations.

The main result of this paper concerns strategies p^* that satisfy the equilibrium condition (3.2).

Theorem 3.1: If p^* is a mixed strategy, then p^* satisfies the equilibrium condition (3.2) under RF if and only if p^* satisfies equation (3.2) under FP.

The proof of Theorem 3.1 is given in Appendix B. It tells us that, when seeking a candidate stable strategy for a game played in a finite population, it does not matter which interpretation of fitness we adopt. Unfortunately, no simple equivalence exists, in general, between stability as it is understood under RF, and stability as it is understood under FP. Still, there are examples in which stability conditions (3.3), (3.5) and (3.7) are identical under both definitions of fitness, and we explore one such example below.

4. EXAMPLE: MATRIX GAMES

Consider a symmetric two-player game in which an individual can adopt one of two pure strategies, A or B. There are four possible outcomes to any contest, and these are described by the 2×2 payoff matrix,

$$G = \begin{matrix} & \text{A} & \text{B} \\ \text{A} & a & b \\ \text{B} & c & d \end{matrix}, \qquad (4.1)$$

where payoffs are given to the row player, for example, an A-player gains a against another A-player, but gains b against a B-player.

This particular matrix game has been studied repeatedly for finite populations (Vickery 1987; Maynard Smith 1988; Schaffer 1988; Neill 2004; Nowak *et al.* 2004). In one study, Nowak *et al.* (2004) propose a definition of evolutionary stability for pure strategies, which invokes both the RF and FP approaches. By their definition, a strategy A is considered *evolutionarily stable* if it satisfies two conditions: (i) the RF of a single mutant (i.e. $i = 1$) in a population otherwise fixed for A is less than that of an A-strategist; and (ii) in a population consisting of $N - 1$ A-individuals and one mutant individual, the mutant has probability less than $1/N$ of ultimately fixing, if the population is held at constant size N. In this section we investigate the consequences of modifying the model of Nowak *et al.* (2004) and allow players to use mixtures of pure strategies according to some probability rule.

Let q and p denote the probability with which mutant and wild-type individuals, respectively, use strategy A. The proportions $1 - q$ and $1 - p$, then, give the probability with which strategy B is used. We will refer to the vectors $\boldsymbol{q} = [q, 1 - q]$ and $\boldsymbol{p} = [p, 1 - p]$ as *mixed strategies*. Assuming that the population is well mixed at the time opponents are chosen, we can calculate an individual's expected payoff as (probability of a mutant opponent) × (expected payoff given mutant opponent) + (probability of a wild-type opponent) × (expected payoff given wild-type opponent). We use the expected payoff to formulate f_i and g_i. Specifically,

$$f_i(q, p) = R_0 + \left[\frac{i - 1}{N - 1}\right]\boldsymbol{q}G\boldsymbol{q}' + \left[\frac{N - i}{N - 1}\right]\boldsymbol{q}G\boldsymbol{p}', \qquad (4.2)$$

$$g_i(q, p) = R_0 + \left[\frac{i}{N - 1}\right]\boldsymbol{p}G\boldsymbol{q}' + \left[\frac{N - i - 1}{N - 1}\right]\boldsymbol{p}G\boldsymbol{p}', \qquad (4.3)$$

where R_0 is a constant that ensures $f_i, g_i > 0$, and a prime denotes the vector-transpose.

Using the fitness $W_i^{\text{RF}}(q, p)$ in equation (2.1), we see that the NE condition (3.2) admits the unique solution

$$p^* = \frac{b(N - 1)/(N - 2) - d - c/(N - 2)}{b - d + c - a}. \qquad (4.4)$$

Equation (4.4) yields a mixed strategy ($0 < p^* < 1$) exactly when the expressions $b - d + c - a$, $(N - 2)(b - d) - (c - b)$ and $(N - 2)(c - a) - (b - c)$ all have the same sign. Using the RF approach, Schaffer (1988) showed that equation (4.4) is a strict NE exactly when

$$b - d + c - a > 0. \qquad (4.5)$$

A simple check of equations (3.5) and (3.7) using W_i^{RF} shows that equation (4.5) is also equivalent to the CS and NIS conditions under RF. Using standard definitions of fitness for infinite populations, Hofbauer & Sigmund

(1988) and Day & Taylor (2003) have presented similar results about the equivalence of stability concepts for matrix games.

By Theorem 3.1, equation (4.4) is also an equilibrium state under FP. And in this case, condition (4.5) again tells the stability story, as the following theorem shows.

Theorem 4.1: The RF stability condition (4.5) also guarantees that p^* in equation (4.4) is simultaneously a strict NE, CS and NIS under FP.

In the mixed-strategies matrix game, we can identify a strategy p^* that satisfies something stronger than Nowak *et al.*'s condition (i): p^* enjoys a RF which exceeds that of any mutant strategy, no matter how many mutants are found in the population. Moreover, the stronger RF condition on p^* appears to be equivalent to a stronger version of Nowak *et al.*'s condition (ii): the probability that p^* becomes fixed in any polymorphic population always exceeds i/N. In the mixed strategies case, then, such 'two-part' definitions of stability—with one part invoking RF and the other invoking FP—are not necessary.

5. CONCLUSIONS AND FUTURE WORK

In finite populations there are at least two ways to define 'fitness'. In large populations reproductive fitness is often the measure of choice (Vickery 1987; Maynard Smith 1988; Schaffer 1988; Neill 2004). In smaller populations, researchers opt for probabilistic notions of fitness (Proulx & Day 2001; Rousset 2003). The main result of this paper states that both notions of fitness provide equivalent candidate 'stable strategies'.

This result is particularly interesting because RF and the mutant FP are, in a sense, very different definitions of fitness. Whereas the former considers only 'short-term' or immediate reproductive gains, the latter adopts a 'long-term' perspective by considering the eventual contribution to the population.

Recent work on two-person games in a finite population has combined the RF and FP interpretations into a single definition of fitness (Nowak *et al.* 2004). We present the so-called 'mixed-strategies' case, in which individuals are allowed to play alternative 'pure' strategies according to some probability rule. In this example, we have found a general equivalence, not only among the different algebraic stability conditions for a given interpretation of fitness but also between the algebraic conditions for the same stability concept under these two different interpretations of fitness.

This work can be extended in several ways. We have assumed that the population is both well mixed and of constant size, but rarely do these assumptions hold in nature. Interesting modifications of our model, then, would consider either a finite population arranged into local social groups (Rousset 2003), or a finite population whose size changes with time.

In addition, our FP model assumes an asymmetry between adults and offspring. Specifically, a newborn offspring will replace an established adult with probability one. The consequences of relaxing this assumption deserve to be explored. To this end, a relevant modification of the current model considers the population to consist of a finite number of territories, each one supporting a

breeding adult. Conflict would then occur between adults (i.e. 'owners') and offspring (i.e. 'intruders') for ownership of these territories. In this case we might also be interested in strategies played conditional on whether one is an owner, or an intruder. Such a situation is reminiscent of the familiar 'Hawk–Dove–Bourgeois' game (Maynard Smith 1982).

APPENDIX A. DERIVATION OF FP FITNESS FUNCTION

Although the Moran model is a continuous-time Markov chain, we are interested in the embedded discrete-time process. This discrete-time process is sometimes called the 'jump chain', because time steps are separated by the 'jumps' made by the continuous-time process between states.

Let $P_{i,j}$ denote the probability that the process jumps from state i to state j. The theory of continuous-time Markov chains tells us that

$$\left.\begin{array}{l} P_{i,i+1} = \dfrac{\lambda_i}{\lambda_i + \mu_i} = \dfrac{f_i}{f_i + g_i}, \\[2mm] P_{i,i-1} = \dfrac{\mu_i}{\lambda_i + \mu_i} = \dfrac{g_i}{f_i + g_i}, \\[2mm] P_{i,i} = 0. \end{array}\right\} \tag{A 1}$$

By conditioning on the outcome of the first jump we get

$$W_i^{\mathrm{FP}} = P_{i,i+1} W_{i+1}^{\mathrm{FP}} + P_{i,i-1} W_{i-1}^{\mathrm{FP}}, \tag{A 2}$$

for $i = 1, \ldots, N-1$, with boundary conditions $W_0^{\mathrm{FP}} = 0$ and $W_N^{\mathrm{FP}} = 1$. We now use a recursive form of equation (A 2), namely,

$$W_{i+1}^{\mathrm{FP}} - W_i^{\mathrm{FP}} = \frac{P_{i,i-1}}{P_{i,i+1}} \left(W_i^{\mathrm{FP}} - W_{i-1}^{\mathrm{FP}}\right), \tag{A 3}$$

to show

$$W_i^{\mathrm{FP}} - W_{i-1}^{\mathrm{FP}} = \frac{P_{i-1,i-2}}{P_{i-1,i}} \times \cdots \times \frac{P_{1,0}}{P_{12}} W_1^{\mathrm{FP}}$$
$$= W_1^{\mathrm{FP}} \prod_{j=1}^{i-1} \frac{g_j}{f_j}. \tag{A 4}$$

It follows that

$$W_i^{\mathrm{FP}} - W_1^{\mathrm{FP}} = W_1^{\mathrm{FP}} \sum_{k=1}^{i-1} \prod_{j=1}^{k} \frac{g_j}{f_j}$$
$$\iff W_i^{\mathrm{FP}} = W_1^{\mathrm{FP}} \left(1 + \sum_{k=1}^{i-1} \prod_{j=1}^{k} \frac{g_j}{f_j}\right). \tag{A 5}$$

Using $W_N^{\mathrm{FP}} = 1$, we see that

$$W_1^{\mathrm{FP}} = \left(1 + \sum_{k=1}^{N-1} \prod_{j=1}^{k} \frac{g_j}{f_j}\right)^{-1}. \tag{A 6}$$

APPENDIX B. PROOF OF THEOREMS
(a) *Proof of Theorem 3.1*
The mixed strategy p^* satisfies equation (3.2) under RF if and only if

$$\frac{\partial f_i / \partial q - \partial g_i / \partial q|_{q=p=p^*}}{g_i(p^*, p^*)} = 0 \tag{B 1}$$

for every $i = 1, \ldots, N-1$. Differentiating W_i^{FP} in equation (2.5) with respect to q and evaluating at $q = p$ yields

$$-\frac{1}{N} \left(\sum_{k=1}^{i-1} \sum_{j=1}^{k} \frac{\partial f_j/\partial q - \partial g_j/\partial q|_{q=p}}{f_j(p,p)}\right)$$
$$+ \frac{i}{N^2} \left(\sum_{k=1}^{N-1} \sum_{j=1}^{k} \frac{\partial f_j/\partial q - \partial g_j/\partial q|_{q=p}}{f_j(p,p)}\right) \tag{B 2}$$

which, by equation (B 1), is zero for any i when $p = p^*$. We conclude that p^* satisfies equation (3.2) under FP.

Conversely, suppose the mixed strategy p^* satisfies equation (3.2) under FP. It follows that equation (B 2) vanishes for $i = 1, \ldots, N-1$ when $p = p^*$. Because the second term in equation (B 2) has the same sign as $\partial W_1^{\mathrm{FP}}/\partial q|_{q=p}$, it vanishes when $p = p^*$. Consequently, the first term in equation (B 2) will also vanish for all $i = 2, \ldots, N-1$ when $p = p^*$. This implies that equation (B 1) holds for all $i = 1, \ldots, N-2$. Since $\partial W_1^{\mathrm{FP}}/\partial q|_{q=p=p^*} = 0$, and since equation (B 1) holds for $i = 1, \ldots, N-2$ we must also have that equation (B 1) holds for $i = N-1$. We conclude that p^* satisfies equation (3.2) under RF. This proves the theorem.

(b) *Proof of Theorem 4.1*
First check the condition (3.3) with W_i^{FP}:

$$\left.\frac{\partial^2 W_i^{\mathrm{FP}}}{\partial q^2}\right|_{q=p=p^*} = -\frac{i}{N^2} \sum_{k=1}^{N-1} \sum_{j=1}^{k} \frac{\partial^2 g_j/\partial q^2 - \partial^2 f_j/\partial q^2|_{q=p=p^*}}{R_0 + \boldsymbol{p}^* \boldsymbol{G} \boldsymbol{p}^{*\prime}}$$
$$+ \frac{N}{N^2} \sum_{k=1}^{i-1} \sum_{j=1}^{k} \frac{\partial^2 g_j/\partial q^2 - \partial^2 f_j/\partial q^2|_{q=p=p^*}}{R_0 + \boldsymbol{p}^* \boldsymbol{G} \boldsymbol{p}^{*\prime}}. \tag{B 3}$$

Substituting $\partial^2 g_j/\partial q^2 - \partial^2 f_j/\partial q^2 = 2(j-1)(b-d+c-a)/(N-1)$ into equation (B 3) yields

$$\left.\frac{\partial^2 W_i^{\mathrm{FP}}}{\partial q^2}\right|_{q=p=p^*} = \frac{b-d+c-a}{N^2(N-1)(R_0 + \boldsymbol{p}^* \boldsymbol{G} \boldsymbol{p}^{*\prime})}$$
$$\times \left(-i \sum_{k=1}^{N-1} k(k-1) + N \sum_{k=1}^{i-1} k(k-1)\right)$$
$$= -\frac{1}{3} \frac{b-d+c-a}{N^2(N-1)(R_0 + \boldsymbol{p}^* \boldsymbol{G} \boldsymbol{p}^{*\prime})} (iN(N+i-3)(N-i)). \tag{B 4}$$

Since $1 \leqslant i \leqslant N-1$ we have both $N-i > 0$ and $N+i-3 \geqslant N-2 > 0$. It follows from equation (B 4), then, that condition (3.3) is given by equation (4.5) under FP.

We can rewrite the CS condition (3.5) as

$$\frac{\mathrm{d}}{\mathrm{d}p} \left[\left.\frac{\partial W_i^{\mathrm{FP}}}{\partial q}\right|_{q=p}\right]_{p=p^*} < 0. \tag{B 5}$$

We now check CS using equation (B 5). From equation (B 2)

we get

$$\frac{d}{dp}\left[\frac{\partial W_i^{FP}}{\partial q}\Bigg|_{q=p}\right]_{p=p^*}$$

$$= -\frac{i}{N^2}\sum_{k=1}^{N-1}\sum_{j=1}^{k}\frac{d}{dp}\left[\frac{\partial g_j/\partial q - \partial f_j/\partial q|_{q=p}}{f_j(p,p)}\right]_{p=p^*}$$

$$+ \frac{N}{N^2}\sum_{k=1}^{i-1}\sum_{j=1}^{k}\frac{d}{dp}\left[\frac{\partial g_j/\partial q - \partial f_j/\partial q|_{q=p}}{f_j(p,p)}\right]_{p=p^*}. \quad (B\ 6)$$

Using Theorem 3.1 and $\frac{d}{dp}\left[\partial g_j/\partial q - \partial f_j/\partial q|_{q=p}\right]_{p=p^*} = (N-2)(b-d+c-a)/(N-1)$, equation (B 6) can be written as

$$\frac{d}{dp}\left[\frac{\partial W_i^{FP}}{\partial q}\Bigg|_{q=p}\right]_{p=p^*} = \frac{(N-2)(b-d+c-a)}{N^2(N-1)(R_0+p^*Gp^{*\prime})}$$

$$\times \left(N\sum_{k=1}^{i-1}k - i\sum_{k=1}^{N-1}k\right)$$

$$= -\frac{1}{2}\frac{(N-2)(b-d+c-a)}{N(N-1)(R_0+p^*Gp^{*\prime})}(i(N-i)). \quad (B\ 7)$$

It follows from equation (B 7) that inequality (4.5) guarantees that equation (B 5) is satisfied.

We now check the NIS condition (3.7).

$$\frac{\partial^2 W_i^{FP}}{\partial p^2}\Bigg|_{q=p=p^*}$$

$$= -\frac{i}{N^2}\sum_{k=1}^{N-1}\sum_{j=1}^{k}\frac{\partial^2 g_j/\partial p^2 - \partial^2 f_j/\partial p^2|_{q=p=p^*}}{R_0+p^*Gp^{*\prime}}$$

$$+ \frac{N}{N^2}\sum_{k=1}^{i-1}\sum_{j=1}^{k}\frac{\partial^2 g_j/\partial p^2 - \partial^2 f_j/\partial p^2|_{q=p=p^*}}{R_0+p^*Gp^{*\prime}}. \quad (B\ 8)$$

We use $\partial^2 g_j/\partial p^2 - \partial^2 f_j/\partial p^2 = -2(1-i/(N-1))(b-d+c-a)$ to show

$$\frac{\partial^2 W_i^{FP}}{\partial p^2}\Bigg|_{q=p=p^*} = -\frac{2(b-d+c-a)}{N^2(R_0+p^*Gp^{*\prime})}$$

$$\times \left[N\sum_{k=1}^{i-1}\left(k-\frac{k(k-1)}{2(N-1)}\right) - i\sum_{k=1}^{N-1}\left(k-\frac{k(k-1)}{2(N-1)}\right)\right]$$

$$= \frac{1}{3}\frac{(b-d+c-a)}{N(R_0+p^*Gp^{*\prime})}\left[\frac{i(N-i)(2N-i)}{N-1}\right]. \quad (B\ 9)$$

It follows from equation (B 9) that inequality (4.5) guarantees equation (3.7).

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