Fertility and Labour Supply in *Femina economica*

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This paper sets out a formal framework for the biological-evolutionary study of human economic behaviour. *Femina economica* is a hypothetical parthenogenetic species with a simple economy. Individuals make decisions about labour supply and fertility subject to time and resource constraints. Labour is of differing types and a parent determines the type of her offspring's labour. Wages are determined as marginal productivities from an economy-wide production function. Three propositions are proved, of which the first shows that under very general conditions there exists a population genetic equilibrium, in which individuals' decisions are assumed to be under genetic control. The second shows that at a population genetic equilibrium, individuals have the same behaviour as they would at an economic equilibrium, in which individuals are assumed to maximise a common utility function. The third proposition shows that if the common utility function fulfils certain conditions, the attainment of an economic equilibrium brings about the same behaviour as a population genetic equilibrium. This suggests a way in which evolutionarily stable behaviour can be brought about without the necessity for changes in gene frequencies. Demographic implications include the possibility of interpreting in Darwinian terms the reductions in offspring number that occur in fertility transitions, and the weak or even negative correlation in economically developed societies between control of resources and offspring number. There are implications for economics of deriving utility maximisation from population genetics.

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1. Introduction

On peut imaginer une société se reproduisant par parthénogenèse ou composée d'hermaphrodites. (de Beauvoir, 1949, p. 40)

This paper provides a formal framework for the biological-evolutionary study of human economic behaviour. The model to be presented holds for the first time several chief aspects in simultaneous formal focus. There is a generational structure in which individuals reproduce, genotypes that can control behaviour, and genes that can spread or not according to their effects on reproduction. The set of behaviours of possible mutants is rich enough to allow a strategic approach, and one equilibrium concept will be defined in terms of evolutionary game theory. People's choices involve not only reproduction, but also the explicitly economic decision about supply of labour, and they are subject to time and budget constraints. A second equilibrium concept will be based on Nash equilibrium, with individuals maximising a utility function. Finally, there is an outline "general equilibrium" in the sense that wages are determined by the aggregate supply of different types of labour, according to an economy-wide production function. The model is both fully biological and fully economic at the same time.

Only with such a wide-ranging model can we ensure a consistent biological-evolutionary approach to human economic behaviour. The hyphenated term "biological-evolutionary" is needed, because there already exist "evolutionary" approaches in economics that arise from analogy with biology (for general introductions, see Hodgson, 1993, 1995; Witt, 1993), but do not study humans as biologists study other animals. Extending the model across biology and economics also exposes to modellers in one discipline formal concerns from the other.

The name *Femina economica* for the hypothetical human-like species studied in the model is biologically justified because the species is assumed to be parthenogenetic for reasons of simplicity, and so all individuals are female. The model places fertility at the heart of economics, making economically appropriate the contrast with *Homo economicus*.

One set of concerns to which the model is relevant centres on two major puzzles, ably and systematically posed by Vining (1986). The first puzzle is the reproductive restraint shown in economically more developed countries, which can be seen both in the drastic reduction in fertility that occurs during so-called "demographic transitions", and by comparing present-day more with less economically developed countries. The second is the absence, in economically more developed countries at least, of the strong and positive relationship between fertility and control of resources that a Darwinian hypothesis would seem to predict. Rogers (1990, 1995) and Harpending & Rogers (1990) tackle these two puzzles with population genetic models. However, the economic side of those models, in terms of the choices of individuals and the economic world they are part of, is extremely primitive.

Questions that are better tackled with a unified model include those that necessarily involve both the biological and economic sides. How do individuals act when they maximise biological fitness in a model that incorporates economic features? How is reproductive value affected by economic considerations? What is the relationship between utility functions and biological fitness? What can the biological nature of humans suggest to us about the forms of utility functions?

The aim in constructing the model was to model humans as a biologist would model any other species in evolutionary terms. This straight away implies that behaviour is determined by genotype. A less obvious implication is that economic elements, such as budget constraints, types of labour, and the determination of wage levels, must be treated as external factors subject to their own laws. The advantage of linking evolutionary biology with economics rather than other aspects of human behaviour, is that it does possess a substantial body of mathematical theory capable of supplying the needed model components. Boyd & Richerson (1986) set themselves a more difficult task because they had to construct a theory of cultural inheritance to fill in the non-biological side of their "dual inheritance theory". The natural selection of genes makes no distinction between the consequences of physical and physiological laws on the one hand, and the consequences of economic laws on the other, and neither does the model to be presented here.

The model is of interest for any hints that might emerge about the relationship between evolutionary biology and human behaviour more widely. On that more general subject, early conceptual work of note includes Darwin (1971), Fisher (1930) and Hamilton (1975); for later empirically oriented work consult reviews by Low *et al.* (1992) for demography, Betzig *et al.* (1988) for behavioural ecology, Dunbar (1995) for anthropology, and Turke (1990) and Pérusse (1993) (each of which is followed by a series of relevant commentaries) for "sociobiology" and "human ethology" and "evolutionary psychology".

The model itself is developed formally in the mathematical appendix, following a biological rather than an economic tradition. A less formal introduction of the model is presented in Section 2, and informal versions of the results in Section 3, where comparisons are drawn with the models of Rogers (1990, 1995) and Harpending & Rogers (1990). The discussion in Section 4 is divided into subsections. It is the introduction of fertility into economic decisions that allows natural selection to act in the model, and Section

4.1 examines how biological ideas have been used in demographic discussions of fertility, and how the model's results may be relevant to demography. Section 4.2 looks at biological questions, such as the role of reproductive value, whether we should expect evolutionary equilibria to be attained in view of the rapidly changing human environment, and the possibility of relaxing assumptions of the model. Section 4.3 looks at implications for economics of the link made with biology in the model, chiefly to do with what properties utility functions might be expected to have when viewed as derived from maximisation of biological fitness. One branch of economics, "New Home Economics", is specifically concerned with decisions involving fertility, and deals with them in a traditionally economic way. The relationship to the biological approach to integration of fertility and economic decisions is discussed in Section 4.4. Finally, the general importance of a technical modelling issue is discussed in Section 4.5, namely whether observed variation in behaviour is interpreted as arising from identical individuals behaving differently, or as flexible responses to pre-existing differences. This brings out an important difference between economic and biological equilibrium concepts, as well as lessons for biologists' traditional expectations of game theory models. The paper ends with a Conclusion.

2. Description of the Model

2.1. THE INDIVIDUAL'S DECISION PROBLEM

Each individual lives as an adult for one generation (or period, for economists), in which she is endowed with one unit of time and one unit of labour, differentiated by type indexed by $j = 1, 2 \ldots n$. A matrix H represents how the adult would behave as each type. Offspring are also differentiated by type, and H_{ij} specifies how much time a type j adult spends in producing type i offspring. The wage per unit labour is w_j. A parent of type j who produces τ units of type i offspring spends τ units of time and τC_{ij} units of resource in doing so. It requires b_j units of resource to keep an adult alive. The b_j and C_{ij} are assumed to be positive. The constraints facing a

parent who has to choose a strategy for each type are therefore the time constraint:

$$\sum_i H_{ij} \leqslant 1 \qquad (1)$$

the resource constraint, subsuming time constraint:

$$b_j + \sum_i C_{ij} H_{ij} \leqslant \left(1 - \sum_i H_{ij} \right) w_j \qquad (2)$$

and non-negativity of offspring production:

$$H_{ij} \geqslant 0 \qquad (3)$$

The left hand side of the resource constraint is expenditure on keeping the adult alive plus the sum of the expenditure on all types of offspring. The right hand side is the earnings from paid employment. A purely economic model would have the individual choose the matrix H to maximise some utility function. In this model H will also sometimes be considered to evolve by natural selection.

Let x_j denote the density of adults that are of type j. Then the amount of labour supplied of type j, to be denoted y_j, in a homogeneous population each of whose members makes choices H is given by

$$y_j = x_j \left(1 - \sum_i H_{ij} \right) \qquad (4)$$

2.2. PRODUCTION AND THE DETERMINATION OF WAGES

The economy produces only one commodity, in amount $f(y)$ in one generation, where y denotes the vector of densities of labour employed of each type. We assume that f is non-negative, continuous, convex, has constant returns to scale and is not everywhere zero. We assume the workers are paid their marginal value in production. Let w denote the wage vector, and p the price of the commodity, normalised so $p + \Sigma_j w_j = 1$. We also assume that the economy is *feasible*. That is, there must exist a vector of labour supply, say $\bar{y}$, such that with some set of associated wages and price $(\bar{w}, \bar{p})$, each type j with $\bar{y}_j > 0$ can earn enough in wages to support itself and engage in at least some reproduction.

If and only if this feasibility condition is upheld can the technology support a population whose ratios of types remain constant over time without transferring resources between individuals.

2.3. GENOTYPES AND REPRODUCTION

There are discrete generations, and an individual lives for one generation as a child and one as an adult. Each individual has a genotype. It will suffice to assume there are at most two genotypes present at any one time, and let them be A and B. Genotype determines the choices of H, according to a schedule based on the wage vector w and price p. Formally, a genotype is a mapping from possible (w, p) to resulting H. Let the choices of H in generation t by genotype $g \in \{A, B\}$ be denoted $H^{g,t}$. Because reproduction is asexual, an offspring has the same genotype as her parent. The density of types with genotype g in generation t can therefore be obtained as

$$x^{g,t} = H^{g,t} x^{g,t-1} \tag{5}$$

A genotype with $H^{g,t}$ constant and equal to H will eventually grow exponentially at rate $\rho(H)$, where $\rho(H)$ denotes the spectral radius of H. The complexity of the model has been concentrated into the calculation of $H^{g,t}$. In particular the wage vector w depends on the frequencies of genotypes A and B, and so the feasible values of H depend on those frequencies. This links the equations for different genotypes, which as presented in eqn (5) seem to be separate. The definition of the model is now complete, and we turn shortly to introduce equilibrium concepts.

In principle, polymorphic equilibria are possible, in which two genotypes are present in stable proportions. Here attention is confined to monomorphic equilibria, in keeping with the evolutionarily stable strategy approach (Maynard Smith, 1982). This is probably reasonable, as the set of possible genotypes includes all possible mappings from (w, p) to H.

It is useful to review now the parameters of the model. b_j is the amount of resource required to support one adult of type j. C_{ij} is the amount of resource required for a type j adult to raise one unit of type i offspring. Finally, there is the production function f. The equilibria found will depend on these parameters.

2.4. EQUILIBRIUM CONCEPTS

A *state of the population* will be represented $((w, p), H, x, y)$. A state is *consistent* if the wages and price (w, p) represent marginal productivities given the labour supply vector y; the time allocation matrix H is non-negative and satisfies the constraints in terms of (w, p) on individual's choices; x is a non-negative right eigenvector of H; and y is the labour supply produced by a population in density x each of whose members is allocating their time according to H. Loosely, the persistence of a consistent state through time is possible, which is part of the requirements for the two equilibrium concepts.

Notice that a consistent population may be growing or shrinking at a constant rate, but that the ratios of types are required to remain fixed. The two equilibrium concepts to be defined below also permit constant growth or shrinkage. It is usual in biological models to assume that a "bland density dependence" maintains the population size (see for example Charlesworth, 1994), so that attention can be focused on the ratios of types. Economists may see the possibility of constructing a model developing that presented here in the same way that Golden Rule models develop the balanced growth model of Gale (1956). [Mitra (1992) gives a succinct technical description of Golden Rule models, and also looks at possibilities of relaxing the assumption of convexity of the production function.] Such a model in the present context could make explicit the population dynamics and the determination of population size.

The first equilibrium concept is *Evolutionarily Stable State*, which is based on the Evolutionarily Stable Strategy (Maynard Smith & Price, 1973; Maynard Smith, 1982). A consistent state of the population $((w, p) H, x, y)$ is an Evolutionarily Stable State if H has the highest spectral radius among time-allocation matrices satisfying the individual's constraints. It would be inaccurate to refer to the state as an "Evolutionarily Stable Strategy" because only H is a strategy, and the rest of the state records information that depends (but non-uniquely) on H and determines the value of playing different possible time-allocation matrices.

Informally, an Evolutionarily Stable State is a consistent state of the population in which there is no genotype that, if introduced as a very small proportion of each type into the population, would ultimately increase in relative proportion to the prevailing genotype.

The second equilibrium concept is the *Offspring-Linear Population Nash Equilibrium*. A consistent population state in combination with a non-negative weighting vector z is an Offspring-Linear Population Nash Equilibrium if, for each type j (including absent types for which $x_j = 0$), the j-th column of H achieves the maximum value of $\Sigma_i z_i h_i$ where h is constrained to satisfy the constraints for an individual of type j.

The central property of an Offspring-Linear Population Nash Equilibrium is that each individual acts as if maximising a weighted sum of the numbers of offspring produced, where the weights are given by z. This weighted sum can be thought of as a common utility function in an economic context. Biological interpretations will be discussed shortly.

3. Results of the Model

Informal versions of the propositions are given here. Formal versions and proofs are given in the Appendix, as are more technical results.

Informal version of Proposition 1: An Evolutionarily Stable State exists in the model of Section 2.

To express the next proposition more understandably in this informal version, we anticipate its content by revealing that the vector z represents the reproductive value of the types. Reproductive value is a biological term that, loosely speaking, measures the contribution of an individual or of a group of individuals to the gene pool of distant generations. The biological interpretation of Proposition 2 is that the quantity maximised is the individual's contribution to the gene pool of distant generations. Each type of offspring has a reproductive value, and the parent makes her choices to maximise the sum of the reproductive values of her offspring.

We further define "relative reproductive value", only for types with positive reproductive value, as the summed reproductive value of the offspring produced by that type, divided by that type's own reproductive value. An "extant" type is one that has a non-zero density in the equilibrium. We may now express the second proposition.

Informal version of Proposition 2: To each Evolutionarily Stable State in the model of Section 2, there exists a corresponding Offspring-Linear Population Nash Equilibrium with the following properties.

1. The reproductive value of each extant type is positive.
2. The relative reproductive values of extant types are all equal.
3. Each absent type with positive reproductive value has a relative reproductive value that is no greater than the relative reproductive value of the extant types.

These first two propositions contain, in principle, potential resolutions of the two puzzles of Vining (1986) discussed in Section 1. The second proposition shows that individuals maximise the sum of the reproductive values of their offspring. Given that offspring types differ in reproductive value, a completely Darwinian model therefore predicts reproductive restraint. At least, parents will not act to maximise their *unweighted* number of offspring. They may have fewer offspring in order to have better offspring. This compatibility between Darwinism and reproductive restraint is at first sight somewhat surprising. The model shows how the kind of quality–quantity trade-off postulated by demographers to explain demographic transitions can be given a Darwinian representation. The Darwinian version does have the methodological virtue that it can, at least in principle, be quantified.

Vining's second puzzle is the correlation or lack of it between wealth and reproductive success within developed societies. Proposition 2 asserts that the relative reproductive values of all the types are equal, even though their absolute reproductive values may be very different. In a simple case in which each type makes only its

own type of offspring, this corresponds to the simple consequence of demographic equilibrium that every type has the same number of offspring. So a very low correlation between wealth and offspring number does not necessarily imply a very low correlation between wealth and reproductive value.

The model's results therefore suggest the *possibility* of resolving Vining's two puzzles. It is at present quite unclear whether reproductive values do differ so greatly between types of offspring that the results do answer Vining. That would require empirical work, as well as more detailed modelling.

The results so far can be compared with those of previous models in this branch of theory. A major aim of the models of Rogers (1990, 1995) and Harpending & Rogers (1990) was to resolve Vining's two puzzles in this way. The present model is a more general resolution for a number of reasons. First, it contains an explicit if simple model of economic choices, as well as of reproductive choices. Second, it is explicit that the individual makes those choices in a way that maximises reproductive value. This point lies latent in the earlier works, though the concept of reproductive value as measuring an individual's contribution to the gene pool of distant generations is fully explored. The maximisation of reproductive value allows links to be made with demography, and with biologists' use of the concept of fitness. It also produces natural expectations that in models with more complex choices there will be again a quantity that individuals act as if maximising at equilibrium, and this is an important general conclusion about the nature of economic and reproductive behaviour.

A formal extension of the scope of the theory that arises from the maximisation of reproductive value is given in the third proposition. To express the proposition informally, it is convenient to retreat from giving z the label "reproductive values", and instead to refer to it more neutrally as the weights in the weighted sum which individuals act as if maximising. Parallel to the usages above, let the "relative weight" of a type with positive weight be the weighted sum of its numbers of offspring divided by the weight of its own type.

Informal version of Proposition 3: Suppose a population is at an Offspring-Linear Population Nash Equilibrium, so that individuals of extant types do act as if maximising a weighted sum of the numbers of offspring types, and individuals of absent types would do so. Further suppose that the following properties hold.

1. The relative weights of extant types are all equal.
2. Each absent type with positive weight has a relative weight that is no greater than the relative weight of the extant types.
3. Each type with zero weight cannot earn enough to reproduce.

Then the population is also in an Evolutionarily Stable State.

This third proposition shows how a certain pattern of flexible responses on the part of utility-maximisers can bring about the same effect as natural selection, without the necessity for changes in gene frequencies. The significance of this result is discussed in Sections 4.2 and 4.3.

4. Discussion

4.1. DEMOGRAPHY

The explanation of human fertility is part of the subject of demography. Biological and economic ideas have been emphasised in the construction of the model, and it is important to understand how these ideas fit in to demographers' views. This section looks at biological ideas about human fertility in two works of mainstream demography, points to work that aims to link biology and demography, and discusses Darwinian perspectives on human fertility suggested by the model of Section 2.

The main business of Wrigley & Schofield (1981) in their magisterial "Population History of England 1541–1871" is to reconstruct measures of fertility and mortality, and they employ sophisticated historical and statistical techniques to this end. Their comments on explanations for fertility, at the level of the individuals involved, are more tentative. They are open-minded about the types of causes at work, discussing on pp. 306–307 the "biological, social, or economic mechanisms" that might link

fertility, mortality and nuptiality. On p. 422 they argue that "mediated by conventions about the timing and incidence of marriage, the impact of changing real wages on marriage patterns over a period of time may be similar to that which would be produced by conscious calculation", despite the fact that "a knowledge of trends in real wages and a conscious attempt to adjust behaviour accordingly" were lacking. This "unconscious strategising" (see also Wrigley, 1978) is strongly redolent of Darwinism, which supposes that our eyes are fashioned to see irrespective of our understanding of optics, and that our behaviour conduces to the propagation of our genes irrespective of how we experience it. In their concluding chapter, they discuss a "niche model" of human reproduction, and refer on p. 462 to "the situation found among some species of birds which breed only after gaining control of an individual territory", citing Wynne-Edwards (1962). Although the biological citation is now somewhat out of date [demographers wishing to learn about current biological theory would do better to start with the discussion specifically for them by Low *et al*. (1992), or enter directly into the evolution literature with the textbook of Ridley (1996)], Wrigley & Schofield certainly seem comfortable with the possibility of admitting biological factors at various levels into the explanation of patterns in human fertility.

A later work by Levine (1987) focusses on explaining people's reproductive decisions, and his account has striking resonances with an active neo-Darwinian approach, resonances to which the author himself makes no reference. He argues for the centrality of "the family" in understanding population history, and defines the family as "the product of strategies of production and reproduction" (p. 4). He insists on the "*interconnectedness* of production and reproduction" (p. 4). The main theme is to explain the patterns of English family life that can be documented from feudal times to the early 20th century, as the product of "an underlying rationality in family formation strategies" that he assumes "to have been responsive to *contemporaneous* changes in the material world" (p. 8). Levine corrects the non-specialist's belief that there was no repro-

ductive restraint before the industrial revolution (p. 69ff). He refers to the tendency to marry someone in a similar social station with the approval of one's parents as operating "through an unconscious rationality" (p. 74). On p. 130, Levine writes "In such a world of pullulating forces, individuals are assumed to make strategic decisions for their own reasons, in order to optimise their perceived circumstances". His "fundamental" belief is that "fertility behaviour is economically rational within the context of socially determined economic goals and within bounds largely set by biological and psychological factors" (p. 161). His peasant demography model and proletarian demography model are stylised representations of the operations of the family as they vary in space and time and between social groups. He explains the models as rational responses to the contingent circumstances of their respective eras. Levine emphasises throughout that principles can be used to explain the response to contingent circumstances, while those contingent circumstances themselves need fit no neat pattern.

Darwinism too supplies an optimising principle, that can be viewed as acting through unconscious rationality, and reacting to historical contingencies. Intriguingly, it seems likely that an active neo-Darwinian account would not contradict Levine's own. The Darwinian account would in theory supply an explicit optimising principle, and so have the advantage of a capacity for quantitative explanation. The model of Section 2 and its results in Section 3 show in outline how such an optimising principle could be derived.

Here is a sketch of a provisional and tentative example in which a Darwinian account could supplement Levine's. In England, the birthrate started to fall dramatically from about 1870. Levine links this fall to the spread of the notion of "respectability" through the working classes. He also points out that around this time the demand for completely unskilled labour was falling fast enough to create an excess of unskilled labourers. Marriage depended on financial independence, and reproduction depended almost exclusively on marriage. Fertility fell fastest among those groups who could educate their children (pp. 191–192). It remained

considerably above average among miners, in whose towns there was an increase rather than a decrease in the demand for unskilled and child labour (p. 207). The tentative Darwinian account is that parents saw the poor economic, and so marital, and so reproductive, prospects of the completely unskilled. Those parents who were in a position to invest effectively in their offspring's health, education and training responded by producing fewer offspring and concentrating their investment, to improve (consciously or unconsciously) their reproductive prospects. This account depends on many assumptions, which could be investigated by historians and demographers. For example, on the Darwinian view we would expect the excess of supply over demand for unskilled labour to have occurred before the reduction in fertility, and to have been observable by, and in fact observed by, those who altered their fertility pattern. We would expect the time of appearance of the reduction in fertility to be geographically and socially linked to the change in the conditions of the labour market. Contemporary accounts of "respectability" might be expected to point to the importance of the low reproductive expectations of unskilled labour. It would be worth investigating whether reduction in offspring number was in fact compensated by an improvement in the reproductive prospects of the offspring. This skeleton Darwinian account may well prove to be untenable. It is proposed here merely to illustrate the kind of historical evidence that could be relevant, and to stress that a Darwinian account can be viewed and judged in historical terms.

The idea of applying Darwinian ideas to demographic phenomena is not new. For example, Low (1991), Low & Clarke (1991) and Clarke & Low (1992) have conducted Darwinian-inspired investigations of demographic phenomena in 19th century Sweden. My aim with this example was to illustrate how well the Darwinian ideas discussed in the present paper resonate with the well-known, canonical work of Levine (1987).

Levine (1987) deliberately adds a humanistic element to the dry accounting air of Wrigley & Schofield (1981), who stress quantitative description and aim at explanation mainly by inter-relating demographic measures. Levine aims to explain by setting out the situation in which people found themselves and appealing to the reader's sense of what she would have done in their place. The Darwinian account does not detract from this humanistic endeavour. It seeks to cast light simultaneously on the actions of the historical subjects and the intuitive understanding appealed to in the reader.

A review of specifically Darwinian explanations in demography is provided by Low et al. (1992), who also expound for non-biologists the relevant areas of modern evolutionary theory. They discuss in depth the approach from "behavioural ecology" to natural fertility, population regulation and reproductive production vs. investment, in each of which there is relevant Darwinian literature. Low et al. portray a convincing case that behavioural ecology has a useful contribution to make in their proposed journey "Toward an Ecological Demography".

For reasons to be discussed in Section 4.2, it is likely that human behaviour does not accord with Darwinian predictions. It is therefore of interest that Proposition 2 from Section 3 does suggest ways of representing non-Darwinian behaviour. For example, people may maximise a function with the wrong weights. Perhaps the weights are out-of-date, or are wrong because of misinformation, or have been psychologically manipulated. One possibility is that the value of social status is over-valued, so that people prefer quality over quantity to too great an extent. It may also be that people's categories are wrong. They may not make fine enough distinctions between different types of offspring. The Darwinian model would still be useful in these circumstances, for suggesting a general framework of maximising weighted sums of offspring number, and for providing within it a standard for comparison.

At a more general level, the model suggests three ways of measuring the quantity of offspring produced by a parent: by number, by reproductive value, and by the resources invested in them. The easiest way is to count offspring, and it is by this measure that fertility transitions are defined. However, was the reduction in offspring number accompanied by a reduction in reproductive value? In other words, did individuals really

change their behaviour in a way that made them biologically worse off? In view of the importance of reproductive values in evaluating Darwinian fitness, this remains an open question, and a vital one for an evolutionary understanding of fertility transitions. It may also be of interest to evaluate strategies for population control by their congruence or conflict with a proper understanding of the Darwinian interests of those affected.

It is also of interest to ask whether the reduction in offspring number in a fertility transition is accompanied by a reduction or an increase in the total amount of resources an adult invests in her lifetime production of offspring. It is in principle possible that the decrease in offspring number was accompanied by an increase in both the Darwinian fitness and reproductive resource use of members of the population. It may be that what saves developed societies from the gloomy prediction of Malthus (1798) is not liberation of individuals from their slavery to reproduction, but rather, that biologically effective reproduction requires economically effective offspring, which in turn requires less vicious and more civilised habits of life for parents.

In conclusion, the model provides a formal structure in a simple model, carrying the implication of an analogous formal structure in more complex models, that supports and extends the application of Darwinian principles to demography.

4.2. BIOLOGY

Various biological issues arise from the model. This section begins with a discussion of reproductive value, considers the question of whether we should expect an evolutionary equilibrium to be approximately attained in a changing environment, and ends by looking at the possibility of relaxing assumptions of the model.

Many of the present model's conclusions are phrased in terms of reproductive value. Introduced by Fisher (1930) in the context of age-structured models, and explored further by Hamilton (1966), it is still a key concept in that area (see Charlesworth, 1994). It is increasingly being employed in other kinds of model (a few

examples are Taylor, 1990; Boomsma & Grafen, 1991; McNamara, 1993; Leimar, 1996). Why is reproductive value such an important concept? The idea that all offspring are not equal was explicit in the work of Lack (1968). He showed that natural selection would lead birds to lay fewer eggs than they could. The reasons included the waste in producing eggs that, once hatched into nestlings, could not be sufficiently fed to survive to fledging; and that expending more time and resources on producing eggs and feeding nestlings prejudiced the survival chances of the parents. Lack's founding work forms part of the framework of modern evolutionary biology.

In simple cases, where all offspring that survive to breed are equal, using reproductive value amounts only to choosing a late enough moment in the life-cycle at which to count offspring. Lack's work falls into this category. However, in more complex cases in which all offspring that survive to breed are not equal, it is necessary to distinguish the types of offspring, and to attach (at least in principle) a numerical reproductive value to each type. The sex ratio argument of Fisher (1930) is a simple example, as it distinguishes female and male offspring.

Two important points can be made about the reproductive values of the types. First, in general they depend on the frequencies of those types in the population. So when strategic behaviour interacts with those frequencies, it is not possible to calculate the reproductive values in advance of knowing the state of the population, and hence the strategies being played. The reproductive values are *endogenous to the equilibrium*. Second, once they are known, the reproductive values provide a quantity that individuals act as if they are maximising at equilibrium. This useful quantity corresponds to what many biologists refer to loosely as ''fitness'' (see Dawkins, 1982, for a review of uses of this concept). Drawing these two points together, fitness *can* be formally constructed to correspond to informal usage. It is then useful for interpreting behaviour at equilibrium, but it does not suffice to find that equilibrium in the first place. Reproductive value thus provides a crucial link between population genetic and game theoretic approaches to the study of behaviour.

In applications, it is likely biologists will need to decide which distinctions it is necessary to make between individuals. If offspring vary in a way that is influenced by the parent on the one hand, and affects the offspring's reproductive success on the other, it is important to recognise those differences when evaluating reproductive success, or fitness. Sex, size, possession of a territory or breeding slot, and inherited social status are obvious possible candidates. Evaluating the reproductive values of types could be done directly, if enough were known about the population, as the left eigenvector of the transition matrix that indicates how many offspring of each type are produced by parents of each type. Another possible approach is to infer reproductive values from the choices made by parents.

Now I turn briefly to a large and controversial topic, the relevance of natural selection models to current human behaviour, as it specially applies here. See Alexander (1990) and Turke (1990) with their following commentaries for an introduction to the general debate. Types of labour and production functions are very new evolutionarily, and are subject to frequent change. It is unreasonable to expect genes with highly specific effects to be selected through the population every time a relevant factor changes, rapidly enough to ensure that human behaviour is usually approximately Darwinian. Change will usually be too rapid in comparison with the speed of selection. On the other hand, we do not require genes with highly specific effects in order to use can openers, operate video machines, devise strategies for chess and bridge, or to read. Yet we do all these things fairly efficiently.

The relevance to current human behaviour of models such as the one presented in this paper stems from an assumption that humans have general purpose cognitive abilities that allow them to react to perceived circumstances. Proposition 3 suggests what kind of general purpose program might evolve that would maintain an Evolutionarily Stable State in the face of changed circumstances, without the need for changes in gene frequencies. Suppose first that humans are constructed to maximise a weighted sum of offspring numbers, with the weights to be evaluated during an individual's lifetime. Further suppose that they gain infor-

mation that allows them to determine the transition matrix H between types, and have evolved to calculate the weights as the left eigenvector of H. Then Proposition 3 states that a population following this rule, if in a consistent state, would also be in an Evolutionarily Stable State. Changes in the production function and resource costs could be responded to, and a new Evolutionarily Stable State attained, with no changes in gene frequencies.

Of course such a rule is unlikely to work perfectly. Knowledge of H will be imperfect, and indeed even the appropriate set of types to distinguish will in reality be unclear. But a strategy broadly of the kind just outlined is likely to be evolutionarily successful because of the generality of its approach, and because it will rapidly bring about evolutionarily appropriate responses to changed conditions. Both these reasons also encourage observers to expect to see evolutionarily appropriate behaviour in a wide range of circumstances, even those of recent origin.

Perhaps other species too have general purpose programs, rather than highly detailed sets of behavioural rules? Certainly, a general purpose program is likely to be more successful within a species in the face of environmental change, and species with more general purpose programs are likely to endure longer than those with highly detailed rules. To give just one suggestive example, Davies (1992) shows that dunnocks (*Prunella modularis*, a European bird also known as the hedge sparrow) exhibit a wide variety of types of breeding group within a small area. There are monogamous pairs, trios with two males, trios with two females, and larger breeding groups. He shows convincingly that the type of group reflects underlying strategic variables such as resource availability, and that the behaviour of an individual is adapted to the type of breeding group to which he or she belongs. It is unlikely that dunnocks have hard-wired rules about each separate type of breeding arrangement. Instead they probably have flexible rules that may include learning.

The final issue for biological discussion is the implications of relaxing some restrictive assumptions of the model of Section 2. The model has asexual individuals. Incorporation of two sexes

would introduce a number of new elements. Let us discuss first for simplicity a case in which a sexual model leads to the formation of permanent monogamous "households" by "marriage". Questions arise of division of productive and reproductive labour between the sexes. Now suppose "households" are not permanent, and "divorce" is possible. A conflict of interest arises between the partners in a household, and here lies the germ of another kind of explanation of reproductive restraint—that the game played between partners in a household results in a solution that is less than fully cooperative, to an extent that will depend on institutional arrangements in respect of divorce, remarriage, and rules of inheritance and child maintenance.

Another unrealistic aspect is the purely economic nature of the types. Instead types could be defined in non-economic ways. The type distinctions will be biologically important if they have any influence over reproduction, for example if an individual's type affects what type of offspring they produce or what type of individual they marry. This applies whether these effects arise in a strong way by explicit social rules, for example type 1 is not permitted to marry type 2; or instead more weakly as correlations, for example type 1 is less likely to marry type 2 because social conventions mean these types rarely meet. Relaxation of assumptions would allow a wide spectrum of social behaviour to be considered within the same basic framework.

4.3. ECONOMICS

The main lesson to be drawn, therefore, is not that preferences are biologically determined in any complete way—but rather, that they are scientifically analysable and even in principle predictable in terms of the inheritance of past genetic and cultural adaptations together with the new adjustments called for by current environmental circumstances. (Hirshleifer, 1977, p. 26)

This section aims to pursue Hirshleifer's proposed program by discussing two kinds of link between utility maximisation studied by economists, represented in the formal development here by the Offspring-Linear Population Nash Equilibrium, and the evolutionary stability

studied by biologists, represented by the Evolutionarily Stable State.

One relationship suggested by the current model is that natural selection has brought about human behaviour which can be viewed as utility-maximising. Proposition 2 shows that at a population genetic equilibrium, there exists a function which each individual acts as if to maximise. It is a weighted sum of offspring produced, the weights being the reproductive values of types. Generalising, it can be suggested that fitness maximisation creates utility maximisation.

Let us see how this works in the model. The set of reproductive values, and so the utility function, is the same for everyone, but is not expressed in terms natural to an economist. This single "underlying utility function" can be unpacked into a set of "imputed utility functions", one for each of the types, that ignore reproduction and are functions of consumption and leisure. For example, we could postulate a utility function for each type k,

$$u_k(c, l) = \alpha_k c^{\beta_k} l^{1 - \beta_k}$$

where c is household consumption and l is the amount of leisure. α_k and β_k are positive constants. The choice of α_k is irrelevant here, and could even vary on an individual basis, but serves to remind us of the incomparability of utilities. If we have an ESS of the model of Section 2, then we can choose $\beta_k = \Sigma_i H_{ik}$, and the reader will readily confirm that each type maximises its $u_k(c, l)$, subject to time and resource constraints, at that equilibrium.

The simplicity of the model makes this example trivial in some ways, but it illustrates the following conclusions. First, the use made of time out of paid employment is likely to depend strongly on child-rearing commitments, and a formulation that classes nappy-changing with water-skiing into a single homogeneous "leisure" constitutes a heroic simplification. From the point of view of the present model, reproduction is central and the first aspects of decision-making that should be articulated are therefore those relating to the rearing of offspring.

Second, the usual economic formulation presupposes that a clear conceptual separation

can be made between people's preferences and properties of the available technology. The biological underpinning suggests on the contrary that the quantity that people will act as if they are maximising, at equilibrium, will depend on all the parameters of the model. Specifically, z is expected to depend on f, as well as on the C_{ij} and b_j.

Third, the maximand provided by the Population Nash Equilibrium is not available as a utility function in a formulation that ignores reproduction. We have however constructed "imputed utility functions", in terms of more usual economic variables. The imputed utility functions are type-dependent, because the types vary in number of children and investment per child. Looking at economics in this light suggests that people's different preferences may result from an underlying common utility function, and from differences between people in variables that are omitted from study in any particular case.

Various conclusions follow from viewing reproductive value as utility. For example, reproductive values are comparable between individuals. Comparability has been of interest to economists because it allows the construction of a social utility function to measure social welfare and so provides a method of choosing between different options in a way that is not interpersonally arbitrary. Ironically, while biological reproductive values are comparable, they are inherently competitive, so that it is impossible to raise everyone's reproductive value. It follows that one natural attempt at a social welfare function, the sum of individuals' reproductive values, is constant (or, more accurately, arbitrary) and independent of social or individual actions (with the arguable exception of those causing the death of all humankind). On the other hand, one can compare the reproductive values of individuals.

Reproductive value is also cardinal, that is, it makes sense to say "X is twice as fit as Y". The reproductive value of groups of individuals can therefore be compared. Selection would also act on average reproductive value when decisions must be taken under uncertainty. One assumption sometimes made about utility is that it tends to negative infinity as consumption tends to

some minimal value. It corresponds to the assumption that an individual will take every possible action to avoid the slightest chance of death. The absolute minimising of the risk of dying is not a property of human behaviour expected on biological grounds. A person should be evolutionarily indifferent to playing double-or-quits with her reproductive value.

A second link between the models of human choice is suggested by Proposition 3. The general purpose rules that are likely to be evolutionarily successful, as discussed in Section 4.2, will incorporate the acquisition of information that helps to determine the individual's utility function, and a behavioral rule that involves choosing actions to maximise that utility function. Maximisation of a function to be determined can be expected to be built in as part of the mechanism that gives rise to an individual's behaviour. Maximisation should then be part of the psychology of human behaviour, consistent with the maximisation of functions that are "best guesses" at, or evolutionarily out-of-date versions of, reproductive value; or even of quite novel functions that, from a biological point of view, would be regarded as "mistakes".

The major implications sketched here of the biological approach for economics are therefore (i) the possibility of constraints on the plausible forms of utility functions, along with their comparability, cardinality and risk-neutrality when measured appropriately, (ii) the centrality of reproduction in the determination of people's preferences and behaviour, (iii) preferences may not, even conceptually, be independent of the available technology, and (iv) biology provides a reason to expect humans to be designed to maximise some quantity that becomes fully determined only during the individual's lifetime.

4.4. NEW HOME ECONOMICS

The New Home Economics of Becker (1991), Becker & Barro (1988), Barro & Becker (1989), and related work (e.g. Cigno, 1991) is the main economic treatment of the subjects, for example marriage, divorce, fertility and legacies, that can most readily be tackled by Darwinian methods. Here the formal bases of the present model and the New Home Economics are compared. Becker

& Barrow (1988) begin with the assumption that a parent's utility depends on her own consumption, on the number of her children, and on the utilities of her children. Their utilities therefore depend in turn on the utilities of their own children. Making some technical assumptions Becker & Barro arrive in their eqn (5) at a *dynastic utility function* "that depends on the consumption and number of children of all descendants of the same family line", thus:

$$U_0 = \sum_{i=0}^{\infty} A_i N_i u(c_i n_i)$$

where i indexes generations forward in time from now, n_i is the number of children and c_i is the consumption per adult in generation i. A_i is the implied degree of altruism of the dynastic head (the decision-maker) towards each descendant in the i-th generation, which approaches zero rapidly enough to guarantee that the sum converges. N_i is the number of descendants in generation i, and u is a standard one-period utility function.

A first attempt at a biological version of what should be maximised in this notation is the long-run rate of increase in number of descendants, as follows

$$\lim_{i \to \infty} N_i^{1/i}$$

A refined version might allow for the ultimate (asymptotic) distribution of capital, and questions arise of whether N_i or $N_i^{1/i}$ will converge more usefully, but these sophistications do not affect the points to be made here.

The biological view is that consumption is irrelevant except insofar as it helps to determine the number and types of descendants. Some consumption is needed directly to acquire the energy to permit work to be done and children to be reared. Other consumption may be needed rather less directly, to acquire or retain a social standing necessary for the production of certain types of offspring. But the formulation of the dynastic utility function in terms of consumption purely for its own sake is inconsistent with the biological viewpoint. Further, it is only the eventual number of descendants that matter, and not the number in any particular intermediate generation.

Despite this formal dichotomy, New Home Economics is in more general terms extremely congenial to the Darwinian approach. It treats those aspects of human life closest to reproduction and assumes a maximisation principle. The conclusions may often not depend critically on what is being maximised, particularly as general forms of utility function are often assumed. The extent to which the conclusions of the New Home Economics, about choice of marriage partner, divorce, and fertility, also hold under an explicitly Darwinian model is worth further study. A technical advantage over the New Home Economics is that the form of the utility function is highly constrained, which may enable more definite predictions to be made.

4.5. EVOLUTIONARY MODELLING WITH TYPES

Some more general points about evolutionary models with different types are made here, which arise from the specific model constructed earlier. If we observe that a society contains two kinds of people, say labourers and lawyers, there are two simple modelling responses. The first is to take the behaviour of the two kinds as fixed, and to model how some individuals become labourers and others become lawyers. This corresponds to making strategies of the kinds, and is the traditional ESS approach to variation in behaviour. The second is to assume that an individual is allotted a kind, but then to study how labourers behave and how lawyers behave assuming they act to best evolutionary advantage. This makes types of the kinds. Reality is likely to be more complicated, with some individual influence over the kind she becomes, and over behaviour within each role, both affected by underlying pre-existing individual differences.

The traditional ESS approach makes the strong conclusion that each strategy should have equal fitness at equilibrium. The types approach by itself makes no such claim. When, as in the model of Section 2, an individual's type is chosen by her parents, we do have the conclusion that each type must have equal relative reproductive value.

The definition of ESS used in the present paper has been adjusted to the existence of a variety of types, so that it involves maximising an eigenvalue, instead of a simple payoff function. This is standard practice where types are involved (e.g. Taylor, 1990; McNamara, 1993; Leimar, 1996). It is necessary because the reproductive values of the different types are not known *a priori* and the eigenvalue calculation effectively works them out. This is quite different from incorporating the dynamics of gene frequencies into the ESS definition, though that would also lead to eigenvalue calculations. Their introduction here follows the ESS philosophy of keeping the gene dynamics as simple as possible—one putative stable allele vs. one candidate mutant—in order to allow the biology to be more sophisticated. This aspect of the definition of ESS represents a more substantial conceptual difference from other equilibrium concepts, such as Population Nash Equilibrium, than the "second condition" of the ESS definition.

Irreducibility of the transition matrix H is a major technical concern with a meaning. If H is irreducible, then all the types are linked by paths of descent. If H is reducible, then there exist subsets of types that do not connect with each other, but are connected within each subset. While it may be reasonable to solve this problem just by assuming that there is some chance of each type giving rise to any other, in simple models in which optimal choices are made, reducibility is a likely outcome. The issue of reducibility is connected with the role of inter-marriage in strife between sections of a community.

One aspect of reducibility is that reproductive values may not be uniquely defined at equilibrium. They are uniquely defined within each internally-connecting subset, up to multiplication by a positive constant. Between subsets, they need satisfy only inequalities which ensure that no type can gain by making types outside its own subset. Reducibility will be an important modelling concept whenever evolutionary models include types.

More realistic evolutionary models in many areas will need to incorporate a variety of types. The requirement that observed kinds should have equal fitness has been seen as a hallmark of the ESS approach. However, that is true only of simple models.

5. Conclusion

The model is an extremely simple representation of an economic society. It is possible to draw tentative conclusions about the outcome of more realistic models that follow the same approach in incorporating models of social institutions and neo-Darwinian assumptions about the evolution of individuals' decisions. The Darwinian part of the model produces behaviour on the part of an individual that maximises the individual's fitness given the choices of all other individuals. However, that fitness is not simply measured as number of offspring, but rather as a weighted sum of offspring produced. The formal impact of social institutions on the model can be seen in two ways. First, they determine which types of offspring it is necessary to distinguish. In this example they are defined by the types of labour. Second, social institutions play an essential rôle in determining the weights employed in calculating fitness. Here the method of wage determination is important. In more realistic models, other social constructs could be important, such as marriage customs, the taxation system, and laws about primogeniture, inheritance and child support. A likely outcome of such models is a categorisation of offspring into types, and a corresponding set of weights such that individuals act so as to maximise their weighted sum of offspring produced.

The sophisticated Darwinian approach to reproduction and economic behaviour taken here is essential for those who take seriously the Darwinian hypothesis about human behaviour. Simpler models that do not recognise types and their different reproductive values will not suffice. The approach may also appeal for methodological reasons to demographers studying fertility, as it suggests a formal framework with fairly restrictive conditions, and so is likely to make fairly sharp predictions. Economists may find food for thought about the currently peripheral place of reproduction in their

discipline, seen against the suggestion that people have a common underlying utility function that is linear in offspring numbers and is independent of consumption. Finally, those who wish to deny on empirical rather than ideological grounds that Darwinian ideas can help to explain human behaviour, will need to be aware of this kind of model. It displaces earlier simpler conceptions that did not distinguish between types, and it provides a theoretical framework for serious modern Darwinian approaches to the quantitative study of human behaviour.

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APPENDIX A

The first subsection of the Appendix proves three technical lemmas, then the second provides formal definitions of terms, and of optimisation programs, that are needed for the main argument. In the next subsection, three lemmas are proved. The three propositions are proved in the fourth and final subsection.

Non-standard notation will be used as follows. If x and A are an n-vector and $n \times n$ matrix, and $I \subset \{1, 2 \ldots n\}$, then $x[I]$ will refer to the vector with elements x_i where $i \in I$, and $A[I]$ will refer to the matrix of values A_{ij} where $i, j \in I$. Elementwise multiplication between conformal matrices will be denoted by $\times$, so $A \times B = C$ means $A_{ij}B_{ij} = C_{ij} \forall i,j$. A non-negative square matrix will be termed stochastic if each column sums to one. Vectors are not categorised as "row" or "column", and the inner product $\Sigma_i x_i z_i$ is written simply as xz. Similarly, $\Sigma_i z_i A_{ij}$ is written zA, $\Sigma_j A_{ij} x_j$ as Ax, and $\Sigma_{ij} z_i A_{ij} x_j$ as zAx. Lower-case Greek letters have been used for scalars, except that p has been used to denote price.

A.1. Technical Preliminaries

The first lemma obtains results about the wages that are consistent with determination as marginal productivities given the economy-wide production function f, and simply provides a convenient point of reference for results that have no claim to novelty. The second lemma is needed to prove the third. The third lemma is thought to be new, and it is hoped may be of value in future studies in which the elements of a non-negative matrix are chosen subject to column-wise linear constraints, with the aim of maximising the matrix's spectral radius.

Lemma 1

Suppose $f: \mathbb{R}_+^n \to \mathbb{R}_+$ is continuous, non-negative, convex and not everywhere zero, and that $f(\mu y) = \mu f(y)$ for $\mu \geqslant 0$. We now define $\mathbb{F}: \mathbb{R}_+^n \to 2^{\mathbb{R}_+^{n+1}} \setminus \{\emptyset\}$. For $y \neq 0$, let

$$\mathbb{F}(y) = \{(w, p): w \geqslant 0, p \geqslant 0, p + \sum_i w_i = 1,$$

$$w(y' - y) \geqslant p(f(y') - f(y)) \, \forall y'\}$$

and let $\mathbb{F}(0)$ equal $\cup_{\{y : y \neq 0\}} \mathbb{F}(y)$.

Then $\mathbb{F}$ is upper semicontinuous on $\{y: y \geqslant 0, \Sigma_j y_j = 1\}$, and $\mathbb{F}(y)$ is convex over the same set. Further, suppose $(w, p) \in \mathbb{F}(y)$ and $(w', p') \in \mathbb{F}(y')$. Then

1. $(w, p) \in \mathbb{F}(\mu y)$, for $\mu \geqslant 0$
2. $w \neq 0$
3. $w(y' - y) \geqslant p(f(y') - f(y))$
4. $wy = pf(y)$
5. $wy' \geqslant pf(y')$
6. $(p'w - pw')y \leqslant 0$
7. $(p'w - pw')(y - y') \leqslant 0$
8. $y \gg 0$ implies $(p > 0$ and $f(y) > 0)$.

Proof

Upper semicontinuity of $\mathbb{F}$ is immediate from the definition, as is convexity of $\mathbb{F}(y)$, for $\Sigma_j y_j = 1$, which excludes the case $y = 0$. Constant returns to scale for f, and the union definition of $\mathbb{F}(0)$ for the case $\mu = 0$, imply Part 1. Part 3 follows directly from the definition of $\mathbb{F}$ for $y \neq 0$. If we choose $y = \mu \bar{y}$, and let μ tend to zero, the preservation of the inequalities in the definition shows that Part 3 is also true for $y = 0$.

Part 4 follows by letting y' equal zero in Part 3, obtaining $wy \leqslant pf(y)$; then by letting $y' = 2y$, obtaining $wy \geqslant pf(y)$.

Suppose contrary to Part 2 that $w = 0$. Then by definition of $\mathbb{F}$, we also have $p = 1$. Part 3 then implies that $f(y') \leqslant f(y)$ for all y'. But by hypothesis there is some value of y, $\tilde{y}$ say, with $f(\tilde{y}) > 0$; and so we can increase $f(y')$ without bound by employing $f(y') = f(\mu\tilde{y}) = \mu f(\tilde{y})$ with large enough μ. Hence $w \neq 0$, proving Part 2. Part 5 follows from substituting Part 4 into Part 3. Multiplying Part 3 by p' yields, together with its symmetrical formula,

$$p'w(y' - y) \geqslant p'p(f(y') - f(y))$$

$$pw'(y - y') \geqslant pp'(f(y) - f(y'))$$

Adding the inequalities yields Part 7, and then letting y' tend to zero gives Part 6. Part 8 follows from Parts 2 and 4, as wy must then be positive, and equal $pf(y)$. □

We now establish notation and some results about the "rates of sequences of types". These are the growth rates of subpopulations that employ a sequence of types in succeeding generations, and choice of fastest growth rates will turn out to define an Evolutionarily Stable State. Complications arise because of non-uniqueness, and Lemma 3 supplies useful strong conditions for the optimality of mixed strategies of reproduction.

Let

$$_{ij}V_m = \{v : v_1 = i, v_{m+1} = j, v_k \in \{1, ,2 \ldots n\}$$

$$\text{for} \quad k \in \{2, 3 \ldots m\}\}$$

$$_iV_m = {}_{ii}V_m$$

$$_{ij}\tilde{V}_m = \{v \in {}_{ij}V_m : v_k = v_{k'} \Rightarrow (k = k', \text{ or } k = 1,$$

$$\text{or} \quad k = m + 1)\}$$

$$_i\tilde{V}_m = {}_{ii}\tilde{V}_m$$

and let the rate of a sequence $v \in {}_{ij}V_m$ in relation to a non-negative matrix Q be defined by

$$\phi_Q(v) = \left(\prod_{k=1}^{m} Q_{v_{k+1}v_k}\right)^{1/m}$$

Now we define sets of "optimal sequences" by letting

$$_i\phi_Q = \max\left\{\phi_Q(v) : v \in {}_i\tilde{V}_m\right\}$$

$$\phi_Q = \max\left\{{}_i\phi_Q : i \in \{1, 2 \ldots n\}\right\}$$

$$_iV_m^* = \{v \in {}_iV_m : \phi_Q(v) = \phi_Q\}$$

$$_{ij}V_m^* = \{v \in {}_{ij}V_m : v' \in {}_{i'}V_m^*, v_{k+k'} = v'_k$$

$$\text{for} \quad k \in \{1, 2 \ldots m + 1\}\}$$

$$_{ij}\tilde{V}_m^* = {}_{ij}V_m^* \cap {}_{ij}\tilde{V}_m$$

Now we define the set of types that can follow a given type j in non-repeating cycles that are optimal given they include j. Let

$$_jU_Q = \{i : v \in {}_j\tilde{V}_m, \phi_Q(v) = {}_j\phi_Q, v_2 = i\}$$

Note that $_jU_Q$ is non-empty by definition of $_j\phi_Q$.

We are now able to define properly placed. Given a square non-negative matrix Q, a conformal substochastic matrix S is said to be *properly placed* on Q if, for each i, j, either $S_{ij} = 0$ or $i \in {}_jU_Q$. This means, loosely, that S is positive only on elements that belong to fastest rate sequences over Q.

Lemma 2

Let Q be a non-negative square matrix of order n,

$$\phi_{\max}(Q) = \max\{Q_{ij}\}$$

and

$$\phi_{\min}(Q) = \min\{\phi_Q(v) : v \in {}_{ij}\tilde{V}_m^*\}$$

Suppose $\phi_Q > 0$. Then

1. For $v \in {}_{ij}V_m$,

$$\phi_Q(v)^m \leqslant \phi_Q^m \left(\frac{\phi_{\max}(Q)}{\phi_Q}\right)^n$$

2. For $v \in {}_{ij}V_m^*$,

$$\phi_Q(v)^m \geqslant \phi_Q^m \left(\frac{\phi_{\min}(Q)}{\phi_Q}\right)^n > 0$$

Proof

We begin by operating on a sequence $v \in {}_{ij}V_m$, and obtaining a formula for its rate in terms of the rates of elements of $_kV_m$. Then we turn to proving Parts 1 and 2. If $v \in {}_{ij}\tilde{V}_m$, then we let $l = 0$ and have finished. Otherwise there is at least one repeated element, and we can find

consecutive subsequence of v, say $c_1 \in {}_{j_1}\tilde{V}_{m_1}$. Replacing the subsequence c_1 with the single element j_1 forms a new sequence $v_2 \in {}_{ij}V_{m-m_1}$. We repeat this process until there are no repeated elements, and let l equal the number of replacements. This yields a series of extracted subsequences c_e, $e \in \{1, 2 \ldots l\}$, along with their lengths m_e. The final sequence v_{l+1} has no repeated elements, so $m - \Sigma m_e \leqslant n$. The definition of rate ensures that

$$\phi_Q(v)^m = \phi_Q(v_{l+1})^{m-\Sigma m_e} \prod_{e=1}^{l} \phi_Q(c_e)^{m_e}$$

Now we prove Part 1. The rate of each c_e is no more than ϕ_Q. The rate of v_{l+1} cannot be greater than $\phi_{\max}(Q)^{m-\Sigma m_e}$. Hence

$$\phi_Q(v)^m \leqslant (\phi_Q)^{\Sigma m_e}(\phi_{\max}(Q))^{m-\Sigma m_e}$$

As already noted, $m - \Sigma m_e \leqslant n$, and the definition of rate implies that $\phi_Q \leqslant \phi_{\max}(Q)$. This proves Part 1.

For Part 2, we are given that $v \in {}_{ij}V_m^*$, which implies there exists $v' \in {}_{i'}V_{m'}$ such that v is a consecutive subsequence of v' and $\phi_Q(v') = \phi_Q$. The process of extraction from v can be applied to the same locations in v', forming a parallel series of sequences v_e'. We then carry on with the process of extraction, continuing the series c_e and v_e' up to $e = l'$. We now show that $\phi_Q(c_e) = \phi_Q$ for $e \in \{1, 2 \ldots l\}$. If not, then either $\phi_Q(c_{\hat{e}}) > \phi_Q$ for some $\hat{e}$ or $\phi_Q(v'_{l'+1}) > \phi_Q$. But these are both impossible, as ϕ_Q is the maximum possible rate for a sequence in ${}_{i''}\tilde{V}_{m''}$ for all i'', m''. Hence $\phi_Q(c_e) = \phi_Q$ for $e \in \{1, 2 \ldots l\}$, as claimed, and we return to considering the original sequence v. The rate of the residual sequence v_{l+1} cannot be less than $\phi_{\min}(Q)$. Hence

$$\phi_Q(v)^m \geqslant (\phi_Q)^{\Sigma m_e}(\phi_{\min}(Q))^{m-\Sigma m_e}$$

As $m - \Sigma m_e \leqslant n$ and $\phi_Q \geqslant \phi_{\min}(Q)$, the weak inequality in Part 2 follows immediately. The strong inequality follows from $\phi_{\min}(Q) > 0$, which we now prove. Suppose to the contrary that $\phi_{\min}(Q) = 0$. Then there must exist $v_{\min} \in {}_{ij}V_m^*$ such that $\phi_Q(v_{\min}) = \phi_{\min}(Q)$. There must also exist $v'_{\min} \in {}_{i}V_{m'}^*$ such that $\phi_Q(v'_{\min}) = \phi_Q$ and $v_{\min}$ is

a consecutive subsequence of $v'_{\min}$. Then $\phi_{\min}(Q) = 0$ implies $\phi_Q(v_{\min}) = \phi_Q(v'_{\min}) = \phi_Q = 0$. But we are given as a hypothesis of the lemma that $\phi_Q > 0$. Hence $\phi_{\min}(Q) > 0$ as required. ☐

Lemma 3

Let Q be a non-negative square matrix of order n, and S a conformal substochastic matrix. Then

1. $$\rho(S \times Q) \leqslant \phi_Q$$

2. Consider the following conditions on Q and S:

$$\rho(S \times Q) = \phi_Q \qquad \text{(i)}$$

$$S \text{ is stochastic} \qquad \text{(ii)}$$

$$S \text{ is properly placed on } Q \qquad \text{(iii)}$$

$$S \times Q \text{ is irreducible} \qquad \text{(iv)}$$

Then

(a) *ii & iii ⇒ i*
(b) *i & iv ⇒ ii & iii*

3. Suppose $(S \times Q)x = \phi_Q x$, $x \geqslant 0$, $x \neq 0$ and let $I = \{i : x_i > 0\}$. Then

(a) $S[I]$ is stochastic and properly placed on $Q[I]$
(b) $S[I]$ has a block diagonal structure in which each block has a spectral radius of ϕ_Q, and is irreducible and stochastic
(c) $\phi_{Q[I]} = \phi_Q$
(d) Suppose $i \in J$ implies $\phi_{Q[J]} < \phi_Q$. Then $x_i = 0$.

Proof

Let $A = S \times Q$, and consider the formula for powers of A in terms of ${}_{ij}V_m$:

$$(A^m)_{ij} = \sum_{v \in {}_{ij}V_m} \phi_A(v)^m$$

$$= \sum_{v \in {}_{ij}V_m} \phi_Q(v)^m \phi_S(v)^m$$

Then employing Part 1 of Lemma 2,

$$(A^m)_{ij} \leqslant \left(\frac{\phi_{\max}(Q)}{\phi_Q}\right)^n \phi_Q^m \sum_{v \in {}_{ij}V_m} \phi_S(v)^m$$

$$= \left(\frac{\phi_{\max}(Q)}{\phi_Q}\right)^n \phi_Q^m (S^m)_{ij}$$

It follows that

$$\max\{(A^m)_{ij}\}^{1/m} \leqslant \left(\frac{\phi_{\max}(Q)}{\phi_Q}\right)^{n/m} \phi_Q \max\{(S^m)_{ij}\}^{1/m}$$

Employing Gelfand's formula for spectral radius (see e.g. Deimling, 1985, p. 79) we conclude that the limits as $m \to \infty$ exist, and

$$\rho(A) \leqslant \phi_Q \rho(S) \leqslant \phi_Q \qquad (A.1)$$

where the second inequality follows because the spectral radius of a substochastic matrix cannot exceed one. This proves Part 1 of the statement of the lemma.

We now turn to proving Part 2a. Let $K = \{i : {}_i\phi_Q = \phi_Q\}$, which is non-empty. It is given that S is stochastic and properly placed on Q, and it is now shown that $S[K]$ is stochastic and properly placed on $Q[K]$. For $j \in K$, it follows immediately from the definitions of ${}_i\phi_Q$ and ${}_jU_Q$ that ${}_jU_Q \subset K$. If S is properly placed on Q, then $S_{ij} = 0$ for $i \notin {}_jU_Q$. Hence $\Sigma_{i \in K} S_{ij} = \Sigma_i S_{ij} = 1$ for $j \in K$, showing $S[K]$ is stochastic. We also have ${}_jU_{Q[K]} = {}_jU_Q$ for $j \in K$. So, as claimed, $S[K]$ is stochastic and properly placed on $Q[K]$. Let $B = S[K] \times Q[K]$. We now study $\rho(B)$. Because $S_{kl} = 0$ for $k \notin K$, $l \in K$, we have the following for $i, j \in K$:

$$(B^m)_{ij} = \sum_{v \in {}_{ij}V_m} \phi_Q(v)^m \phi_S(v)^m$$

Only those terms are non-zero for which $v \in {}_{ij}V_m^*$, for otherwise $\phi_S(v) = 0$. It follows from Part 2 of Lemma 2, that

$$(B^m)_{ij} \geqslant \phi_Q^m \left(\frac{\phi_{\min}(Q)}{\phi_Q}\right)^n (S^m)_{ij}$$

and so

$$\max\{(B^m)_{ij}\}^{1/m} \geqslant \phi_Q\left(\frac{\phi_{\min}(Q)}{\phi_Q}\right)^{n/m} \max\{(S^m)_{ij}\}^{1/m}$$

Gelfand's formula again shows the limits exist as $m \to \infty$. B is a diagonal submatrix of A, so we know that $\rho(A) \geqslant \rho(B)$. Hence we obtain

$$\rho(A) \geqslant \rho(B) \geqslant \phi_Q \rho(S[K]) = \phi_Q$$

In combination with Part 1 of the lemma, this proves $\rho(A) = \phi_Q$ as required.

Next, we turn to Part 2b. $S \times Q$ is irreducible by hypothesis, from which it follows that S itself is irreducible. Remark 2 on p. 63 of Gantmacher (1960) shows that for irreducible substochastic S

$$\rho(S) = 1 \Leftrightarrow S \text{ is stochastic}$$

Equation (A1) together with condition (i) imply that $\rho(S) = 1$, so establishing condition (ii).

If condition (iii) does not hold, then there must be i, j, k such that $S_{ij} > 0$, $i \notin {}_jU_Q$, $k \in {}_jU_Q$. Define $\bar{Q}$ as equal to Q except that $\bar{Q}_{ij} = Q_{ij} + \tau$, where $\tau > 0$ is chosen to ensure ${}_jU_{\bar{Q}} = \{i\} \cup {}_jU_Q$. Let $\bar{S}$ be defined to ensure that $S \times Q = \bar{S} \times \bar{Q}$. Note that $\bar{S}_{ij} < S_{ij}$ but the elements are otherwise equal. The argument establishing Part 1 can be repeated for $\bar{S}$ and $\bar{Q}$ to establish that

$$\rho(\bar{S} \times \bar{Q}) \leqslant \phi_{\bar{Q}} \rho(\bar{S})$$

But $\rho(\bar{S}) < 1$, as $\bar{S}$ is irreducible and strictly substochastic. Hence

$$\rho(S \times Q) = \rho(\bar{S} \times \bar{Q}) < \phi_Q$$

This contradicts condition (i) and completes the proof of Part 2b.

Finally, we turn to Part 3. The "Normal Form of a Reducible Matrix" (see Gantmacher, 1960, p. 75) provides a block decomposition of $S[I]$ as follows.

$$\begin{bmatrix} S^{11} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S^{22} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \ldots & 0 & 0 & 0 & 0 & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & \ldots & 0 & S^{gg} & 0 & 0 & 0 & 0 \\ S^{g+1,1} & S^{g+1,2} & \ldots & \ldots & \ldots & S^{g+1,g+1} & 0 & 0 & 0 \\ S^{g+2,1} & S^{g+2,2} & \ldots & \ldots & \ldots & \ldots & S^{g+2,g+2} & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ S^{s,1} & S^{s,2} & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & S^{s,s} \end{bmatrix}$$

where (a) for each i, $g + 1 \leqslant i \leqslant s$, at least one of the S^{ij} for $j \leqslant i - 1$ is non-zero, and (b) each diagonal block is irreducible. Theorem 6 on p.77 of Gantmacher (1960) shows that as $S[I]$ has a strictly positive right eigenvector, both $\rho(S^{ii}) = \rho(S[I])$ for $1 \leqslant i \leqslant g$ (the isolated blocks), and $\rho(S^{ii}) < \rho(S[I])$ for $g + 1 \leqslant i \leqslant s$. We can apply Part 2b to each isolated block, showing that S^{ii} is stochastic for $1 \leqslant i \leqslant g$. As S itself is stochastic, it follows that $S^{ki} = 0$ for $k \neq i$. But then we must have $g = s$, for otherwise $S^{g+1,g+1}$ exists, and by definition at least one of the $S^{g+1,j}$ would have to be non-zero for $1 \leqslant j \leqslant g$. Hence $S[I]$ has a block diagonal structure in which each block has a spectral radius of ϕ_Q, and is irreducible and stochastic, proving Part 3b. It also follows from Part 2b that each block of $S[I]$ is properly placed on $Q[I]$. $S[I]$ inherits from its blocks stochasticity and proper placement on $Q[I]$, proving Part 3a.

To establish Part 3c, we apply Part 2a to $S[I]$ and $Q[I]$.

There remains Part 3d, which follows immediately from the conclusion that $\phi_{Q[I]} = \phi_Q$. $\square$

A.2. Definitions of Equilibrium Concepts and Programs

This subsection defines optimisation programs that will be needed in later proofs. The optimisation programs are then used to define equilibrium concepts. One key aspect in the technical development is employing the result of Gale (1972), which in Lemma 4 is used to link ProgA to ProgL, which allows the two equilibrium concepts to be linked. Also defined here in formal terms are some concepts explained in the text.

The first two optimisation programs are ProgESS and ProgPNE, as follows.

H max $\rho(H)$,   ProgESS($\bar{w}, \bar{p}$)

$\qquad H_{ij} \geqslant 0$,

$$\left(1 - \sum_i H_{ij}\right)\bar{w}_j - \bar{p}b_j - \bar{p}\sum_i C_{ij}H_{ij} \geqslant 0$$

h max $\bar{z}h$,   ProgPNE($\bar{j}, \bar{z}, \bar{w}, \bar{p}$)

$\qquad h \geqslant 0$,

$$\left(1 - \sum_i h_i\right)\bar{w}_{\bar{j}} - \bar{p}b_{\bar{j}} - \bar{p}\sum_i C_{ij}h_i \geqslant 0$$

A state $((w, p), H, x, y)$ is *consistent* if

1. $H \geqslant 0$, $\rho(H) > 0$
2. $x \geqslant 0$, $x \neq 0$
3. $Hx = \rho(H)x$

4. $y_j = \dfrac{x_j(1 - \Sigma_i H_{ij})}{\Sigma_j x_j(1 - \Sigma_i H_{ij})}$

5. $p > 0$
6. there exists w' such that
   (a) $(w', p) \in \mathbb{F}(y)$
   (b) $w_j = \max\{w'_j, pb_j\}$
7. H is feasible in ProgESS(w, p)

A consistent state of the population $((\hat{w}, \hat{p}), \hat{H}, \hat{x}, \hat{y})$ is an *Evolutionarily Stable State* if $\hat{H}$ solves ProgESS $(\hat{w}, \hat{p})$.

A consistent state of the population $((\hat{w}, \hat{p}), \hat{H}, \hat{x}, \hat{y})$ with an associated n-vector $\hat{z} \geqslant 0$ is an *Offspring-Linear Population Nash Equilibrium* if $\hat{z}\hat{x} = 1$ and, for each j, the j-th column of $\hat{H}$ solves ProgPNE($j, \hat{z}, \hat{w}, \hat{p}$). Note that the behaviour of absent types (with $\hat{x}_j = 0$) is required to be optimal by this definition. An Offspring-Linear Population Nash Equilibrium will be denoted as $((\hat{w}, \hat{p}), \hat{z}, \hat{H}, \hat{x}, \hat{y})$.

Next we define a program and its "linearisation" following the balanced-growth model of Gale (1956).

(H, x) max α,   ProgA($\bar{w}, \bar{p}$)

$\qquad H_{ij} \geqslant 0$,

$\qquad x_j \geqslant 0$,

$$\sum_j x_j = 1,$$

$\qquad (Hx)_j \geqslant \alpha x_j$,

$$\left(1 - \sum_i H_{ij}\right)\bar{w}_j - \bar{p}b_j - \bar{p}\sum_i C_{ij}H_{ij} \geqslant 0$$

(H, x) max $\dfrac{\bar{z}Hx}{\bar{z}x}$,   ProgL($\bar{z}, \bar{w}, \bar{p}$)

$\qquad H_{ij} \geqslant 0$,

$\qquad x_j \geqslant 0$,

$$\sum_j x_j = 1,$$

$$\left(1 - \sum_i H_{ij}\right)\bar{w}_j - \bar{p}b_j - \bar{p}\sum_i C_{ij}H_{ij} \geqslant 0,$$

$$\bar{z}x > 0$$

The strict inequality is required to ensure that the maximand is defined for feasible (H, x), and needs careful attention when the existence of a solution is being claimed. When a solution does exist, the strict inequality is irrelevant, and so it has been ignored in the Lagrangean for ProgL, which is given next, together with the first order conditions and complementary slackness conditions evaluated at $H = H^L$, $x = x^L$. In applications of these results, it will always be true that $\bar{z}x^L = 1$, and so this is assumed for ease of reading.

$$\mathcal{L} = \frac{\bar{z}Hx}{\bar{z}x} + \sum_{ij}\Gamma_{ij}H_{ij} + \sum_u \sigma_u x_u + \kappa\left(\sum_j x_j - 1\right)$$

$$+ \sum_j \lambda_j\left(\bar{w}_j - \bar{p}b_j - \sum_t H_{tj}(\bar{w}_j + \bar{p}C_{tj})\right) \text{ (A.2)}$$

and

$$\frac{\partial \mathcal{L}}{\partial H_{kl}} = 0 = \bar{z}_k x_l^L + \Gamma_{kl} - \lambda_l(\bar{w}_l + \bar{p}C_{kl}) \text{ (A.3)}$$

$$\frac{\partial \mathcal{L}}{\partial x_l} = 0 = (\bar{z}H^L)_l - (\bar{z}H^L x^L)\bar{z}_l + \sigma_l \quad \text{(A.4)}$$

$$\begin{cases}\Gamma_{ij} \geqslant 0 \\ H_{ij}^L \geqslant 0\end{cases} \begin{cases}\sigma_j \geqslant 0 \\ x_j^L \geqslant 0\end{cases}$$

$$\text{(A.5)}$$

$$\begin{cases}\lambda_j \geqslant 0 \\ (1 - \Sigma_t H_{tj}^L)\bar{w}_j - \bar{p}b_j - \bar{p}\Sigma_t C_{tj}H_{tj}^L \geqslant 0\end{cases}$$

The terms in κ have been omitted for ease of reference, as

$$0 = \sum_l x_l^L \frac{\partial \mathcal{L}}{\partial x_l^L} = \kappa$$

As a final definition, an economy will be said to be *feasible* if there exists $\bar{y} \geqslant 0$, $\bar{y} \neq 0$, such that there exists $(\bar{w}, \bar{p}) \in \mathbb{F}(\bar{y})$ for which

$$\bar{y}_i > 0 \text{ implies } \bar{w}_i > \bar{p}b_i$$

In a feasible economy, each extant type can support itself and have at least some resource left over for reproduction.

A.3. Lemmas

Three lemmas are proved here. Lemma 4 moves from a solution to ProgESS to a solution to ProgL. Lemma 5 moves from a solution to ProgL to eigensystem conditions. Lemma 6 proves continuity and convexity results about the solution to ProgESS in preparation for the fixed-point argument in Proposition 1. A key point in the technical development is the use of Lemma 3 to find the solutions to ProgESS.

Lemma 4

Suppose H^* solves ProgESS$(\bar{w}, \bar{p})$, $\alpha^* \equiv \rho(H^*) > 0$, $x^* \geqslant 0$, and $H^*x^* = \alpha^*x^* \neq 0$. Then there exists z^*, such that

1. $z^* \geqslant 0, z^*x^* = 1$
2. (H^*, x^*) solves ProgL$(z^*, \bar{w}, \bar{p})$

Proof

We first prove that (H^*, x^*) solves ProgA$(\bar{w}, \bar{p})$. H^* is feasible in ProgA, as the constraints on H are the same in ProgESS and ProgA. If H^* is irreducible, then eqn (40) on p. 65 of Gantmacher (1960) states that

$$\max_{\{x \geqslant 0, x \neq 0\}} \min_j \frac{(H^*x)_j}{x_j} = \rho(H^*)$$

Thus the maximum α attainable in ProgA by (H^*, x) is $\rho(H^*)$. This conclusion also holds if H^* is reducible, for we then consider the "Normal Form of a Reducible Matrix" (see Gantmacher, 1960, p. 75) and apply the same argument to the irreducible diagonal blocks with the highest spectral radius. This highest value is attained whenever $H^*x = \rho(H^*)x$, and in particular by (H^*, x^*).

Suppose (H', x') attains $\alpha' > \alpha^*$ in ProgA. Then the same results of Gantmacher (1960) show that $\rho(H') \geqslant \alpha'$. But H' is feasible in ProgESS, and has $\rho(H') > \rho(H^*)$, contradicting the optimality of H^* in ProgESS. Therefore, no such (H', x') exists, and so (H^*, x^*) solves ProgA, as required.

Gale (1972) shows, though in a somewhat different notation, that for a solution (H^*, x^*) to ProgA$(\bar{w}, \bar{p})$ there exists $z^* \geqslant 0$ such that $z^*x^* = 1$ and (H^*, x^*) solves ProgL$(z^*, \bar{w}, \bar{p})$, proving Parts 1 and 2.

Lemma 5

Suppose $\bar{z} \geqslant 0$, (H^*, x^*) solves ProgL$(\bar{z}, \bar{w}, \bar{p})$, $\alpha^* \equiv \rho(H^*) > 0$, $x^* \geqslant 0$, $H^*x^* = \alpha^*x^* \neq 0$ and $\bar{z}x^* = 1$. Let $I = \{i : x_i^* > 0\}$. Then

1. $\bar{z}[I] \gg 0$
2. $\alpha^*\bar{z}[I] = \bar{z}[I]H^*[I]$
3. $\alpha^*\bar{z} \geqslant \bar{z}H^*$
4. $\bar{w}_j - \bar{p}b_j > 0$ implies $\bar{z}_j > 0$
5. $x_j^* > 0$ implies that the inequalities

$$\begin{cases} H_{ij}^* \geqslant 0 \\ \bar{z}_i \dfrac{\bar{w}_j - \bar{p}b_j}{\bar{w}_j + \bar{p}C_{ij}} \leqslant \alpha^*\bar{z}_j \end{cases}$$

hold with complementary slackness.

Proof

$\bar{z}_k = 0$ implies by eqn (A.3) that for all l, either $H_{kl}^* = 0$ or $\lambda_l = 0$. $\lambda_l = 0$ in turn implies that $x_l^* = 0$, for otherwise by eqn (A.3) we would have $\bar{z}_i = 0$ for all i, contrary to the hypothesis of the Lemma that $\bar{z}x^* = 1$. Hence $\Sigma_l H_{kl}^* x_l^* = 0$, and the eigen property of x^* then yields $x_k^* = 0$. So $x_j^* > 0$ implies $\bar{z}_j > 0$, proving Part 1.

ProgL$(\bar{z}, \bar{w}, \bar{p})$ is solved by (H^*, x^*), and so its first order conditions and complementary slackness conditions hold. The hypotheses of the lemma give $\bar{z}H^*x^* = \alpha^*\bar{z}x^* = \alpha^*$, and so eqn (A.4) yields the following inequalities, holding with complementary slackness.

$$\begin{cases} x_j^* \geqslant 0 \\ \alpha^*\bar{z}_j \geqslant \Sigma_i \bar{z}_i H_{ij}^* \end{cases}$$

The eigenvector condition of the lemma implies that $H_{ij}^* = 0$ for $i \notin I$, $j \in I$, which with those inequalities establishes Part 2. The second inequality itself is Part 3.

To prove Part 4, we first show there exists k such that $\bar{w}_k - \bar{p}b_k > 0$ and $\bar{z}_k > 0$. Suppose to the contrary that $\bar{z}_j > 0$ implies $\bar{w}_j - \bar{p}b_j = 0$. Then $\bar{z}_j > 0$ also implies, through the budget constraint of ProgL, that $H_{ij}^* = 0$ for all i. Part

3 shows that $H_{ij}^* = 0$ for $\bar{z}_i > 0$, $\bar{z}_j = 0$, so it follows that $\bar{z}_i > 0$ implies $H_{ij}^* = 0$ for all j. Now the eigen property of x^* shows $\Sigma_j H_{ij}^* x_j^* = \alpha^* x_i^* = 0$. But we have shown that $\bar{z}_i > 0$ implies $x_i^* = 0$, contradicting the hypothesis of the Lemma that $\bar{z}x^* = 1$.

Thus we may choose k so that $\bar{w}_k - \bar{p}b_k > 0$ and $\bar{z}_k > 0$. Now suppose, contrary to Part 4, that there exists l such that $\bar{w}_l - \bar{p}b_l > 0$ but $\bar{z}_l = 0$. Construct $(\hat{H}, \hat{x})$ by $\hat{H} = 0$ except that

$$\hat{H}_{kl} = \frac{\bar{w}_l - \bar{p}b_l}{\bar{w}_l + \bar{p}C_{kl}} > 0,$$

and $\hat{x} = 0$ except that $\hat{x}_k + \hat{x}_l = 1$. Then by choosing $\hat{x}_k$ small enough we can ensure that

$$\frac{\bar{z}\hat{H}\hat{x}}{\bar{z}\hat{x}} = \frac{\bar{z}_k\hat{H}_{kl}\hat{x}_l}{\bar{z}_k\hat{x}_k} > \frac{\bar{z}H^*x^*}{\bar{z}x^*}$$

contradicting the hypothesis of the lemma that (H^*, x^*) solves ProgL.

Turning to Part 5, we begin by multiplying eqn (A.3) by H_{kl}^* and summing over k, yielding

$$0 = (\bar{z}H^*)_l x_l^* - \lambda_l \sum_k H_{kl}^*(\bar{w}_l + \bar{p}C_{kl})$$

We can then multiply eqn (A.4) by x_l, and use this to substitute for $(\bar{z}H^*)_l$ in the left hand term, and apply the complementary slackness condition for λ in eqn (A.5) in the right hand term, to obtain

$$0 = \alpha^*\bar{z}_l x_l^* - \lambda_l(\bar{w}_l - \bar{p}b_l)$$

Now $x_l^* > 0$ implies $\bar{z}_l > 0$ by Part 1, and so the above equation shows that $\bar{w}_l - \bar{p}b_l > 0$ also. We can therefore divide by $\bar{w}_l - \bar{p}b_l$ to obtain, for $x_l^* > 0$,

$$\lambda_l = \frac{\alpha^*\bar{z}_l x_l^*}{\bar{w}_l - \bar{p}b_l}$$

Substituting back into eqn (A.3) yields Part 5. $\square$

Lemma 6

Suppose $p > 0$ and $w_j \geqslant 0$. Let

$$Q_{ij} = \max\left\{0, \frac{w_j - pb_j}{w_j + pC_{ij}}\right\}$$

$$\tilde{w}_j = \max\{pb_j, w_j\}$$

and

$$\mathscr{F}^1(w, p) = \{H : H = S \times Q,$$

S is stochastic and properly placed on $Q\}$

Then $\mathscr{F}^1$ is uppersemicontinuous and $\mathscr{F}^1(w, p)$ is convex for all (w, p). Furthermore $H \in \mathscr{F}^1(w, p)$ implies that H solves ProgESS$(\tilde{w}, p)$ with value ϕ_Q.

Proof

Q is a continuous function of (w, p), and the set of S that is stochastic and properly placed on Q is convex, and considered as a function of Q is uppersemicontinuous. It follows that $S \times Q$ is uppersemicontinuous in (w,p). Hence $\mathscr{F}^1$ is uppersemicontinuous and $\mathscr{F}^1(w, p)$ is convex.

The set of feasible H in ProgESS$(\tilde{w}, p)$ is

$$\mathbb{H} \equiv \{H : H = S \times Q, S \text{ is substochastic}\}$$

It follows from Part 1 of Lemma 3 that $\rho(H') \leqslant \phi_Q$ for $H' \in \mathbb{H}$. But $\mathscr{F}^1(w, p) \subset \mathbb{H}$, and Part 2a of Lemma 3 shows that $H \in \mathscr{F}^1(w, p)$ implies $\rho(H) = \phi_Q$ and so H solves ProgESS$(\tilde{w}, p)$ with value ϕ_Q.

A.4. Propositions

The meaning and interpretation of the Propositions are discussed in the text. Note the use of Lemma 3 in linking to ProgESS during the proof of Proposition 3.

Proposition 1

An Evolutionarily Stable State exists in the model of Section 2.

Proof

We claim that there exists $((w^*, p^*), H^*, x^*, y^*)$ that satisfies the conditions for an Evolutionarily Stable State, and proceed by constructing a multivalued mapping $\mathscr{F}: \Omega \to 2^\Omega \backslash \{\emptyset\}$, parameterised by $p_{\min}$, where

$$\Omega = \{((\tilde{w}, \tilde{p}), (w, p), H, x, y):$$

$$\tilde{w} \geqslant 0, \tilde{p} \geqslant 0, \tilde{p} + \sum_j \tilde{w}_j = 1, w \geqslant 0, p \geqslant p_{\min},$$

$$p + \sum_j w_j = 1, H \geqslant 0, \sum_i H_{ij} \leqslant 1, x \geqslant 0,$$

$$\sum_j x_j = 1, y \geqslant 0, \sum_j y_j = 1\}$$

We define $\mathscr{F}$ by

$$((\tilde{w}', \tilde{p}'), (w', p'), H', x', y') \equiv \omega' \in \mathscr{F}(\omega)$$

$$\equiv \mathscr{F}(((\tilde{w}, \tilde{p}), (w, p), H, x, y))$$

iff

$$(\tilde{w}', \tilde{p}') \in \mathbb{F}(y)$$

$$(w', p') = \begin{cases} (\tilde{w}, \tilde{p}) & \tilde{p} \geqslant p_{\min} \\ \left(\dfrac{1 - p_{\min}}{1 - \tilde{p}} \tilde{w}, p_{\min}\right) & \tilde{p} < p_{\min} \end{cases}$$

$$H' \in \mathscr{F}^1(w, p) =$$

$$\left\{\bar{H} : Q_{ij} = \max\left\{0, \frac{w_j - p b_j}{w_j + p C_{ij}}\right\}, \bar{H} = S \times Q,\right.$$

S is stochastic and properly placed on $Q\Big\}$

$$x' \in \mathscr{F}^2(H) \equiv \left\{\bar{x} : H\bar{x} = \rho(H)\bar{x}, \bar{x} \geqslant 0, \sum_i \bar{x}_i = 1\right\}$$

$$y' \in \mathscr{F}^3(x, H)$$

$$\equiv \left\{\bar{y} : \beta\bar{y}_j = x_j\left(1 - \sum_i H_{ij}\right), \bar{y} \geqslant 0, \sum_j \bar{y}_j = 1\right\}$$

$\mathscr{F}$ is upper semicontinuous and $\mathscr{F}\omega$ is convex for all ω, because the analogous properties hold for each of the individual component mappings. The only difficult cases are $\mathbb{F}(y)$ and $\mathscr{F}^1(w, p)$, dealt with in Lemmas 1 and 6, respectively.

By Kakutani's theorem (see for example Mas-Colell *et al.*, 1995, p. 953) there therefore exists for $p_{\min} = 1/t$ a fixed point $((\tilde{w}^t, \tilde{p}^t), (w^t, p^t), H^t, x^t, y^t)$ of $\mathscr{F}$, for $t \in \{2, 3 \dots \infty\}$. If $p^t > 1/t$ for some $\hat{t}$, then $((\tilde{w}^{\hat{t}}, \tilde{p}^{\hat{t}}), (w^{\hat{t}}, p^{\hat{t}}), H^{\hat{t}}, x^{\hat{t}}, y^{\hat{t}})$ is also a fixed point for all $t \geqslant \hat{t}$ and for all $p_{\min} \leqslant 1/\hat{t}$. We now show that there must exist such a $\hat{t}$. Suppose to the contrary that $p^t = 1/t$ for all t. Then the

sequence of fixed points is on a compact set and so we may replace the sequence with a convergent subsequence that tends to, say, $((\tilde{w}, \tilde{p} = 0), (w, p = 0), H, x, y)$. Let $I = \{i : y_i > 0\}$, which is non-empty. We will show in turn that $w[I] = 0$; $x^t[I] = 0$ for sufficiently large t; and $y[I] = 0$, providing the contradiction.

(a) To prove that $w[I] = 0$. Lemma 1 shows that $wy = pf(y)$, and as $p = 0$, it follows that $y_i > 0$ implies $w_i = 0$.

(b) To prove that $x^t[I] = 0$ for sufficiently large t. Because $H^t \in \mathcal{F}^1(w^t, p^t)$, we know that $H^t = S^t \times Q^t$ where S^t satisfies the conditions of Part 3d of Lemma 3 which we now apply. We therefore proceed to show that $w_i = 0$, $i \in J$ implies $\phi_{Q^t[J]} < \phi_{Q^t}$ for sufficiently large t, as this will establish that $x_i^t = 0$ for sufficiently large t, as required. At this point we need to use notation and concepts developed in Section A.1. Let $\mathbb{S}(v)$ denote the subset of elements of $\{1, 2 \ldots n\}$ present in the sequence v. Then we need to show that for sufficiently large t,

$$\max \{\phi_{Q^t[J]} : J \cap I \neq \emptyset\}$$
$$= \max \{\phi_{Q^t}(v) : v \in {}_{ij}\tilde{V}_y, \mathbb{S}(v) \cap I \neq \emptyset\} <$$
$$\min \{\phi_{Q^t}(v) : v \in {}_{ij}\tilde{V}_m, \mathbb{S}(v) \cap I = \emptyset\} \leq \phi_{Q^t}$$

(A.6)

The outer relations hold by definition, leaving the central inequality to be shown. The minimum tends to 1, because $p^t \to p = 0$, and $\mathbb{S}(v) \cap I = \emptyset$ so that $w_j^t \to w_j > 0$. Hence

$$Q_{ij}^t = \frac{w_j^t - p^t b_j}{w_j^t + p^t C_{ij}} \to 1$$

for all Q_{ij}^t involved in the calculation of the rates. To pursue the maximum, let

$$\theta_k = \lim_{t \to \infty} \left(\frac{p^t}{w_{v_k}^t + p^t C_{v_{k+1} v_k}} \right),$$

$$\theta_{\min} = \min \{\theta_k\}, \quad K = \{k : \theta_k > 0\}$$

If $\theta_{\min} > 0$, then the maximum approaches a limit strictly less than one, and we have established the inequality (A.6). If $\theta_{\min} = 0$, the limit equals one, and is attained only by sequences satisfying $\mathbb{S}(v) \cap K = \emptyset$. We now proceed to compare the rates of sequences attaining the minimum and

maximum, to first order in p^t. We may write the rate as

$$\phi_{Q^t}(v) = 1 - \frac{p^t}{m} \sum_k \frac{b_{v_k} + C_{v_{k+1} v_k}}{w_k^t} + O^2(p^t)$$

Our task has now reduced to showing that

$$\min \left\{ \sum_k \frac{b_{v_k} + C_{v_{k+1} v_k}}{m w_k^t} + O(p^t) : \right.$$

$$\left. \mathbb{S}(v) \cap I \neq \emptyset, \mathbb{S}(v) \cap K = \emptyset \right\} >$$

$$\max \left\{ \sum_k \frac{b_{v_k} + C_{v_{k+1} v_k}}{m w_k^t} + O(p^t) : \mathbb{S}(v) \cap I = \emptyset \right\}$$

for sufficiently large t. But in the minimum, at least one of the w_i^t tends to zero whereas in the maximum, none does. Hence the minimum increases without limit as $t \to \infty$ while the maximum remains bounded. This establishes that the inequality holds for large enough t, and so completes the proof that $x^t[I] = 0$ for sufficiently large t.

(c) To prove that $y[I] = 0$. $x^t[I] = 0$ implies that $y^t[I] = 0$, only provided $\sum_k x_k^t (1 - \sum_i H_{ik}^t) > 0$, which is true because $p^t > 0$ ensures that $\sum_i H_{ij}^t < 1$. Hence $y^t[I] = 0$ for sufficiently large t, establishing $y[I] = 0$ as claimed. This is the required contradiction.

The steps (a) to (c) have completed the proof that there must exist $\hat{i}$ such that $((\tilde{w}^{\hat{i}}, \tilde{p}^{\hat{i}}), (w^{\hat{i}}, p^{\hat{i}}), H^{\hat{i}}, x^{\hat{i}}, y^{\hat{i}})$ is a fixed point of $\mathcal{F}$ for $p_{\min} = 1/\hat{i}$, and with $p^{\hat{i}} > 1/\hat{i}$. It is therefore also a fixed point of $\mathcal{F}$ for all smaller $p_{\min}$. Let

$$w_j^* = \max \{w_j^{\hat{i}}, p^{\hat{i}} b_j\} \quad p^* = p^{\hat{i}} \quad H^* = H^{\hat{i}}$$

$$x^* = x^{\hat{i}} \quad y_j^* = x_j^* \left(1 - \sum_i H_{ij}^*\right)$$

The form of $\mathcal{F}$, together with Lemma 6, shows that $((w^*, p^*), H^*, x^*, y^*)$ satisfies all the conditions of an Evolutionarily Stable State except one element of consistency. What remains to prove is that $\rho(H^*) > 0$.

We first show that $w^{\hat{i}} \not\leq p^{\hat{i}} b$. It is an assumption of the model that the economy is

feasible, and so let y' and $(w', p') \in \mathbb{F}(y')$ satisfy the feasibility condition that $y_i' > 0$ implies $w_i' > p'b_i$. If we assume, contrary to what we aim to show, that $w^i \leqslant p^i b$, we obtain, recalling that $p^i > 0$,

$$y_i' > 0 \text{ implies } p^i w_i' > p^i p' b_i \geqslant p' w_i^i$$

However, Part 6 of Lemma 1 provides that

$$y'(p^i w' - p' w^i) \leqslant 0$$

establishing a contradiction. Hence $w^i \nleqslant p^i b$, as claimed.

There must therefore be i such that $w_i^i > p^i b_i$, which implies that a positive maximand can be attained in ProgESS(w^i, p^i). A solution must therefore have a positive value, and so $\rho(H^i) > 0$, as required. $\square$

Proposition 2

Suppose $((w^*, p^*), H^*, x^*, y^*)$ is an Evolutionarily Stable State in the model of Section 2, and let $I = \{i : x_i^* > 0\}$. Then there exists $H^{**} \geqslant 0$ and $z^* \geqslant 0$ such that

1. $H_{ij}^* = H_{ij}^{**}$ for $j \in I$
2. $((w^*, p^*), H^{**}, x^*, y^*)$ is an Evolutionarily Stable State
3. $z^* x^* = 1$
4. $((w^*, p^*), z^*, H^{**}, x^*, y^*)$ is an Offspring-Linear Population Nash Equilibrium
5. $z^*[I] \gg 0$
6. $\alpha^* z^*[I] = z^*[I] H^*[I]$
7. $\alpha^* z^* \geqslant z^* H^*$
8. $x_j^* > 0$ implies that the inequalities

$$\begin{cases} H_{ij}^* \geqslant 0 \\ z_i^* \dfrac{w_j^* - p^* b_j}{w_j^* + p^* C_{ij}} \leqslant \alpha^* z_j^* \end{cases}$$

hold with complementary slackness.

Proof

The suppositions of Lemma 4 hold with $\bar{w} = w^*$, $\bar{p} = p^*$, giving the existence of z^* such that $z^* \geqslant 0$ and $z^* x^* = 1$, proving Part 3, and such that (H^*, x^*) solves ProgL(z^*, w^*, p^*).

Now we define H^{**} by $H_{ij}^{**} = H_{ij}^*$ for $j \in I$, establishing Part 1, and by choosing a solution to ProgPNE(j, z^*, w^*, p^*) for the j-th column where $j \notin I$. H^{**} is feasible in ProgL, and (H^{**}, x^*) is easily verified to be a solution.

H^{**} is feasible in ProgESS, so to prove Part 2, it will suffice to show that $\rho(H^{**}) \geqslant \rho(H^*)$. Part 1 shows that $\rho(H^{**}[I]) = p(H^*[I])$, and, as a diagonal submatrix cannot have a spectral radius higher than the original matrix, $\rho(H^{**}) \geqslant \rho(H^{**}[I])$. We need now only show that $\rho(H^*[I]) = \rho(H^*)$, but this follows immediately from the consistency of an Evolutionarily Stable State. This completes the proof of Part 2.

We now prove that $((w^*, p^*), z^*, H^{**}, x^*, y^*)$ is an Offspring-Linear Population Nash Equilibrium. First, we show that the j-th column of H^{**} solves ProgPNE(j, z^*, w^*, p^*). This is true by definition for $j \notin I$. Suppose that for some $j \in I$ there exists $\hat{h}$, feasible in ProgPNE(j, z^*, w^*, p^*), with $\tau = z^* \hat{h} - (z^* H^{**})_j > 0$. Let $\hat{H}$ equal H^{**} except that the j-th column equals $\hat{h}$. Then $(\hat{H}, x^*)$ is feasible in ProgL, and

$$\frac{z^* \hat{H} x^*}{z^* x^*} = \frac{z^* H^{**} x^* + \tau x_j^*}{z^* x^*} > \frac{z^* H^{**} x^*}{z^* x^*}$$

contradicting the solution of ProgL by (H^{**}, x^*). Hence the j-th column of H^{**} solves ProgPNE(j, z^*, w^*, p^*), as required. The conditions of Lemma 5 are met with $\bar{z} = z^*$, $\bar{w} = w^*$ and $\bar{p} = p^*$, and its Part 4 shows that $w_j^* - p^* b_j > 0$ implies $z_j^* > 0$, completing the conditions for an Offspring-Linear Population Nash Equilibrium, and the proof of Part 4.

Recalling that (H^*, x^*) solves ProgL(z^*, w^*, p^*), the remainder of the proposition follows directly from Lemma 5.

Proposition 3

Suppose $((w^*, p^*), z^*, H^*, x^*, y^*)$ is an Offspring-Linear Population Nash Equilibrium, and let $I = \{i : x_i^* > 0\}$. Suppose that for some $\alpha^* > 0$ we have

1. $\alpha^* z^*[I] = z^*[I] H^*[I]$
2. $\alpha^* z^* \geqslant z^* H^*$

Then $((w^*, p^*), H^*, x^*, y^*)$ is an Evolutionarily Stable State.

Proof

Let

$$Q_{ij} = \max \left\{ 0, \frac{w_j^* - p^* b_j}{w_j^* + p^* C_{ij}} \right\}$$

The feasible values for H in ProgPNE are such that $H = S \times Q$ where S is a substochastic matrix. Let S^* be such that $H^* = S^* \times Q$.

For the next stage of the proof, restrict attention to j such that $w_j^* - p^* b_j > 0$. This guarantees that the value of ProgPNE(j, z^*, w^*, p^*) is positive, and so that $\Sigma_i S_{ij}^* = 1$. We let

$$\gamma_j = \max_i \left\{ z_i^* Q_{ij} \right\}$$

and claim that the following pairs of inequalities hold with complementary slackness

$$\begin{cases} H_{ij}^* \geqslant 0 \\ z_i^* Q_{ij} \leqslant \gamma_j \end{cases} \qquad (A.7)$$

$$\begin{cases} x_j^* \geqslant 0 \\ \gamma_j \leqslant \alpha^* z_j^* \end{cases} \qquad (A.8)$$

To establish (A.7), we note that Offspring-Linear Population Nash Equilibrium provides that $H_{ij}^* > 0$ implies $\gamma_j = Q_{ij} z_i^*$, while the definition of γ_j implies $\gamma_j \geqslant Q_{ij} z_i^*$.

To establish (A.8), we first prove that $\gamma_j \leqslant \alpha^* z_j^*$. Multiplying the inequalities in eqn (A.7) by S_{ij}^* and summing over i, we obtain

$$\sum_i z_i^* S_{ij}^* Q_{ij} = \gamma_j \sum_i S_{ij}^* = \gamma_j$$

Condition (2) of the lemma establishes that the l.h.s. is less than or equal to $\alpha^* z_j^*$, proving the inequality. It is now established for later use that $z_j^* > 0$. Otherwise by the inequality just proved, $\gamma_j = 0 = \max \{z_i^* Q_{ij}\}$, which implies that $Q_{ij} = 0$ for all i, which contradicts the standing assumption that $w_j^* - p^* b_j > 0$.

To complete the proof of the complementary slackness in (A.8), we need to show that $x_j^* > 0$ implies $\gamma_j = \alpha^* z_j^*$. Multiplying the inequalities in eqn (A.7) by S_{ij}^* and summing over I, we obtain

$$\sum_{i \in I} z_i^* S_{ij}^* Q_{ij} = \gamma_j \sum_{i \in I} S_{ij}^*$$

The l.h.s. equals $\alpha^* z_j^*$ by Condition 1 of the lemma. We turn to prove the r.h.s. equals γ_j. Consistency of the Population Nash Equilibrium implies that $H^* x^* = \rho(H^*) x^*$, and so $H_{ij}^* = 0$ for $j \in I$, $i \notin I$. Hence $\Sigma_{i \in I} S_{ij}^* = \Sigma_i S_{ij}^* = 1$, establishing that the r.h.s. equals γ_j, as required. This completes the proof of the complementary slackness condition (A.8). We now lift the restriction on j.

In the remainder of the proof, we first employ the notation of Section A.1, in combination with the complementary slackness conditions just established, to prove in turn that (i) $\alpha^* = \phi_Q = \phi_{Q[I]}$ and (ii) $p(H^*) = \phi_Q$. Then we show that the value of ProgESS is ϕ_Q, which implies that H^* solves ProgESS. The conclusion of the lemma then follows directly.

Consider a sequence $v \in {}_i \tilde{V}_m$. We claim that $\phi_Q(v) \leqslant \alpha^*$. Consider first the case in which there is a k such that $w_{v_k}^* - p^* b_{v_k} = 0$. Then $Q_{v_{k+1} v_k} = 0$ and so $\phi_Q(v) = 0 \leqslant \alpha^*$ as required.

We need therefore consider further only sequences for which $w_{v_l}^* - p^* b_{v_l} > 0$ for all l. The first part of the proof established that if j is an element in such a sequence, then the complementary slackness conditions (A.7) and (A.8) apply, and $z_j^* > 0$. Using all three of these results, we obtain

$$\prod_k Q_{v_{k+1} v_k} \leqslant \prod_k \frac{\gamma_{v_k}}{z_{v_{k+1}}^*}$$

$$\leqslant (\alpha^*)^m \frac{z_{v_1}^* z_{v_2}^* \dots z_{v_{m-1}}^* z_{v_m}^*}{z_{v_2}^* z_{v_3}^* \dots z_{v_m}^* z_{v_1}^*} = (\alpha^*)^m$$

and hence

$$\phi_Q(v) \leqslant \alpha^*$$

as required. This shows that $\phi_Q \leqslant \alpha^*$.

It was shown earlier that $S^*[I]$ is stochastic, and so there is a sequence v such that $x_{v_k} > 0$ and $S_{v_{k+1} v_k}^* > 0$. The other parts of the complementary slackness conditions then hold with equality for such sequences, and the previous calculation holds with equality throughout. Hence $\phi_Q = \alpha^*$. All the elements of such sequences are in I by definition, and so $\phi_{Q[I]} = \alpha^*$. This establishes (i).

The attainment of ϕ_Q by all sequences $v \in {}_i V_m$ such that $x_{v_k} > 0$ and $S_{v_{k+1} v_k}^* > 0$ shows that $S^*[I]$ is properly placed on $Q[I]$. It was earlier established that $S^*[I]$ is stochastic, and so Part

2a of Lemma 3 proves that $\rho(H^*[I]) = \phi_{Q[I]}$, and by (i) we have $\rho(H^*[I]) = \phi_Q$. Part 1 of Lemma 3 implies that $\rho(H^*) \leqslant \phi_Q$, but the spectral radius of a diagonal submatrix cannot exceed that of the original matrix. Hence $\rho(H^*) = \phi_Q$, establishing (ii).

To complete the proof, it remains only to state that, by Lemma 6, the value of ProgESS is ϕ_Q. For this shows that H^* solves ProgESS, and so $((w^*, p^*), H^*, x^*, y^*)$ is an Evolutionarily Stable State, as claimed.

$\square$