

Economics Letters 66 (2000) 241-248

economics letters

www.elsevier.com/locate/econbase

A biological approach to economics through fertility

Alan Grafen*

Department of Zoology, Oxford OX1 3PS, UK Received 21 April 1999; accepted 23 June 1999

Abstract

Individual choice of labour supply and fertility is studied, in a simple multi-generational general equilibrium model in which behaviour may be determined by genes. Equilibrium concepts from economics (Nash equilibrium) and biology (evolutionary stability) are linked in three propositions. © 2000 Elsevier Science S.A. All rights reserved.

Keywords: Biology; Fertility; Labour supply; Nash equilibrium; Evolutionary stability

JEL classification: A12; J20

1. Introduction

The New Home Economics (Becker and Barro, 1988; Barro and Becker, 1989; Becker, 1991), and related work (e.g., Cigno, 1991) is the main economic treatment of those subjects that can most readily be tackled by Darwinian methods. Becker and Barro (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 and Barro arrive in their Eq. (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

0165-1765/00/ = see front matter © 2000 Elsevier Science S.A. All rights reserved. PII: 0165-1765(99)00206-2

^{*}Tel.: +44-1865-277-438; fax: +44-1865-277-435.

E-mail address: alan.grafen@sjc.ox.ac.uk (A. Grafen)

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.

The biological approach can be introduced by explaining its view of the dynastic utility function. Consumption should be 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.

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.

A more fundamental biological approach, however, would be unwilling to assume the existence of an 'as-if' maximised quantity, and would insist on deriving the existence and nature of that quantity from a population genetic model in which genes determined behaviour. The model of Grafen (1998) was designed to be as simple as possible for this purpose, but presented for a biological audience. The model has enough economic structure to create economic choices for consumers, and enough biological structure to allow a biological treatment of those decisions. Here, the model and results are presented for economists.

2. Description of the model

2.1. The individual's decision problem

Each individual lives as an adult for one period, in which she is endowed with one unit of time and one unit of labour, differentiated by type indexed by j = 1, 2, ..., 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

$$H_{ij} \ge 0$$

$$\sum_{i} H_{ij} \le 1$$

$$b_{j} + \sum_{i} C_{ij}H_{ij} \le \left(1 - \sum_{i} H_{ij}\right)w_{j}$$

The left-hand side of the third constraint is expenditure on keeping the adult alive plus the sum of the expenditures 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_i , in a homogeneous population each of whose members makes choices *H* is given by

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

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, concave, and has constant returns to scale. 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 $p + \sum_{j} w_{j} = 1$.

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, $x^{g,t}$, can therefore be obtained as

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

A genotype with $H^{g,t}$ constant and equal to H will eventually grow exponentially at rate $\rho(H)$, 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 above 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. One further technical point explained further in Grafen (1998) is that, in keeping with common practice in biological models, the growth-rate of the population at equilibrium need not be one. It is implicitly assumed that 'bland density-dependent' factors maintain the population size without altering the relative proportions of types, which is the main focus of the model.

The parameters of the model are, therefore, b_i , the amount of resource required to support one adult

of type j, C_{ij} , the amount of resource required for a type j adult to raise one unit of type i offspring, and 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 an 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, with fixed proportions of densities of the types.

The first equilibrium concept is *evolutionarily stable state*, which is based on the evolutionarily stable strategy (Maynard Smith and 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 for the given values of (w, p).

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* (PNE). 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 jth column of H achieves the maximum value of $\sum_i z_i h_i$, where h is constrained to satisfy the individual's constraints for an adult 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

Results are presented here without proofs, for which the reader is referred to Grafen (1998).

Proposition 1. If there is a consistent state, then there is an evolutionarily stable state (ESS).

A consistent state will exist provided some distribution of types can produce enough to pay for strictly more than their own maintenance.

The requirement in the following proposition that all types are present at the ESS is not made in Grafen (1998). It is made here to simplify presentation and notation. Note that if we have an ESS with absent types, then by dropping those types from the model, the ESS remains an ESS. Hence even in this restricted version, the first proposition shows that the second is not vacuous.

Proposition 2. Suppose ((w^* , p^*), H^* , x^* , y^*) is an ESS, and suppose $x^* \gg 0$. Then there exists $\alpha^* > 0$, and $z^* \ge 0$ such that

z*x* = 1, z* ≫ 0
 α*z* = z*H*
 ((w*, p*), z*, H*, x*, y*) is an offspring-linear PNE
 the inequalities

$$\begin{cases} H^*_{ij} \ge 0 \\ z^*_i \frac{w^*_j - p^* b_j}{w^*_j + p^* C_{ij}} \le \alpha^* z^*_j \end{cases}$$

hold with complementary slackness.

Thus, if behaviour is determined genetically, then at an equilibrium, individuals take decisions as if maximising a weighted sum of offspring numbers. The weights are a left eigenvector of H, and have a biological interpretation as 'reproductive value', which is an old concept in biology that is gaining a deserved central place in modern theory (Tuljapurkar, 1989; Boomsma and Grafen, 1991; Taylor, 1996; McNamara, 1997; Grafen, 1998, 1999). Economic choices are, therefore, made according to a maximisation principle, and we may view this as a biological derivation of utility-maximisation. The nature of utility may seem unusual in that fertility is central and consumption per se plays no role. On the other hand, an economist studying this population who ignored reproduction, or who ignored differences between offspring types, would undoubtedly be able to impute utility functions that did involve consumption to explain the behaviour of the consumers.

The central role of fertility is natural in a Darwinian framework. How much of human behaviour can be reconstructed on the basis that what people really care about is the quantity and quality of their offspring? If we ignore quality of offspring, then the problems of demographic transitions and of the absence of strong positive wealth–fertility correlations in advanced economies make this project untenable (Vining, 1986). Once we accept that there is quality variation, and that quality can have a Darwinian interpretation, namely 'reproductive value', then the biological approach can be taken further. More work will obviously be required to discover how much further.

Let us tentatively consider the consequences of equating utility and reproductive value. Reproductive value is comparable between people. It can be summed over a set of people and so the total reproductive value can be compared between groups. In the presence of uncertainty reproductive value is maximised risk-neutrally. The idea that all possible actions will be taken to avoid death is not supported by the biological view.

It is doubtful that gene frequency changes actually bring about biological equilibrium in human populations, as the environment changes too quickly. The next proposition suggests a deeper biological strategy that could be fixed by gene frequency changes, but which is so general that it will maintain biologically appropriate responses to changing environments. Again the restriction that all types are present is not made in Grafen (1998). Again we can delete all absent types from the model, so the previous propositions together show that this final proposition, even with its assumption of no absent types, is not vacuous.

Proposition 3. Suppose ((w^* , p^*), z^* , H^* , x^* , y^*) is an offspring-linear PNE, and that $x^* \gg 0$. Suppose that for some $\alpha^* > 0$ we have $\alpha^* z^* = z^*H^*$. Then ((w^* , p^*), H^* , x^* , y^*) is an ESS. The more general strategy is that an individual is programmed to maximise a weighted sum of offspring numbers, but that the types and the weights to be attached to them are learnt during the first phase of life before life-decisions need to be taken. This proposition states that if the types are right, and if the weights are computed as a left eigenvector of the population projection matrix H, then if the population arrives at an economic equilibrium, it will also have achieved a biological equilibrium. The types are 'right' if they respect the differences in labour-types recognised in the economy, and these may change as the economy develops. The weights need to be learnt if technological change alters the production function and the value of different types of labour, or if any of the costs associated with maintaining self or rearing offspring change. The left eigenvector produces the reproductive values, and so corresponds to asking, for a given projection matrix H, how much each type contributes to the gene pool in distant generations. Knowledge of biological genealogies is clearly of importance to such a strategist. The significance of arriving at a biological equilibrium is that no mutation causing a further change in behaviour would be selected for.

This result suggests that it may be worth pursuing Darwinian explanations of behaviour in modern settings. It also suggests a penumbra around Darwinian accounts, in which non-Darwinian behaviour may result from acquiring the wrong weights or the wrong type distinctions. They may be wrong because of time lags, or incomplete information, or systematic manipulation of information. In this case, individuals do not maximise their reproductive value, but their behaviour can be viewed as resulting from running a program in a new environment that was designed to maximise reproductive value in a previous one. This is a particular version of a standard viewpoint in evolutionary psychology (Barkow et al., 1992).

4. Discussion

Grafen (1998) did not notice a similar model presented by Robson and Wooders (1997), which shares a generational structure with endogenous population densities, and the assumptions of a single good and a finite number of types of labour, and of a concave production function of the labour inputs with constant returns to scale. The differences will help to pinpoint the aims of this present model.

The models share the aim of combining biology and economics in the study of human behaviour (see Robson, 1999, for a review of such work), as distinct from the commoner aim of employing analogies from one subject in the service of the other. Robson and Wooders focus on the central decision of how production should be divided between the types of individual. There is no decision for individuals to take, at least explicitly. Growth rate of the population is maximised by the 'platinum rule' of allocating according to marginal products. The biological competition is at the level of populations. Those societies adopting the platinum rule will grow faster than those that do not, and so come to represent a larger and larger fraction of the human population.

By contrast, the present model simply assumes wages are determined by marginal products, and focusses on individual decision-making in that context. Individuals have a free choice of the amount of labour to supply, and of the type of labour their children should be educated into, and the results hold for arbitrary values of b, C and f, the costs of subsistence and of rearing offspring, and the production function. The importance of the richness of choice is that the present model aims to show a general equivalence between the outcome of biological evolution and economic equilibrium at the

level of individual choices, and in particular to show that biological evolution results in individuals acting as maximising agents in a wide variety of circumstances.

Robson and Wooders' model raises the interesting issue, not considered by Grafen (1998), of whether the ESS in the present model attains a social maximum of growth rate. There appears to be scope for externalities because the earnings of one type cannot be transferred to pay for the reproduction of another. The biological viewpoint is generally that individual-level maximisations do not lead to higher level efficiencies, but also that those higher-level efficiencies are of little relevance. For some economic purposes, however, the social efficiency of the biological equilibrium may well be of interest.

The potential implications for economics of the individual-level optimisations studied in the present model relate most strongly to decisions involving fertility (including demographic transitions, population control programs and wealth–fertility correlations), child maintenance, inheritance and education. If individuals make choices even roughly in line with the somewhat sophisticated but fundamentally biological suggestions presented here, then this could have important consequences for understanding human behaviour, and so perhaps for policy-making, in these areas.

Acknowledgements

I am grateful to Arthur Robson and Eric Maskin for helpful discussions of the relevance of my earlier paper to economists, at a meeting on Evolutionary Models of Social and Economic Behaviour held at Pennysylvania State University in March, 1999.

References

- Barkow, J., Cosmides, L., Tooby, J. (Eds.), 1992. The Adapted Mind:Evolutionary Psychology and the Generation of Culture, Oxford University Press, London.
- Barro, R.J., Becker, G.S., 1989. Fertility choice in a model of economic growth. Econometrica 57, 481-501.
- Becker, G.S., 1991. In: A Treatise on the Family, Enlarged edition, Harvard University Press, Cambridge, MA, First edition published in 1981.
- Becker, G.S., Barro, R.J., 1988. A reformulation of the economic theory of fertility. The Quarterly Journal of Economics 103, 1–25.
- Boomsma, J.J., Grafen, A., 1991. Colony-level sex ratio selection in the eusocial *Hymenoptera*. Journal of Evolutionary Biology 3, 383–407.
- Cigno, A., 1991. In: Economics of the Family, Oxford University Press, London.
- Grafen, A., 1998. Fertility and labour supply in femina economica. Journal of Theoretical Biology 194, 429-455.
- Grafen, A., 1999. Formal darwinism, the individual-as-maximising-agent analogy, and bet-hedging. Proceedings of the Royal Society, Series B 266, 799–803.
- Maynard Smith, J., 1982. In: Evolution and the Theory of Games, Cambridge University Press, Cambridge.
- Maynard Smith, J., Price, G.R., 1973. The logic of animal conflict. Nature 246, 15-18.
- McNamara, J.M., 1997. Optimal life histories for structured populations in fluctuating environments. Theoretical Population Biology 51, 94–108.
- Robson, A.J., 1999. The biological basis of economic behavior. In preparation.
- Robson, A.J., Wooders, M., 1997. On the growth-maximizing distribution of income. International Economic Review 38, 511–526.

- Taylor, P.D., 1996. Inclusive fitness arguments in genetic models of behaviour. Journal of Mathematical Biology 34, 654–674.
- Tuljapurkar, S., 1989. An uncertain life: demography in random environments. Theoretical Population Biology 35, 2275–2294.
- Vining, D.R., 1986. Social versus reproductive success—the central theoretical problem of human sociobiology. Behavioral and Brain Sciences 9, 167–260.