For Love or Money: The Evolution of Reproductive and Material Motivations[*]

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1994

Abstract

The model developed here is used to study the evolution of reproductive strategy in a sexual population with heritable wealth. In contrast to earlier haploid models, the present model implies that at evolutionary equilibrium the wealthy must out-reproduce the poor. Thus, the negative correlation between wealth and fertility in many modern populations is probably not an evolutionary equilibrium. At evolutionary equilibrium, there are strong correlations of long-term fitness both with wealth and with fertility. This suggests that selection will have favored a psychology with both material motivations (a desire for wealth) and reproductive motivations (a desire for sex and children). Since the two correlations are of roughly equal magnitude, there is no reason to suppose that either motivation will dominate.

1 Two questions

What reproductive strategies are favored by natural selection in a world where wealth can be inherited? Heritable wealth introduces several interesting wrinkles. First, there is the trade-off between the number of one's children and their wealth. A parent cannot simultaneously maximize both. Second, there is the question of how fitness should be defined. It makes no sense to equate fitness with the number of children, because the parent whose children are many may lose in competition with parents whose children are fewer but wealthier.

These observations suggest two questions. First,

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- *Is it true that at evolutionary equilibrium the wealthy must out-reproduce the poor?*

An affirmative answer would follow from the assumptions that (a) selection favors those who produce the most offspring, and that (b) a wealthy person has all the opportunities available to a poor person and more. If this were true, then selection should lead to an equilibrium at which the wealthy produce at least as many offspring as the poor. Yet human females do not behave this way, and this has been a source of consternation for evolutionary ecologists (Vining, 1986). But I have already suggested that assumption (a) need not hold when wealth can be inherited. Thus, there may be no cause for consternation.

A second question involves the psychology of motivations. I shall distinguish *reproductive motivations* (the desire for children) from *material motivations* (the desire for wealth). I will assume without proof that (1) the strength of selection for reproductive motivations depends on the correlation r_{kids} between fitness and the number of one's surviving offspring, and that (2) the strength of selection for material motivations depends on the correlation r_{wealth} between fitness and wealth. These assumptions imply that if $r_{\text{wealth}} \gg r_{\text{kids}}$, then selection should favor a psychology dominated by material motivations, while the opposite should be true then $r_{\text{wealth}} \ll r_{\text{kids}}$. In the absence of heritable wealth $r_{\text{kids}} = 1$ and $r_{\text{wealth}} < r_{\text{kids}}$. Thus, selection should favor a psychology in which reproductive motivations were dominant. It is not clear what to expect when wealth is heritable. Thus, I shall ask:

- *Under what circumstances, if any, is r_{wealth} large relative to r_{kids}?*

2 Previous work

Henry Harpending and I have written two previous papers on this subject. In the first (Rogers, 1990), I calculated optimal reproductive strategies in a model with heritable wealth. I will not describe that model in detail, since it differs from the one described below in only one respect: the earlier model assumed clonal inheritance: that each each individual was genetically identical to her single parent. The clonal model was convenient because the fitness of an individual could be equated with the ratio of increase of the clone comprising her descendants. Under mild assumptions, this ratio converges to a stable value λ. The optimal reproductive strategy is the one that maximizes λ.

λ can also be interpreted as the dominant eigenvalue of a matrix $\mathbf{G}$, whose ijth entry is the expected number of offspring of wealth i per parent
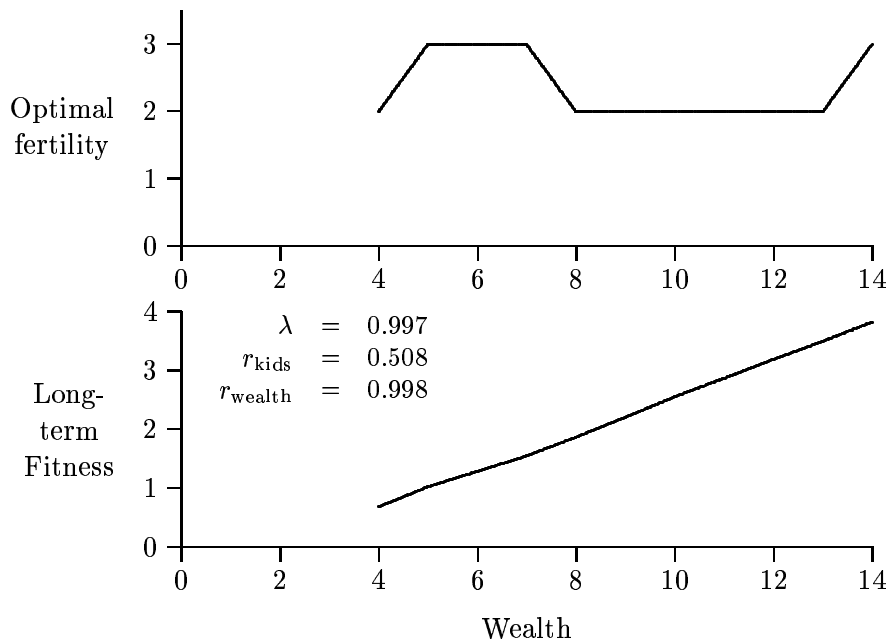
Figure 1: An evolutionary equilibrium under clonal inheritance
Source: Figure 2 of Rogers (1990).

of wealth j. The procedure for calculating $\mathbf{G}$ involved assumptions similar to those in the sexual model described below, and will not be repeated here. Once an optimal strategy has been found, the clonal assumption also makes it easy to calculate the *stable wealth distribution* h, (the vector whose ith entry is the equilibrium proportion of the population in wealth category i), and the vector w of *long-term fitnesses* (whose ith entry is proportional to the number of descendants that an individual of wealth i will produce in the long run, that is, in the limit as time goes to infinity). These vectors are, respectively, the column- and row-eigenvectors of $\mathbf{G}$ that are associated with λ, the dominant eigenvalue. They are analogous to the *stable age distribution* and the vector of *reproductive values* from classical demography (Keyfitz, 1968).

The optimal strategy under one set of assumptions (see the original paper for details) is described in figure 1. That result provided surprising answers to both of the questions raised above: Even at evolutionary equilibrium, fertility need not be a non-decreasing function of wealth, and r_{wealth} may greatly exceed r_{kids}. In a world such as that described in figure 1, fertility would be a poor measure of fitness, and selection should favor a

psychology dominated by material motivations. The paper went on to show that $r_{\text{wealth}} > r_{\text{kids}}$ in harsh environments, whereas $r_{\text{wealth}} < r_{\text{kids}}$ in mild ones. Thus, selection should favor material motivations most strongly in harsh environments.

The model underlying these conclusions was unrealistic in many ways, but two of these seem especially important. The first is that of clonal inheritance. Under this system, my descendant ten generations hence would—apart from the minor effect of mutation—be genetically identical to me. Under sexual reproduction, on the other hand, this descendant would share few genes with me. Thus, increasing the wealth of this descendant would increase my fitness more in the clonal case than in the sexual case. My assumption of clonal inheritance probably inflated the importance of heritable wealth.

A second assumption introduced an opposite bias. I assumed that, in addition to inheriting wealth, each individual earned some wealth on her own. This earned wealth was a Poisson random variable, with a distribution that did not depend on the wealth inherited. Thus, offspring of rich parents earned the same amount on average as the offspring of poor parents. In reality, inherited wealth often facilitates the acquisition of additional wealth. It would have been more reasonable to assume a positive regression of earned on inherited wealth. Thus, my independence assumption probably reduced the effect of heritable wealth.

Since the two false assumptions produce opposite biases, it is not clear whether their net effect makes heritable wealth more or less important than it should be. To find out, we need a model that incorporates sexual reproduction. Harpending and I (1990) extended the linear mathematics of the first paper to the sexual case. However, that algebra holds only at demographic equilibrium, and does not provide a means of finding this equilibrium. Thus, we were unable to calculate optimal reproductive strategies.

Below, section 3 will extend the earlier model to deal with sexual reproduction and to make earned wealth depend on inherited wealth. Section 4 will describe the algorithm used for finding evolutionary equilibria. Results are presented in section 5 and discussed in section 6.

3   Model of a monoecious sexual population

The model incorporates sexual reproduction, but has only one sex: each individual is able to mate with any other. I am assuming, in other words, monoecious sexual reproduction. This allows me to incorporate the effects of

sex while neglecting the complexities that are introduced by separate sexes. In addition, I assume that generations are discrete and non-overlapping. Individuals of each generation are classified into a finite number K of discrete wealth categories.

In order to find optimal reproductive strategies, we must be concerned with two kinds of equilibria: demographic and evolutionary. A population at demographic equilibrium is one with in which the relative frequencies of individuals within wealth classes do not change. This demographic process is described in section 3.1. A population is at evolutionary equilibrium when its members have a genotype with higher fitness than any other genotype would have when rare. The evolutionary process is described in section 3.2.

3.1   A genetically homogeneous population

A homogeneous population can be described by the number $n_i(t)$ of individuals of wealth i in generation t, where $i = 0, 1, \ldots, K-1$. The column-vector whose ith entry is $n_i(t)$ will be denoted by $\mathbf{n}(t)$. The total population size in generation t is $N(t) = \sum_k n_k(t)$.

To describe the production of each new generation, I extend Pollak's (1990) birth-matrix–mating-rule model to deal with the case in which offspring are classified into K categories. The expected number of wealth i in generation $t+1$ can be written as

$$n_i(t+1) = \sum_{jk} b_{ijk} u_{jk}[\mathbf{n}(t)] \tag{1}$$

where b_{ijk} is the expected number of offspring of wealth i produced by a mating between parents of wealths j and k, and $u_{jk}[\mathbf{n}(t)]$ the expected number of such matings, a function of $\mathbf{n}(t)$. A demographic equilibrium is defined by a vector $\mathbf{n}(t)$ such that $\mathbf{n}(t+1)$ is proportional to $\mathbf{n}(t)$. The conditions under which such equilibria exist can be specified under restricted versions of this model (Caswell, 1989; Pollak, 1990), but are unknown in the general context considered here. In later sections, equilibria are found numerically using an algorithm based on recursion 1.

To show how this recursion relates to the linear mathematics of clonal populations (Rogers, 1990; Rogers, 1992) (or of classical demography), I re-express it as

$$\mathbf{n}(t+1) = \mathbf{G}\mathbf{n}(t) \tag{2}$$

where $\mathbf{G}$ is a matrix whose ijth entry g_{ij} is the expected number of offspring

of wealth i per parent of wealth j. Equating the two recursions shows that

$$g_{ij} = \sum_k b_{ijk} \frac{u_{jk}[\mathbf{n}(t)]}{n_j(t)} \tag{3}$$

In general, $\mathbf{G}$ is a function of $\mathbf{n}(t)$, and will change each generation. Thus, we cannot project the population into the future simply by iterating (2) with constant $\mathbf{G}$. The familiar linear mathematics of classical demography no longer apply.

On the other hand, if the population does reach an equilibrium, the linear mathematics become useful. It is reasonable to assume that the mating function $u_{ij}[\mathbf{n}]$ is homogeneous of degree 1, i.e. that

$$u_{ij}[a\mathbf{n}] = a u_{ij}[\mathbf{n}]$$

for any scalar a[1]. This says, for example, that doubling the number of individuals will double the number of matings between each pair of wealth categories. When this assumption holds, g_{ij} will depend only on the relative frequencies of individuals within wealth categories. At equilibrium, these relative frequencies do not change and therefore neither does g_{ij}. Equation 2 is then linear, and the standard results of stable population theory apply (Rogers, 1990; Harpending and Rogers, 1990; Rogers, 1992). Given particular assumptions about b_{ijk} and $u_{jk}[\mathbf{n}]$, we can use numerical methods to find equilibria and then interpret them in the ordinary way. We can, for example, use the methods described above in section 2 to calculate the ratio λ of increase, the vector w of long-term fitnesses, and the stable wealth distribution h. What we cannot do is specify, in general, the conditions under which equilibria will exist.

Adding sources of variation to a model usually makes it harder to study, rather than easier. Yet adding genetics to this model provides a way around its nonlinearity. The trick is to ask a slightly different question. Rather than seeking demographic equilibria, we seek to determine the circumstances under which a rare allele can invade a population dominated by some other allele. A strategy that cannot be invaded is an "evolutionarily stable strategy," or ESS (Maynard Smith, 1982).

3.2   When can a rare allele invade?

Consider the dynamics of a rare allele B in a population dominated by a common allele A. Superscripts 1, 2, and 3 will indicate genotypes AA,

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[1] A rationale for this assumption is discussed by Pollak (1990, p. 406).

AB, and BB, respectively. For example, $n_j^{(2)}(t)$ denotes the number of AB individuals of wealth j in generation t, and $u_{jk}^{(2,1)}[\mathbf{n}^{(1)}(t),\mathbf{n}^{(2)}(t)]$ is the expected number of matings in which one parent has genotype AB and wealth j while the other has genotype AA and wealth k.

Since B is rare, we need consider only two genotypes (AA and AB), and two types of mating ($AA \times AA$ and $AA \times AB$). The other genotypes and mating types are negligibly rare. Prior to the introduction of B, all individuals were of genotype AA, and I assume that this population was at equilibrium. At this equilibrium, the relative frequency of individuals of wealth i is a constant $p_i^{(1)}$, and in each generation the population increases by a constant ratio $\lambda^{(1)}$, i.e. $N^{(1)}(t+1) = \lambda^{(1)}N^{(1)}(t)$. While B is rare, its effect on the demographic parameters of AA will be small. Thus, any departures of AA from this equilibrium will be small enough to neglect. The AA component of the population will continue to increase by a factor of $\lambda^{(1)}$ each generation.

The AB component of the population reproduces itself via matings of type $AA \times AB$, whose offspring are evenly divided between genotypes AA and AB. Of these, the AA offspring can be ignored since they are rare compared with the offspring of $AA \times AA$ matings. The AB offspring, on the other hand, are of central concern: their number in each generation is approximately equal to the number of copies of the B allele. Thus, if AB increases at a ratio faster than $\lambda^{(1)}$ then the B allele will increase when rare. This ratio of increase is determined from the equation,

$$n_i^{(2)}(t+1) \quad = \quad \frac{1}{2}\sum_{jk} b_{ijk}^{(2,1)} u_{jk}^{(2,1)}[\mathbf{n}^{(1)}(t),\mathbf{n}^{(2)}(t)] \tag{4}$$

The factor of $1/2$ here arises because only half of the offspring produced by an $AA \times AB$ mating are of genotype AB. This factor does not appear in equation 1, a fact that seems to impose a two-fold disadvantage upon the AB component of the population. However, this apparent disadvantage is exactly offset by less obvious advantage: the number of unions (i.e. the sum of u_{jk}) equals half the number of individuals in equation 1, but equals the total number of AB individuals in equation 4 (see equations 7 and 11 below).

Equation 4 can also be expressed as

$$\mathbf{n}^{(2)}(t+1) = \mathbf{G}^{(2,1)}\mathbf{n}^{(2)}(t) \tag{5}$$

where $\mathbf{G}^{(2,1)}$ is a matrix whose ijth entry

$$g_{ij}^{(2,1)} = \frac{1}{2} \sum_k b_{ijk}^{(2,1)} \frac{u_{jk}^{(2,1)}[\mathbf{n}^{(1)}, \mathbf{n}^{(2)}]}{n_j^{(2)}} \tag{6}$$

is the expected number of offspring of wealth i per parent of wealth j. So far, the algebra is identical to that of the homogeneous population considered above. The important difference here is that equation 5 is approximately linear when allele B is rare, provided that $u_{jk}^{(2,1)}$ is homogeneous of degree 1 and is a function only of $n_j^{(2)}$ and $n_k^{(1)}$.

To see why this is so, expand $u_{jk}^{(2,1)}[n_k^{(1)}, n_j^{(2)}]$ in Taylor series about $n_j^{(2)} = 0$, drop terms in $(n_j^{(2)})^2$, and note that $u_{jk}^{(2,1)}[n_k^{(1)}, 0] = 0$ since there can be no matings involving AB when this genotype is absent. This gives

$$g_{ij} \approx \frac{1}{2} \sum_k b_{ikj} \frac{\partial u_{jk}^{(2,1)}[n_k^{(1)}, 0]}{\partial n_j^{(2)}}$$

Since $n_j^{(2)}$ does not appear here, it is clear that g_{ij} does not vary with the number of AB individuals. Neither does it vary with $n_k^{(1)}$. This follows from the fact that, since $u_{jk}^{(2,1)}$ is homogeneous of degree 1, the derivative here is homogeneous of degree 0 (Varian, 1984, p. 330).

For example, if mating is at random, and all AB individuals find mates, then

$$u_{jk}^{(2,1)} = n_j^{(2)} p_k^{(1)} \tag{7}$$

and

$$g_{ij}^{(2,1)} = \frac{1}{2} \sum_k b_{ijk}^{(2,1)} p_k^{(1)} \tag{8}$$

The relative frequencies $p_k^{(1)}$ are approximately constant, since the AA component of the population is at approximate equilibrium.

The constancy of $g_{ij}^{(2,1)}$ implies that the AB component of the population will converge to a stable distribution of wealth categories given by the leading right-eigenvector of $\mathbf{G}^{(2,1)}$, and will then grow at a ratio given by the corresponding eigenvalue $\lambda^{(2,1)}$ of this matrix. Since the AA component of the population is still increasing at ratio $\lambda^{(1)}$, it follows that B will increase in frequency when rare if and only if

$$\lambda^{(2,1)} > \lambda^{(1)} \tag{9}$$

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This argument applies also to the case in which B is common and A is rare. In that case, B increases when

$$\lambda^{(2)} > \lambda^{(1,2)} \tag{10}$$

where $\lambda^{(2)}$ is the equilibrium growth ratio of a pure BB population, and $\lambda^{(1,2)}$ the ratio of increase of AB in a population dominated by BB.

Inequalities analogous to 9 and 10 are widely used within evolutionary ecology for populations structured by age (Charlesworth, 1980, section 4.3). The present results generalize these to the case of populations structured by arbitrary categories, such as social class or levels of wealth.

3.3 Mating

I assume that mating is at random, both with respect to wealth category and genotype. Under this assumption, the unions matrix $u_{jk}^{(2,1)}$ for rare individuals of genotype AB is given by equation 7. In a homogeneous population, the unions matrix for AA individuals is

$$u_{ij}[\mathbf{n}(t)] = \frac{n_i(t)n_j(t)}{2N(t)} \tag{11}$$

The denominator $2N(t)$ is chosen to make $\sum_{ij} u_{ij}[\mathbf{n}(t)] = N(t)/2$, as is appropriate if all individuals form pairs.

3.4 Reproduction

A reproductive strategy will be represented as a vector whose ith entry determines the allocation to fertility when the bearer's wealth is i. For example, if there were only $K = 3$ levels of wealth, one feasible reproductive strategy is $v = (0, 0, 1)$. An individual with this strategy would allocate 0 units of wealth toward fertility if her own wealth was either 0 or 1, and 1 unit if her own wealth was 2.

I assume that the two individuals in a union make independent allocations to fertility, as determined by their own wealth and strategy, and independent of the allocation made by their partner. These assumptions serve simplicity more than realism, and might usefully be revised in future work.

A family's allocation to fertility is the sum of the allocations made by the two partners. For example, consider a union between two individuals who share strategy v, but who have wealth 1 and 2 respectively. According to strategy v, the first parent's fertility allocation will be 0, that of the second

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1. The family's fertility allocation will be the sum of these, or 1. The wealth not allocated to fertility is inherited by the children produced. Our example family has wealth $1 + 2 = 3$, and bequeaths 2 units of wealth to its children. Inherited wealth is divided among the children as evenly as possible.

A family that allocates x units of wealth to fertility will produce

$$m(x) = \begin{cases} 0 & x < s \\ \text{Round}\left[m_+(1 - e^{-\alpha(x-s+1)})\right] & x \geq s \end{cases} \qquad (12)$$

children. $m(x)$ is called the "fertility function," and is graphed in the upper panel of figure 2. No children are produced at all if the family allocation is less than s, the "starvation threshold." Above this threshold, fertility increases with allocation at a decreasing rate toward a maximal value, m_+. The rate of increase is determined by a third parameter, α. $m(x)$ is rounded to the nearest integer for computational convenience.

I assume that heterozygous AB individuals exhibit, with equal probability, either the strategy of AA or that of BB.

3.5 Earned wealth

In addition to inherited wealth, each offspring earns some wealth on her own. The wealth y earned by an individual who inherits x units of resource is a Poisson random variable with mean

$$E\{y\} \equiv \beta + \gamma x$$

γ can be interpreted as the regression of earned on inherited wealth. When $\gamma = 0$, earned and inherited wealth are independent as my earlier paper assumed.

If $x + y \geq K$, then the individual's wealth is truncated back to $K - 1$. This truncation models nothing in the real world, and is done solely for computational convenience. In the earlier paper (Rogers, 1990), I showed that it made little difference.

These assumptions are sufficient to determine all of the quantities defined in sections 3.1 and 3.2.

4 Searching for equilibria

4.1 Demographic equilibria

The simplest algorithm for finding demographic equilibria begins with some arbitrary initial wealth distribution and iterates equation 1 until the wealth
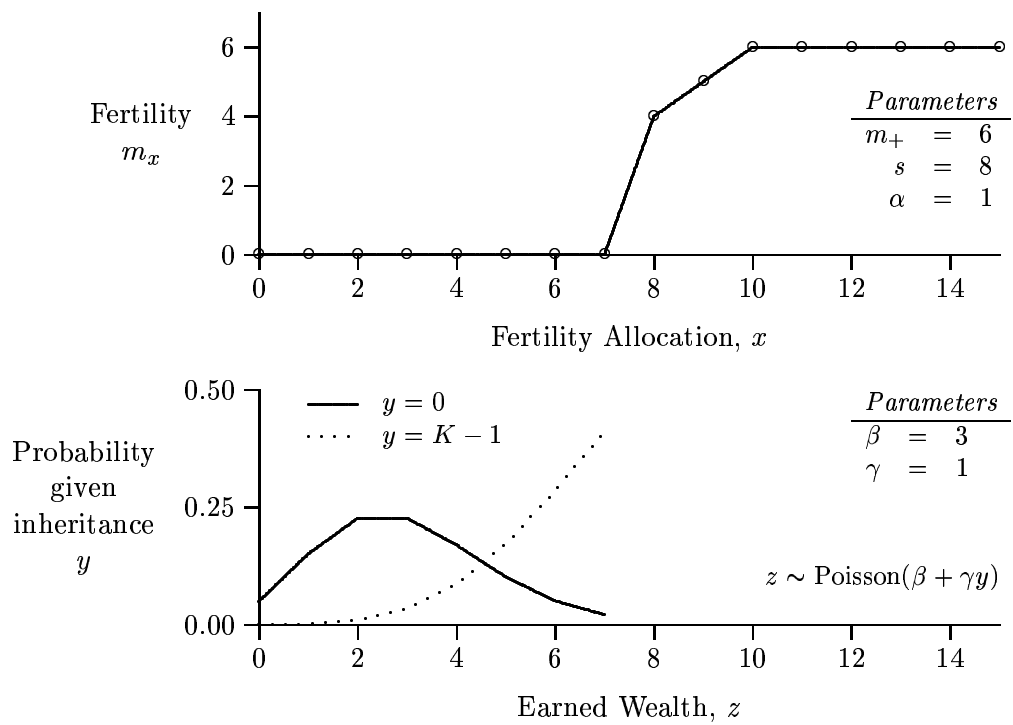
Figure 2:
The upper panel shows how many offspring are gained for given investments of wealth. The lower panel shows the truncated Poisson probability distribution of earned wealth. The solid line there applies to all individuals when $\gamma = 0$, and to those who inherit nothing when $\gamma > 0$. The dotted line shows the distribution of earned wealth given the maximal inheritance, $K - 1$, in the case when $\gamma = 1$.

distribution becomes nearly constant. Then, the ratio of increase is calculated as $\lambda = N(t+1)/N(t)$. I will refer to this as the method of forward iteration. Unfortunately, if an accurate answer is desired, this method usually takes a large number of iterations. However, a small number of iterations— I use no more than six—is usually sufficient to reach the neighborhood of an equilibrium. Then, the equilibrium can be "polished" using the faster method of inverse iteration.

The method of inverse iteration is a well-known algorithm for finding selected eigenvectors of a matrix. Given initial estimates of λ and of the stable wealth distribution, each inverse iteration improves these estimates. I modified the standard algorithm (Press et al., 1988, pp. 394–395) only slightly, by using equation 3 to recalculate $\mathbf{G}$ at the beginning of each iteration. The resulting algorithm usually converged rapidly.

When the inverse iterations did not converge, the two-stage process was repeated again with a new, randomly chosen, initial vector. As many as five initial vectors were tried. This algorithm nearly always converged. Furthermore, extensive experimentation failed to identify any cases in which different initial vectors lead to different equilibria. Thus, the demographic equilibria in this model appear to be unique.

4.2 Evolutionary equilibria

For each set of parameter values, the goal is to find an *evolutionarily stable strategy*, or ESS (Maynard Smith, 1982). An ESS is a strategy whose fitness is higher, when common, than that of any possible invading strategy. My search algorithm begins with an arbitrary initial strategy, and pits this against each possible one-step perturbation. Here, a one-step perturbation is a strategy that differs from the old by ± 1 in exactly one position. When a better strategy is found, the new strategy replaces the old and the process begins again. The search ends when it finds a strategy that cannot be improved by any one-step perturbation.

In comparing an old strategy A with a new one B, I calculate four ratios of increase:

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\begin{aligned}
\lambda^{(1)} &= \text{ratio for pure } AA \text{ population} \\
\lambda^{(2,1)} &= \text{ratio for rare } AB\text{s with } AA \text{ common} \\
\lambda^{(1,2)} &= \text{ratio for rare } AB\text{s with } BB \text{ common} \\
\lambda^{(2)} &= \text{ratio for pure } BB \text{ population}
\end{aligned}
$$

I will say that AB invades AA if $\lambda^{(1)} < \lambda^{(2,1)}$ and that AB invades BB if

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$\lambda^{(2)} < \lambda^{(1,2)}$. In comparing two strategies there are four cases to consider.

First, if AB invades AA but not BB, then BB is an ESS but AA is not. In this case, the search algorithm replaces A with B and continues.

Second, if AB invades BB but not AA, then A is retained and B rejected.

If neither of these cases holds, then there is at least one internal equilibrium which may be either stable or unstable. In these cases, the search algorithm accepts B if $\lambda^{(2)} > \lambda^{(1)}$, and rejects it if this inequality is reversed. Ties occur when $\lambda^{(1)} \approx \lambda^{(2)}$, to within the limits of numerical precision. When an upper bound on optimal investment is sought, ties are decided in favor of the strategy investing more. The reverse is true when a lower bound is sought.

This procedure ignores internal equilibria (mixed ESSs), and consequently may stop at a strategy that is not an ESS. However, in practice this seldom happens. Almost always, the upper and lower bound on optimal investment enclose a region that is stable against invasion from outside the region.

5   Results

Figures 3 and 4 illustrate optimal reproductive strategies calculated from two sets of parameter values. The second differs from the first in that β is reduced from 3 to 1, and γ increased from 0 to 1. Thus, figure 4 describes a world in which wealth is harder to earn for those who inherit little, but easier to earn for those with an ample inheritance. The two optimal reproductive strategies are identical for wealth levels 0 through 4. At higher wealth levels, less is allocated to fertility in figure 4 than in figure 3. This makes sense: inherited wealth has become more important, so wealthy parents are emphasizing quality at the expense of quantity.

Note that fertility is a non-decreasing function of wealth in both figures. With sexual reproduction, I have been unable to find parameter values that generate a decreasing or non-monotone relationship such as that shown for the case of clonal inheritance in figure 1. I cannot guarantee that non-monotone equilibria do not exist under sexual reproduction, but I have yet to find one. This provides a tentative negative answer to the first of the two questions with which I began. It seems unlikely that the negative relationship observed in many western countries can represent an evolutionary equilibrium.

Let us turn now to the second question, which asks when, if ever, the correlation of long-term fitness with wealth exceeds that with fertility. The
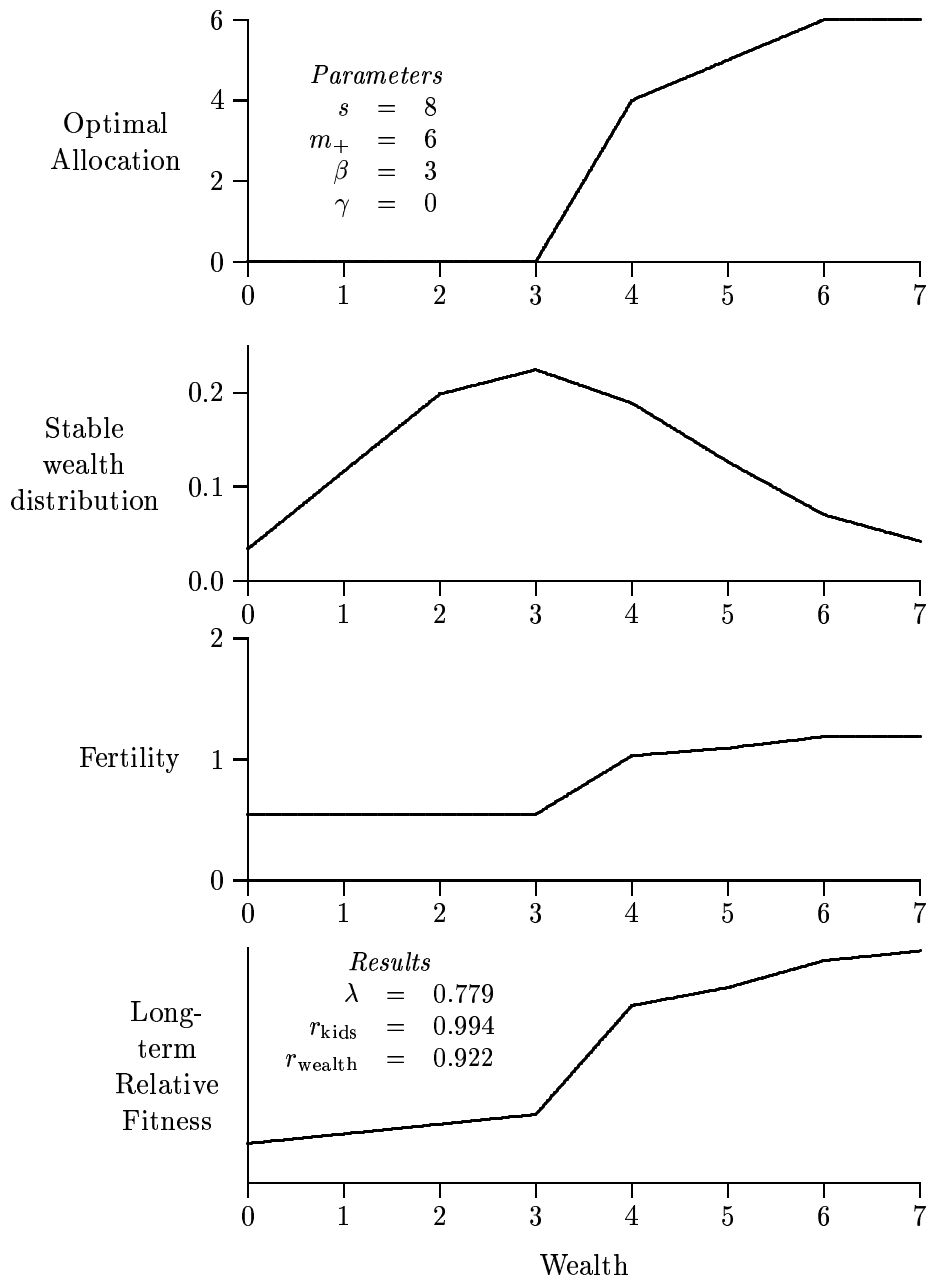
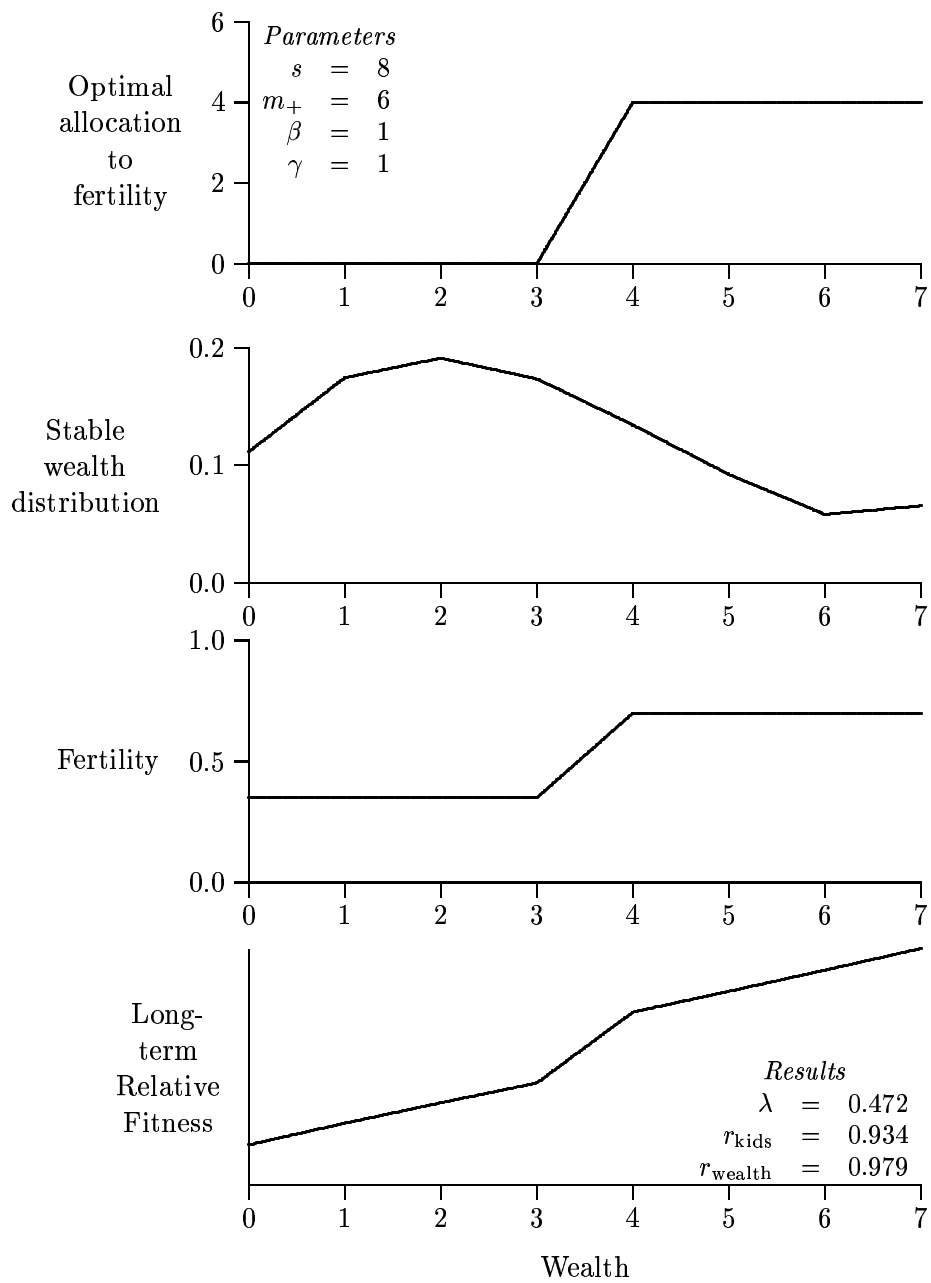Figure 3: An optimal strategy with $\gamma = 0$

Figure 4: An optimal strategy with $\gamma = 1$

stable wealth distributions in the two figures shows that at equilibrium, mean wealth is lower in the second. Thus, figure 4 appears to describe a harsher world than than in figure 3—an impression that is confirmed by the two values of λ. Note that $r_{\text{wealth}} > r_{\text{kids}}$ in the harsher environment, while the reverse is true in the milder environment. This pattern is consistent with that found under clonal inheritance in my earlier paper (Rogers, 1990) (see section 2).

But before reaching any conclusion, let us examine a wider range of parameter values. This is done in figure 5 for the case in which earned wealth is independent of that inherited ($\gamma = 0$).

The two perspective drawings in the figure show how r_{kids} and r_{wealth} vary over a wide range of value of s and β. In each drawing, the environment is harshest at the left corner, where the starvation threshold (s) is large and mean earned wealth (β) small. The environment improves as one moves from left to right, and is mildest in the right corner.

In my earlier paper, r_{kids} was near zero in harsh environments, near unity in mild ones, and undefined at the extreme right-hand corner of the drawing (Rogers, 1990, fig. 5). Here, in figure 5, the pattern is similar in that r_{kids} increases from left to right, but it is never as low as in the other analysis. Sexual reproduction seems to have greatly increased the correlation between fertility and long-term fitness. Thus, fertility is a much better proxy for fitness than the earlier study implied.

In the earlier paper, r_{wealth} was near unity in harsh environments, and decreased to low values in mild ones. Its pattern in figure 5 is quite different, having highest values in environments of intermediate quality. Thus, the conclusions of the previous paper do not hold when sexual reproduction is added to the model.

But as I suggested above, the original model was unrealistic in two important respects, and only one of these is corrected in figure 5. This figure, like my original analysis, assumes that earned and inherited wealth are independent. This second problem is corrected in figure 6, which assumes that the regression of earned on inherited wealth is $\gamma = 1$. This figure exhibits a pattern much like that of the original analysis. The correlation r_{kids} between fertility and fitness is highest in mild environments, while the correlation r_{wealth} between wealth and fitness is highest in harsh environments. Thus, harsh environments may in fact select for a material motivations, and mild environments for reproductive motivations.

But although the present analysis does confirm the pattern detected earlier, it has different implications concerning the magnitude of the correlations. This is seen most easily in figure 7. There, panel A graphs the
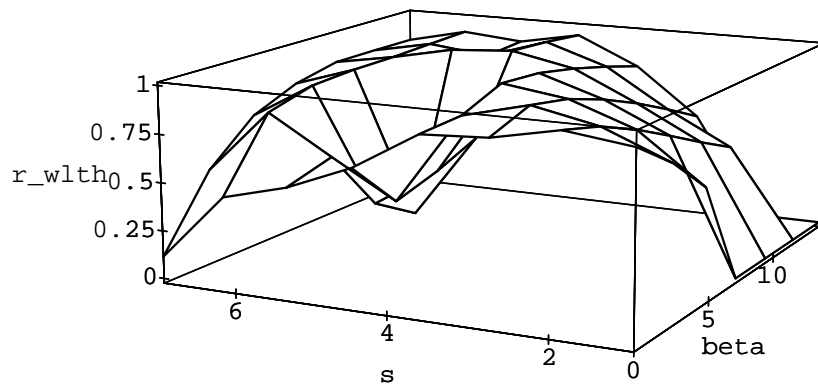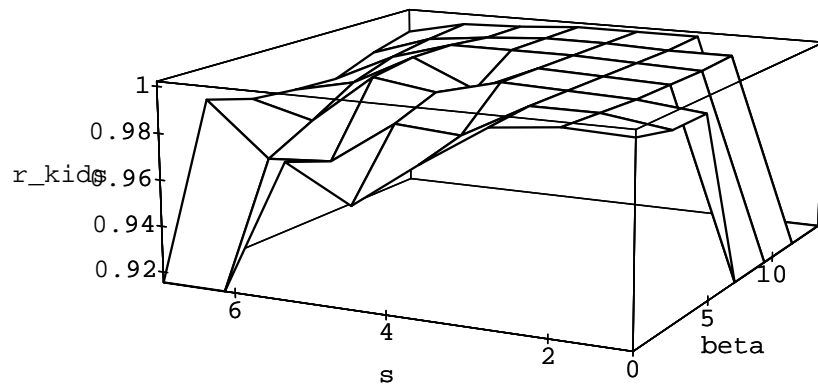
Figure 5: Response of r_{kids} and r_{wealth} to s and β
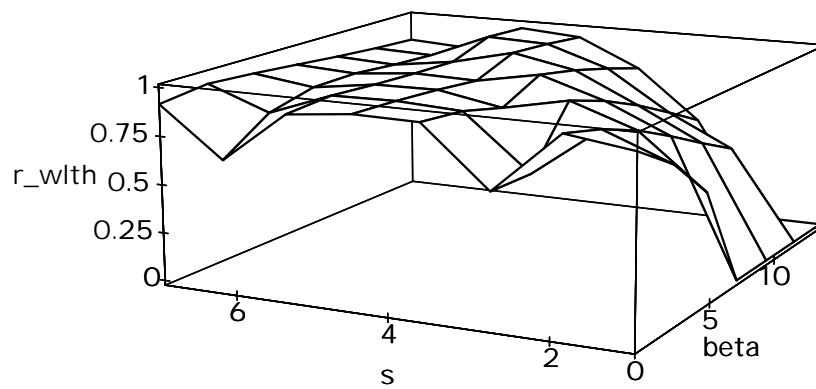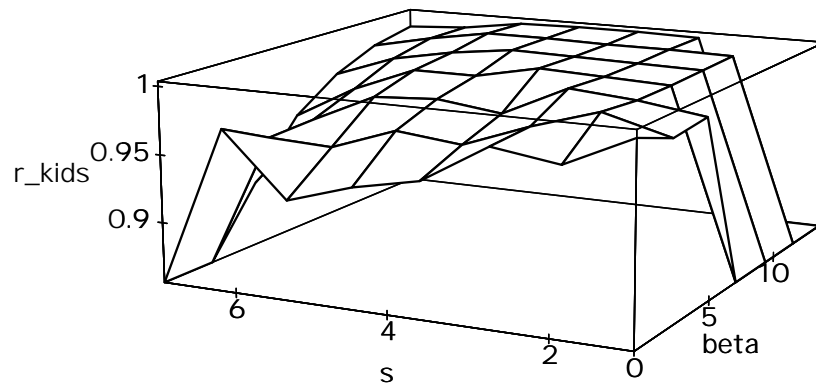Parameters: $m_+ = 6$, $\gamma = 0$.

Figure 6: Response of r_{kids} and r_{wealth} to s and β
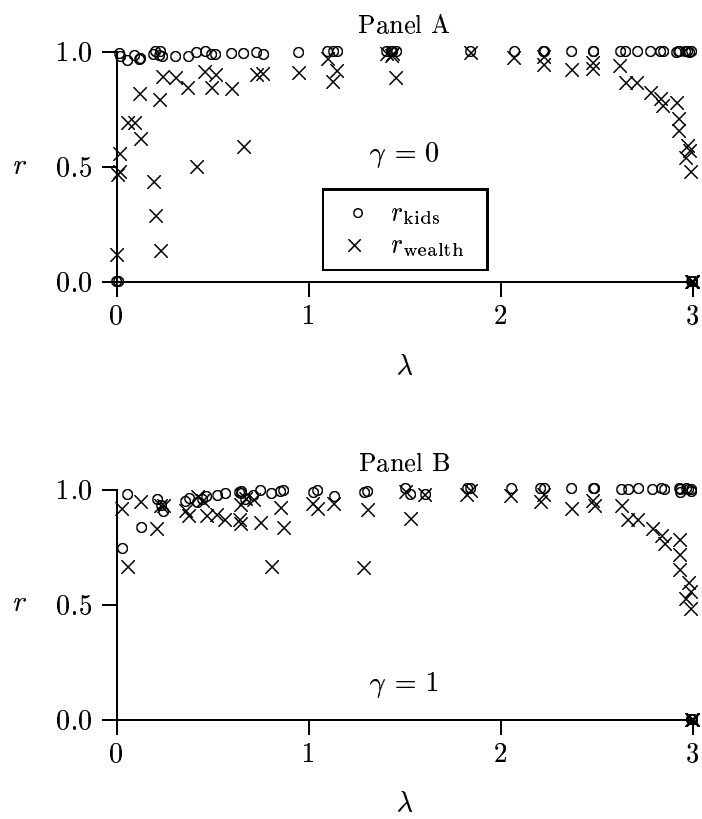Parameters: $m_+ = 6$, $\gamma = 1$.

Figure 7: r_{kids} and r_{wealth} against λ

correlations in figure 5 against λ, the ratio of increase, and panel B does the same for the correlations in figure 6. What is impressive about these correlations—especially those in panel B—is that most of them are very large. The range of λ here is unrealistic. We can safely ignore all but the region near $\lambda = 1$. In this region, both correlations are always large. Thus, the present model implies that fertility and wealth are *both* excellent proxies for fitness. In a world such as that described here, there is no reason to expect either kind of motivation to dominate.

6 Discussion

Modern economics recognizes a variety of motivations, including the desire for children (Becker, 1981). Nonetheless, many economic models accord primary importance to material motivations. For example, Friedman (1953, p.171) observes that the assumption of "single-minded pecuniary self-interest... works well in a wide variety of hypotheses in economics bearing on many of the mass phenomena with which economics deals." Both the intuitive appeal of this theory and its predictive success argue that material motivations are important. Yet it does not follow that their importance is paramount.

Human sociobiology would explain material motivations in terms of their effect on short-term reproductive success. Those who acquire more resources are able to devote more resources to producing offspring, and thus gain higher fitness. In this theory, material motivations are subordinate to reproductive ones. We desire material goods only in order to facilitate reproduction. Thus, we should not desire more resources than we can use for reproduction. The very wealthy should not desire additional wealth.

In this account, the theory of reproductive motivations is more general than that of material motivations, for it tells us when the latter theory will apply. Thus, the theory of reproductive motivations subsumes that of material motivations. The latter is a simplified approximation to the former, applicable only in a restricted set of circumstances.

But there is evidence contrary to this view. The very wealthy go on increasing their own wealth, in spite of the negligible effect this has on their own reproduction. Data from western countries often show a negative relationship between wealth and the fertility of females (Vining, 1986). This is easy to understand in a theory of material motivations, since the opportunity cost of child care is higher for the wealthy than for the poor. These data are, however, hard to reconcile with a theory that makes reproductive

motivations paramount. Similarly, the theory of reproductive motivations struggles with the "demographic transition," a historical decline in the fertility of developed countries. As productivity increased in these countries, the limits to fertility must have relaxed. Thus, a theory of reproductive motivations implies that fertility should rise with productivity, rather than falling as it did in fact. The theory of material motivations makes short work of this problem: The rising productivity of these countries would increase the opportunity cost of time devoted to child care, favoring a shift to smaller families.

The results presented here suggest a way to reconcile these data with the supposition that human motivations evolved by natural selection. In a world with heritable wealth, wealth has value over and above its effect on the number of one's offspring. By continuing to earn, a rich person can increase the wealth of descendants several generations removed. Thus, the marginal effect of wealth on fitness may remain positive even among the very wealthy. Furthermore, the model suggests that wealth and fertility may be of roughly equal value in estimating fitness. At evolutionary equilibrium, material and reproductive motivations should both be important. In such a world, material motivations would be in no sense subordinate to reproductive ones. Resources should be valued even when they have no immediate effect on reproduction.

Acknowledgements

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