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ECONOMICS

EVOLUTION, FERTILITY AND THE AGEING POPULATION

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DISCUSSION PAPER 13.02

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Abstract: We propose that the recent rise in the fertility rate in developed countries is the beginning of a broad-based increase in fertility towards above-replacement levels. Environmental shocks that reduced fertility over the past 200 years changed the composition of fertility-related traits in the population and temporarily raised fertility heritability. As those with higher fertility are selected for, the "high-fertility" genotypes are expected to come to dominate the population, causing the fertility rate to return to its pre-shock level. We show that even with relatively low levels of genetically based variation in fertility, there can be a rapid return to a high-fertility state, with recovery to above-replacement levels usually occurring within a few generations. In the longer term, this implies that the proportion of elderly in the population will be lower than projected, reducing the fiscal burden of ageing on developed world governments. However, the rise in the fertility rate increases the population size and proportion of dependent young, presenting other fiscal and policy challenges.

Key words: fertility, human evolution, ageing population, population growth

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1. Introduction

Demographic change is projected to present fiscal and economic challenges to governments in forthcoming decades, particularly in developed countries. Population ageing caused by reduced fertility and increasing life expectancy has been predicted to increase the demands placed on pension systems and aged-care services at a time when the relative tax base is forecast to be declining (for example, Lee & Mason (2011)). This twin assault on government finances has led developed world governments to expect deterioration in their fiscal positions.

While a range of assumptions underpins these projections, the focus of this paper is on the fertility rate, which is a key determinant of demographic developments over the longer term. Fertility has been declining in most developed countries since the demographic transition in the late nineteenth century. After the post-war baby boom in the 1950s and early 1960s, fertility continued to decline before rebounding slightly in recent years. The total fertility rate in developed countries dropped from 2.81 in 1950-55 to 1.56 in 1995-2000, before recovering to 1.66 in 2005-10 (United Nations 2011). The recent increase in fertility in developed countries does not depend on immigration. It is present in countries with few immigrants, such as Japan (United Nations 2011), and is typically exhibited amongst native born populations once immigration is excluded (for example, Tromans et al. (2009)). In view of the recent increase in fertility, many population forecasts have been revised but few project a return of fertility to the replacement level of about 2.1 children per woman. For example, the United Nations (2011) predicts that the fertility rate in developed countries will increase to 1.97 by 2045-50 in its medium fertility scenario.

Evolutionary biology suggests that fertility will bounce back after an environmental shock. Since the Industrial Revolution, shocks such as changes in income, contraception

and female roles have changed the composition of fertility-related traits under selection and temporarily raised the proportion of variability in fertility in the population that can be attributed to genetic variation. That is, the shocks have increased the heritability of fertility. Following the increase, the prevalence of fertility-related genes is subject to evolution by natural selection. Those genes associated with higher fertility have a selective advantage and thereby increase their frequency, which increases the fertility rate over time. Consequently, heritable traits and behaviours that lead individuals to have few or no children eventually disappear from the population.

Based on these insights from evolutionary biology, we propose that the recent rise in the fertility rate is the beginning of a broad-based increase in developed world fertility towards above-replacement levels. Using quantitative genetic models, we model the evolution of the fertility rate, population size and population structure following an environmental shock that reduces fertility. We show that even with relatively low levels of genetically based variation in fertility, there is a return to a high-fertility state, with recovery to above replacement levels usually occurring within a few generations.

Our hypothesis is relevant for the design of pension systems and aged care services. The postulated increase in fertility would reduce the fiscal burden to the extent that it reduces the proportion of elderly in the population. However, a rise in the fertility rate will also increase population growth and the proportion of dependent young, presenting new fiscal and economic policy challenges.

2. Heritability of fertility

Selection for high fertility requires variation in fertility in the population and a genetic basis for the intergenerational transmission genetic of this variation. Fisher's (1930)

fundamental theorem of natural selection states that the “rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time.” Fitness is defined as the average contribution of a genotype to the gene pool in the next generation. Fisher’s theorem implies that variation in traits in a population can only persist where they have a weak relationship with fitness. If there were a strong relationship with fitness, those traits associated with higher fitness would rapidly outcompete traits with lower fitness, resulting in the lower fitness traits being selected out of the population. This implication has often led researchers to assume that the heritability of fertility, a primary factor affecting fitness, would effectively be zero. Accordingly, any variation in fertility would be due to environment. Consistent with this, Murphy (1999) has shown that the relationship between the fertility of parents and children was close to zero in populations preceding the demographic transition in the nineteenth century.

However, as Fisher recognised, variation in traits that affect fitness may exist in the population for extended periods, particularly where there are large and continuous perturbations in the environment. Environmental change can alter the selective pressure upon a genotype. Neutral genes that were not under selection (or already in their steady-state equilibrium) may suddenly become decisive factors as to whether an organism survives or reproduces in the new environment. For example, an ancestral gene relating to salt retention had an allele (variant of a gene) in Africa that did not increase salt retention. When humans moved out of Africa into cooler latitudes where salt retention was costly, the previously neutral allele spread rapidly (Cochran & Harpending 2009; Thompson et al. 2004).

A range of environmental shocks may have affected the heritability of fertility. In the economic literature, examples of possible shocks include: increased entry of women

into the workforce (Becker 1960; Galor & Weil 1996); preference for decreased quantity and increased quality of children in response to increased income (Becker & Lewis 1974); substitution from quantity to quality of children in response to increased technological progress and changing returns to human capital (Galor & Weil 2000; Galor & Moav 2002); decreased child mortality (Preston 1978); and a series of contraceptive devices of increasing effectiveness and ease of use (Becker 1960). In this paper, we deal with a generic shock to fertility as for the purposes of our hypothesis it is sufficient that that variation in fertility is heritable after the decline.

There is substantial empirical evidence that the heritability of fertility has increased after the demographic transition. Fisher (1930) analysed the number of children by women as a function of the number of children born to their mothers. He found that a woman could expect 0.21 additional children for each additional child that her mother had and 0.11 additional children for each additional child that her grandmother had. Since the second-generation effect was one half of the first-generation effect, Fisher suggested that the correlation between mother and child must be almost exclusively due to "organic" inheritance. Using those estimates, he concluded that heritability of fertility at that time was 0.4 (40 per cent of the variation in fertility is explained by genetic factors).

Recent studies support the view that fertility has become heritable and is transmitted between generations. Murphy (1999) found that while the relationship of fertility between parents and children before the demographic transition are close to zero, they average around 0.2 in post-demographic transition societies, with the estimates increasing in recent periods. Rodgers et al. (2001a), who analysed data for Danish twins from the 1950s, attribute one quarter of the variation in fertility to genetic factors. In a review of recent literature, Rodgers et al. (2001b) concluded that "Fertility differentials

are genetically influenced, and at least part of the influence derives from behavioural precursors that are under volitional control, which are themselves genetically mediated."

Kohler et al. (1999) examined data obtained for Danish twins for the periods 1870 to 1910 and 1953 to 1964. Each period covers a time of substantial fertility decline, with the first period covering the demographic transition and the second the end of the baby boom. The heritability of fertility varied from close to zero in the pre-transition period to approximately 0.4 to 0.5 during the demographic transition, and it remained strong for the 1953 to 1964 cohort. The continuing high heritability of fertility is suggestive of multiple shocks or shocks hitting different groups within the population at different times.

Using a Danish database, Murphy and Knudsen (2002) found strong intergenerational correlation between fertility of parents and children. They observed that "Those from larger families not only provide a disproportionate contribution to the next generation, they also have an even greater impact on numbers of more distant kin. The 8.8 per cent of those born in 1968-69 who had four or more siblings accounted for 15.1 per cent of births to this cohort by the end of 1994".

3. Evolutionary dynamics

To be policy relevant, the selective effect on fertility related traits must be rapid enough to occur within relevant policy horizons. There is considerable evidence for rapid evolutionary change in human history. For example, the invention of agriculture has resulted in the spread of alleles related to lactose and gluten tolerance and malaria resistance (Voight et al. 2006). Genomic evidence also suggests that human evolution

has accelerated, with genomic surveys identifying significant genetic selection (Hawks et al. 2007).

Rapid genetic change is also evident following disease induced environmental shocks. For example, Stephens et al. (1998) noted that the increase in prevalence of the CCR5-Δ32 AIDS resistance gene from one in 10,000 of the population to one in 10 within 700 years (approximately 28 generations) required a selection coefficient[1] of 28 per cent (dominance) or 37 per cent (additive). They hypothesised that the gene provided a fitness advantage because it was also associated with resistance to the medieval plague. Similarly, Mead et al. (2009) found a rapid spread during the 20th century of an allele that provided immunity to kuru in Papua New Guinea, with selection coefficients generally around 30 per cent and as high as 64 per cent in some communities. Relating to fertility, Milot et al. (2011) observed that in a frontier French-Canadian population, the average age of first reproduction dropped from 26 to 22 over 140 years. As the trait of age of first reproduction is highly heritable, the reduction in age was evidence of selection acting on an existing trait.

Despite growing research into and evidence of the heritability of fertility, there has been limited research into its consequences. Fisher (1930) noted that a higher fertility genotype would eventually dominate the population if fertility had a heritability greater than zero. Based on a fertility ratio of two to one between the more and less fertile genotypes (which was in line with the data Fisher examined), he demonstrated that a population consisting of 97 per cent of the less fertile genotype and three per cent of the more fertile one would have equal prevalence of each within five generations.

[1] A selection coefficient measures the proportional amount that a phenotype is less fit than the phenotype with the highest fitness.

More recently, Foster (2000) proposed that the inherited “need to nurture” is sufficiently strong that the majority of women will want to bear at least one child. She concluded that has likely approached the limits of its decline. Murphy and Wang (2002) developed a model of population dynamics based on England and Wales between 1850 and 2050. Even with low intergenerational inheritance of fertility, the simulations reveal that the 2050 population would be 2.5 times larger than where there is no inheritance. The authors suggest that the heritability of fertility has played an important role in supporting developed world fertility rates, low as they are. Rowthorn (2011) showed that if religiosity is heritable (for which there is substantial evidence), the higher fertility of more religious individuals will cause the religiosity allele to spread in the population, thereby boosting fertility and population levels.

4. Three models of fertility

This section sets out three models of fertility: a diploid model, a model with varying heritability, and an age-structured haploid model. Humans are diploid; that is, they have two complete sets of chromosomes, one from each parent. In contrast, a haploid organism possesses only one set of chromosomes. Due to the simplicity of the first model, we model the human population as diploid organisms. However, the study of the evolution of social behaviour in humans is usually based on observable phenotypes (Grafen 1991). This allows abstraction from complications concerning genetic inheritance, such as diploid reproduction, multi-gene traits, interactions between genes and phenotypic expression. As a diploid approach is unwieldy in the third model, which focuses on age structure, we take a phenotypic approach in that model. Thus, the population is treated as haploid, with the allele for high or low fertility effectively a phenotypic character transmitted from parent to child. The second model, which

features varying heritability, does not distinguish between diploid and haploid organisms.

4.1. A diploid model of human fertility

The population consists of male and female agents who live for one period in which they pair and have children. The children, who inherit their genes from their parents, form the population in the next generation. There are equal numbers of males and females born in each generation.

Two alleles code for each trait; that is, agents are diploid. Female fertility is determined by the alleles at her fertility locus of her chromosomes, with two fertility-related alleles present in the population representing high and low fertility ($i = H, L$). This results in three potential genotypes: *HH*, *HL* and *LL*. Each child receives one allele from each parent, with the particular allele from each parent contributed with a 50 per cent probability. The genotype of the male does not influence the fertility of his female partner, but may influence the genotype of his children.

A single environmental fertility shock takes place at time t_0. Before t_0, all female genotypes have the same phenotypic fertility, with n^{ii} being the number of children born by females of genotype *ii*. As fertility is perfectly correlated with fitness in this model, each genotype has the same fitness before t_0 and any change in prevalence of the fertility alleles would be the result of random sampling between generations.

$$n_t^{HH} = n_t^{HL} = n_t^{LL} \qquad \forall t < t_0 \tag{1}$$

Following the fertility shock, the fertility rate of genotype *LL* decreases, while the fertility of genotype *HH*, who are immune to the shock, is unchanged. The fertility of

the heterozygote genotype *HL* is dependent on which allele is dominant. The fertility of each genotype following the shock is:

$$\begin{aligned} n_t^{LL} &= (1-s)n_t^{HH} \qquad 0 \le s \le 1 \\ n_t^{HL} &= (1-hs)n_t^{HH} \qquad h \in 0,1 \end{aligned} \qquad \forall t \ge t_0 \tag{2}$$

The selection coefficient *s* indicates the proportional reduction in fertility (and fitness) for genotype *LL* that is caused by the shock. The dominance coefficient *h* indicates the relative fertility of the female heterozygote. The high-fertility *H* allele is dominant and the low-fertility *L* allele recessive when $h = 0$, and vice versa when $h = 1$. This gives the following fertility relation, where at least one of the inequalities is a strict inequality:

$$n_t^{HH} \ge n_t^{HL} \ge n_t^{LL} \qquad \forall t \ge t_0 \tag{3}$$

The frequency of each allele is represented by π_t^i. As each person has two alleles, the proportion of each of the three genotypes in the population, π_t^{ii}, is a function of the prevalence of the allele.[2] The proportion of each genotype in generation *t* is:

$$\pi_t^{\bar{i}\bar{i}} = \frac{X_t^{\bar{i}\bar{i}}}{X_t} \tag{4}$$

X_t is the total population and X_t^{ii} is the population of each genotype.

If there is random mating, the number of each genotype in generation $t + 1$ is:

$$X_{t+1}^{HH} = \frac{1}{2}\left(\left(\pi_t^{HH}\right)^2 n^{HH} + \pi_t^{HH}\pi_t^{HL}\left(\frac{n^{HH}+n^{HL}}{2}\right) + \frac{1}{4}\left(\pi_t^{HL}\right)^2 n^{HL} \right) X_t \tag{5}$$

[2] As there is selection occurring, these are not in the Hardy-Weinberg frequencies, although they are a close approximation. The Hardy-Weinberg equilibrium involves constant allele and genotype frequencies:

$$\pi^{HH} = \left(\pi^H\right)^2 \qquad \pi^{HL} = \pi^H\left(1-\pi^H\right) \qquad \pi^{LL} = \left(1-\pi^H\right)^2$$

$$X_{t+1}^{HL} = \frac{1}{2}\left(\pi_t^{HH}\pi_t^{HL}\left(\frac{n^{HH}+n^{HL}}{2}\right) + \pi_t^{HL}\pi_t^{LL}\left(\frac{n^{HH}+n^{LL}}{2}\right) + \frac{1}{2}\left(\pi_t^{HL}\right)^2 n^{HL} + 2\pi_t^{HH}\pi_t^{LL}\left(\frac{n^{HH}+n^{LL}}{2}\right)\right) X_t \quad (6)$$

$$X_{t+1}^{LL} = \frac{1}{2}\left(\left(\pi_t^{LL}\right)^2 n^{LL} + \pi_t^{HL}\pi_t^{LL}\left(\frac{n^{HL}+n^{LL}}{2}\right) + \frac{1}{4}\left(\pi_t^{HL}\right)^2 n_t^{HL}\right) X_t \quad (7)$$

For any selection coefficient greater than zero, the frequency of the high-fertility allele and high-fertility phenotypes will increase. This is the case both when the high-fertility allele is recessive and dominant. Further detail on the rate of increase is provided in Appendix B.

To provide an illustration of the speed of the return to a high-fertility state, we conducted simulations with a population with an initial total fertility rate of 3.6, falling to 1.8 after a fertility shock. These fertility rates approximate the baby boom peaks and fertility rate lows experienced in Australia and the United States before the recent rebound in fertility (United Nations 2011). The fertility rate of the high-fertility phenotype is unaffected by the shock, whereas the fertility rate of the low-fertility phenotype is determined by the selection coefficient *s*. The selection coefficient is chosen so that total fertility rate equals 1.8 immediately after the shock. Simulations were conducted for different initial values for the prevalence of the high-fertility phenotype of between one and 40 per cent of the population (see Table 1 in Appendix A).

When the high-fertility allele is dominant, the high-fertility phenotype (genotypes *HH* and *HL*) quickly dominates the population and the total fertility rate rapidly returns to pre-shock levels (Figure 1). The long-run total fertility rate does not depend on the size of the fertility shock because the low-fertility allele is always selected out of the

population. The speed of the return to the pre-shock total fertility rate, however, depends on the initial prevalence of the high-fertility phenotype. If the high-fertility phenotype forms only one per cent of the population, fertility increase to above replacement within seven generations and it takes more than 20 generations until fertility returns to previous levels. If it comprises 40 per cent of the population, the first generation following the shock has fertility above replacement and total fertility approaches previous levels within 10 generations.

Figure 1: Total fertility rate with dominant high-fertility allele

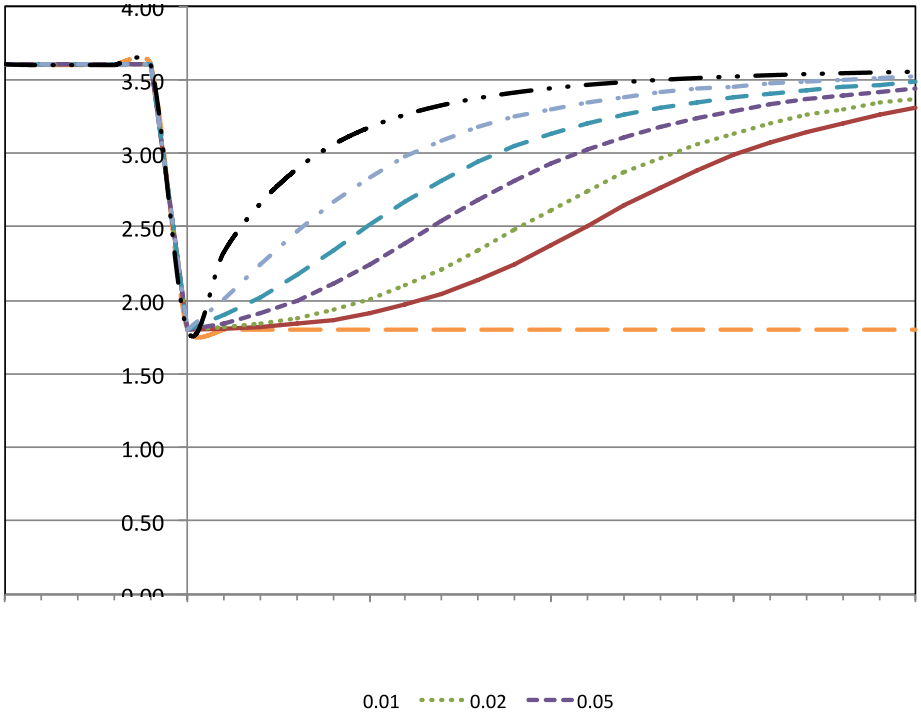
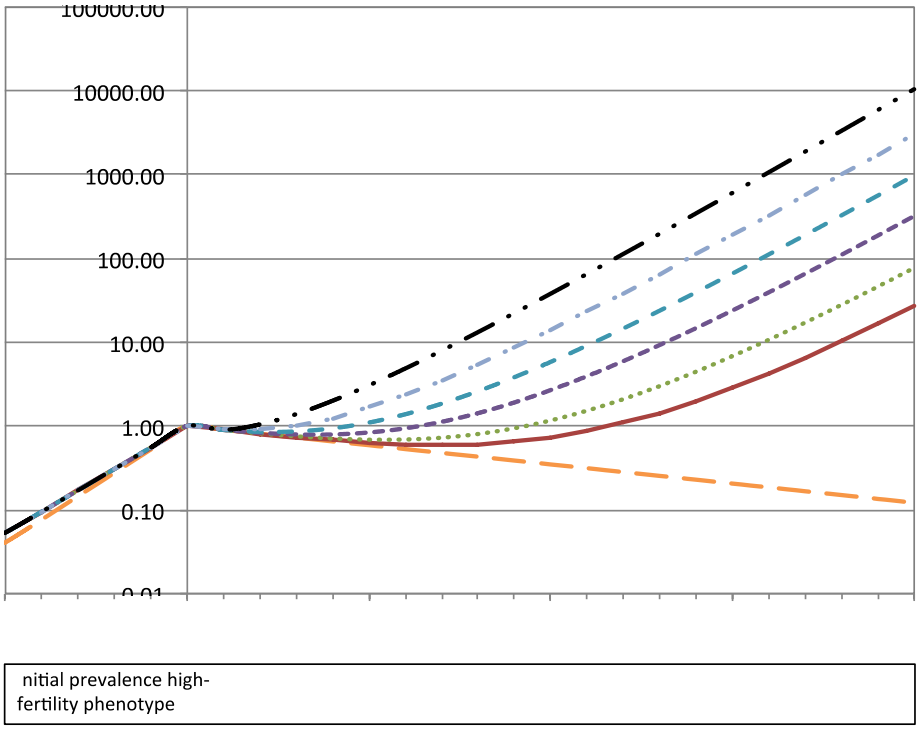


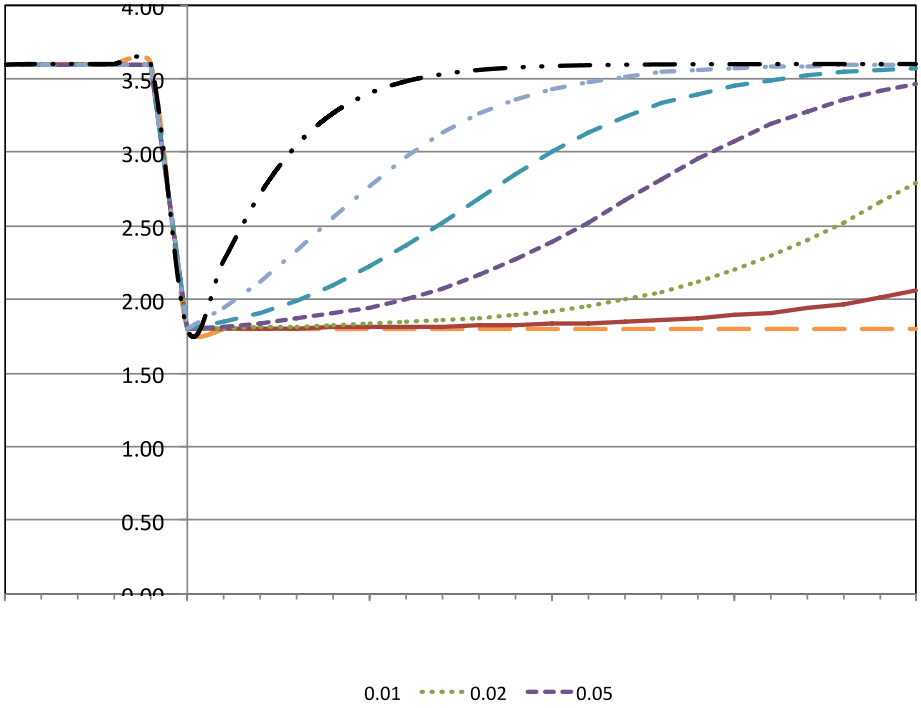
Figure 2 shows that selection for the high-fertility phenotype is important for population projections. Whatever the initial prevalence of the high-fertility phenotype, the population after 20 generations is orders of magnitude higher than if the total fertility rate remained at 1.8. In the case of an initial one per cent prevalence of the high-fertility phenotype, the population is over double that of the constant fertility case after 10 generations, while for higher initial prevalence the population is an order of magnitude or more higher.

Figure 2: Population with dominant high-fertility allele



Where the high-fertility allele is recessive, there is greater variation in the rate of increase in the fertility rate after the shock than in the dominant case (Figure 3). If the high-fertility phenotype (genotype *HH*) forms only one per cent of the population, it takes 19 generations until the fertility rate increases above replacement and many more generations until the old fertility rate is restored. If the high-fertility phenotype comprises 40 per cent of the population, the first generation following the shock has fertility above replacement and the total fertility rate approaches previous levels within six generations.

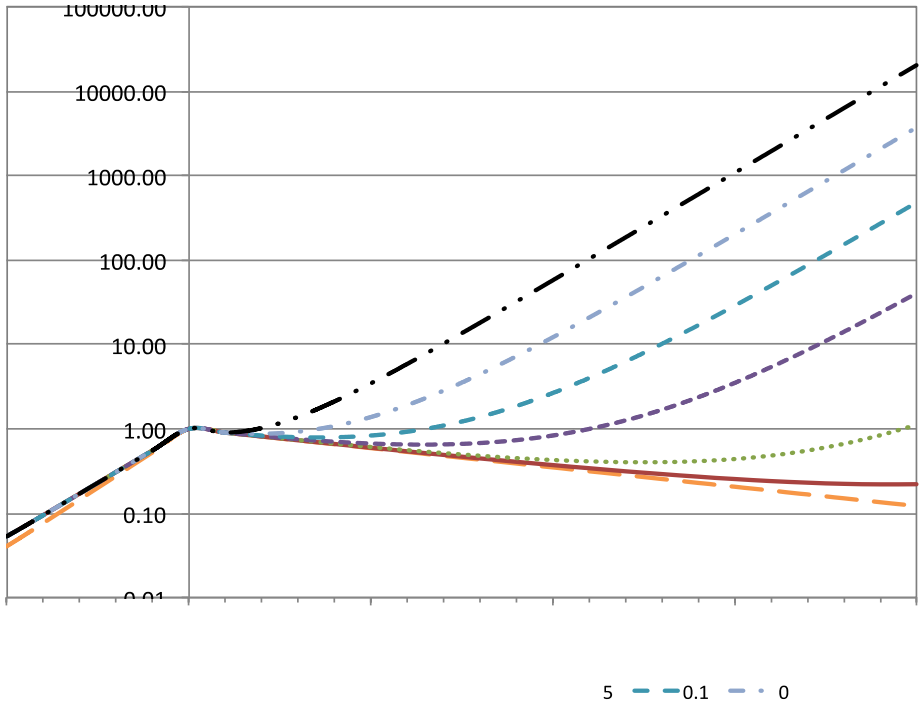
Figure 3: Total fertility rate with recessive high-fertility allele



The greater range of change in fertility in the case of the recessive allele is due to the greater range of frequency of the high-fertility allele implied by the initial phenotype frequencies. In the dominant case, the frequency of the high-fertility allele ranges from 0.5 per cent to 22 per cent as the high-fertility phenotype changes from one per cent to 40 per cent of the population. When the high-fertility allele is recessive, the frequency of the high-fertility allele ranges from 10 per cent to 63 per cent for similar high-fertility phenotype prevalence. Further detail on the rates of change for the recessive and dominant cases is provided in Appendix B.

The population growth in each scenario also varies more when the high-fertility allele is recessive than when it is dominant (Figure 4). If less than five per cent of the starting population is the high-fertility phenotype, it takes 12 or more generations before the population passes its initial level, although by this time the population is over four times that of a case with no variation in fertility.

Figure 4: Population with recessive high-fertility allele



Finally, it is unlikely that the high populations as shown in some scenarios in Figures 2 and 4 would be realised in full without interruption. Other shocks, possibly related to hitting Malthusian limits, would be expected to restrict fertility and total population growth. That said, the current world population is many times larger than would have been thought possible in Malthus's day. This observation is also relevant to the models described below.

4.2. A model of heritability of fertility

In the previous model children fully inherit fertility from their parents. This contrasts with the observation that heritability of fertility is below one and is often measured at around 0.2 to 0.4 in modern populations. In this section, we present a model of family size in which we vary the heritability of fertility.

The population is composed of male and female agents who are paired into families.[3] In each generation, the female gives birth to zero, one or more children. The frequency of the number of children is given by a binomial distribution, with conditional mean μ_t and variance σ_t^2. The maximum number of children (n) is set at 10. This approximates Hutterite fertility, which is considered a good example of an unrestricted fertility rate (Clark 2007). The frequency of families with i children at generation t, f_t^i, is given by:

$$f_t^i = \frac{n!}{i!(n-i)!}\left(p_t\right)^i\left(1-p_t\right)^i \qquad (8)$$
$$\mu_t = np_t \qquad \sigma_t^2 = np_t\left(1-p_t\right)$$

Given a mean μ_t and n = 10, these equations determine the probability p_t, the variance σ_t^2 and f_t^i.

The mean number of children that a child has in their family is greater than the mean number of children in each family as there are more children in the larger families. The proportion of children who are in a family with i children, π_t^i, is:

$$\pi_t^i = \frac{if_t^i}{\mu_t} \qquad (9)$$

The mean number of children that each child has in the family to which it was born is:

$$c_t = \sum_{i=0}^{n} i\pi_t^i \qquad (10)$$

Equation (10) determines the family size if fertility is completely heritable. If each child born in generation t had the same number of children as their parents, the population in generation t + 1 would have a mean of c_t children in each family. This would represent

[3] Whether agents are haploid or diploid does not affect this model.

an increase in the mean number of children born to each family as those from larger families come to form a larger part of the population.

If fertility is not fully heritable, the increase in family size can be modelled using the breeder's equation, which provides an estimate of the evolutionary change in a phenotypic trait under selection (Lush 1937). Under the breeder's equation, the change in the mean family size from one generation to the next is proportional to the selection differential and the narrow sense heritability of fertility (h^2). The selection differential is the difference between the mean fertility of the parents (μ_t) and the mean number of children that each child has in their family (c_t),

$$\Delta \mu_t = h^2 \left(c_t - \mu_t \right) \tag{11}$$

$$\mu_{t+1} = \mu_t + h^2 \left(c_t - \mu_t \right) \tag{12}$$

Using these equations, we can calculate the effects of different heritability levels on the rate of change in population fertility, where the mean number of children per family is equal to the total fertility rate. Iterating forward, the new mean number of children as calculated by equation (12) is input into equation (8) to give the family structure of the new generation.

Figure 5 shows the results of a simulation with initial mean family size of 1.8 (which is effectively the total fertility rate). Even at relatively low heritability, the increase in fertility is rapid. For a heritability of 0.2, the fertility is above replacement within two generations. As fertility is constrained by an upper bound of 10 children per family, fertility and population projections are higher than for the diploid model presented earlier in this paper where fertility is effectively constrained at 3.6. Population growth is

also rapid in all scenarios of heritability (Figure 6). This model indicates that increases in fertility may still be relatively rapid, even where heritability of fertility is below one.

Figure 5: Total fertility rate with varying heritability

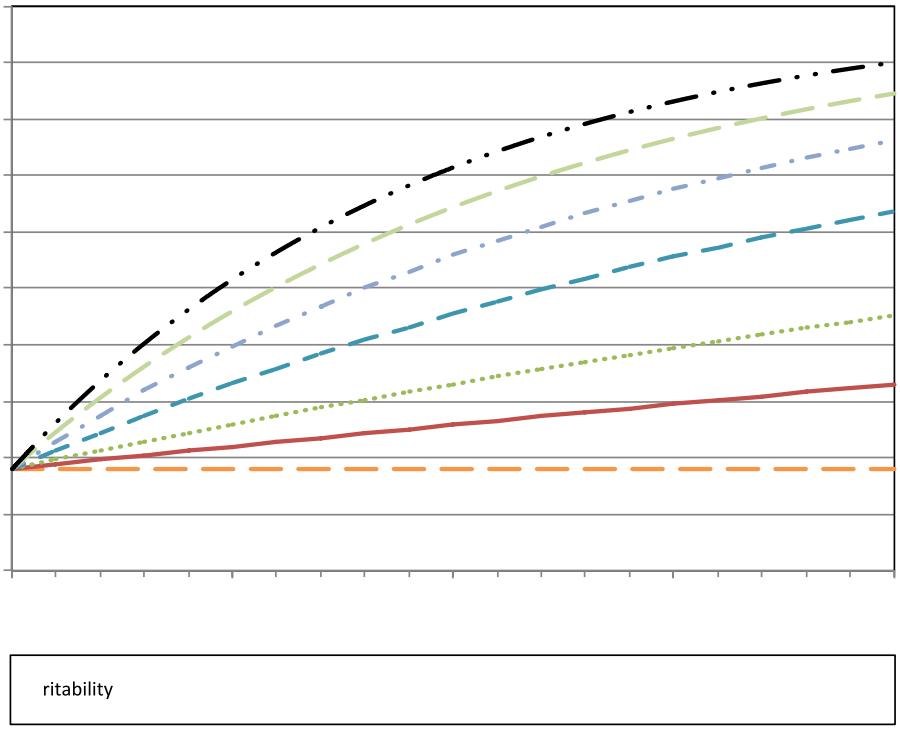
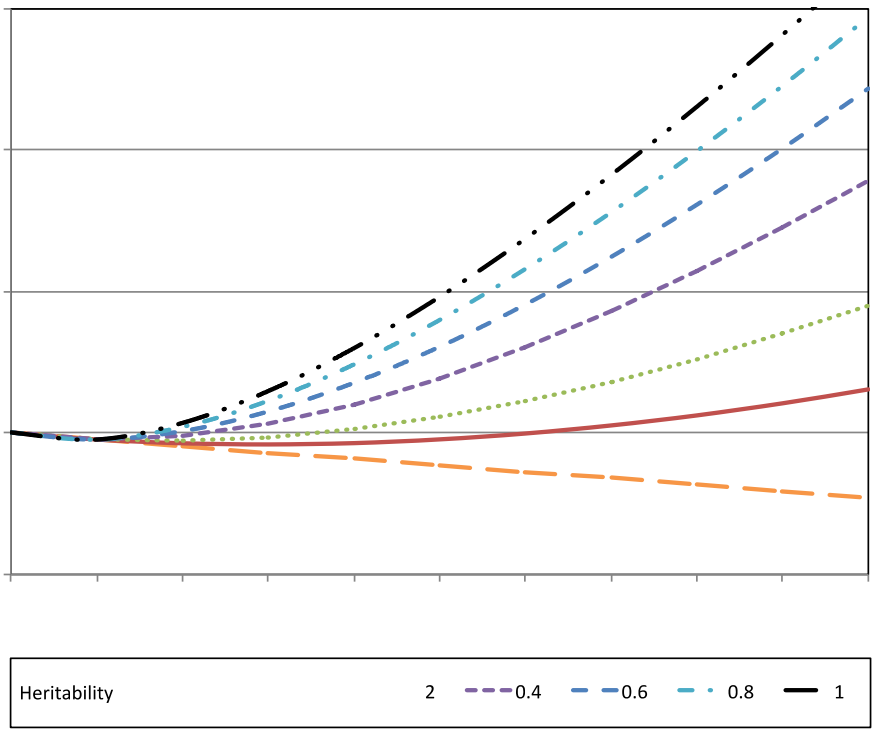


Figure 6: Population with varying heritability



4.3. A haploid age-structured model

Many of the economic challenges arising from low fertility rates pertain to the age structure of the population, rather than the fertility rate in itself. In this section, we present an age-structured model that shows how the age structure affects the short-run dynamics.

The population in the age-structured model is composed of haploid male and female agents, who are grouped into five-year age cohorts. In each five-year period, females bear children, with equal numbers of males and females born each generation. Children born in one five-year period become the population of 0 to 4 year olds in the next five-year period. Agents also have a probability of death, which does not vary between males and females and remains constant through time. The average fertility rate for each age cohort in period t_0 and the death rate approximate those in a modern, industrialised economy. The population structure in period t_0 is similar to that in United States and Australia in 1960 following the baby boom, giving a starting point that now lies 50 years in the past. The fertility rates, death rates and initial population structure are shown in Table 2 in Appendix A.

The fertility of a female is determined by a single allele at her fertility locus. Two alleles determine fertility, with these alleles representing high and low fertility respectively ($i = H, L$). The allele inherited by the child may come from either parent, with a 50 per cent probability for each.

A single environmental fertility shock takes place at t_0. Each genotype has a different response to the shock, with $n^{i\tau}$ being the number of children born by females of genotype i for age cohort τ. The selection coefficient s, which is the same for each age cohort, indicates the relative response of the different genotypes to the fertility shock.

$$n_t^{L\tau} = \left(1-s\right) n_t^{H\tau} \qquad 0 \le s \le 1 \qquad \forall t \ge t_0 \tag{13}$$

The population proportion of genotype *i*, belonging to age cohort τ, is:

$$\pi_t^{i\tau} = \frac{X_t^{i\tau}}{X_t} \tag{14}$$

X_t is the total population and $X_t^{i\tau}$ is the population of genotype *i* in age cohort τ.

The number of children of each genotype in generation $t + 5$ is:

$$X_{t+5}^{i(0-4)} = \frac{1}{2} X_t \sum_{\tau=0-4}^{100+} \pi_t^{i\tau} n^{i\tau} \tag{15}$$

The total fertility rate at time *t* is:

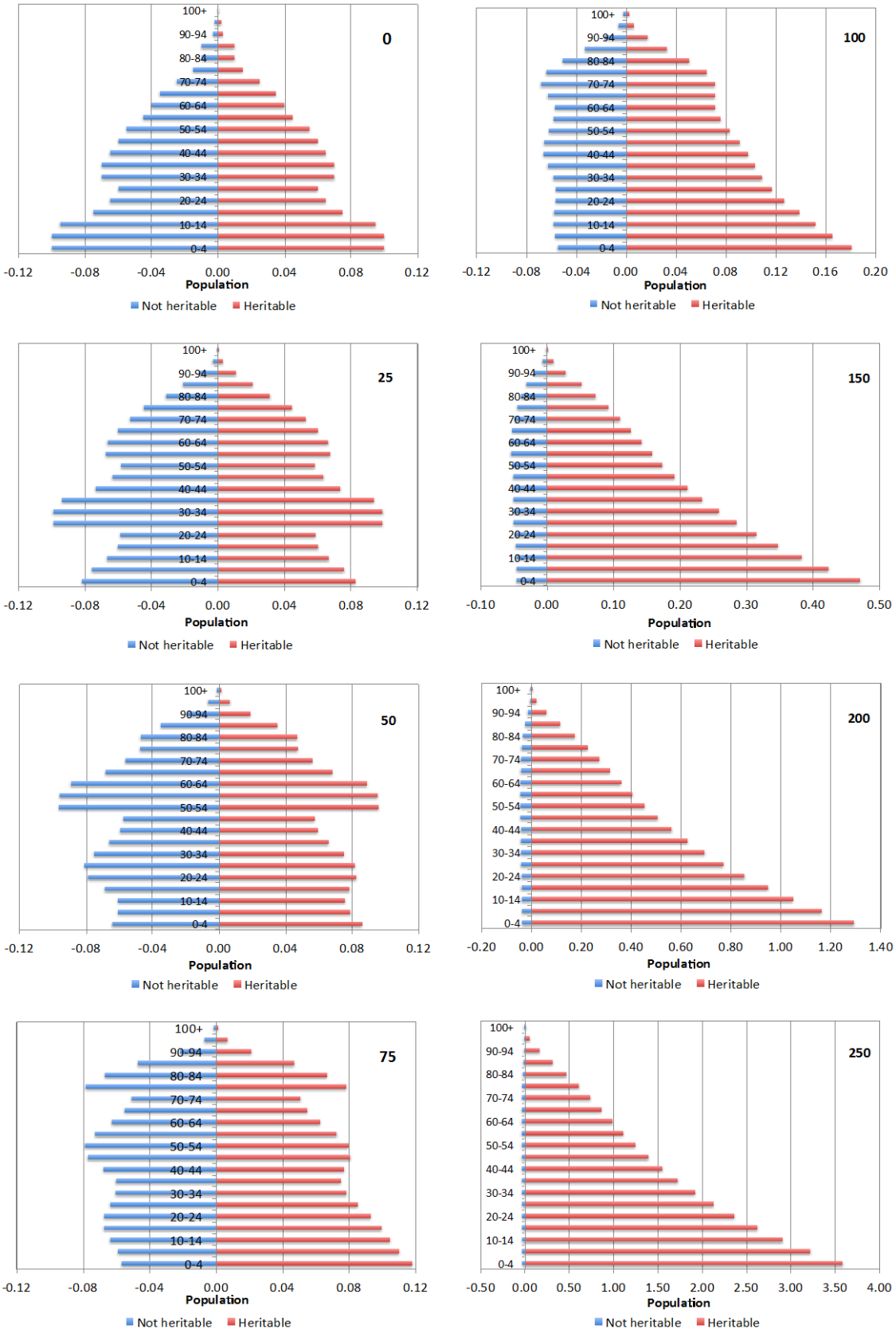
$$n_t = \sum_{\tau=0-4}^{100+} \frac{X_t^{H\tau} n^{H\tau} + X_t^{L\tau} n^{L\tau}}{X_t^{H\tau} + X_t^{L\tau}} \tag{16}$$

As a numerical example, we ran a simulation where the initial total fertility rate is 1.8, the high-fertility genotype initially comprises 20 per cent of the population and the ratio of fertility between the high and low-fertility genotypes is 3.0 (i.e. $s = 0.66$) after a fertility shock. This implies fertility rates of approximately 1.3 and 3.9 for the low and high-fertility genotypes.

Figure 7 shows the age structure of the population over a 250-year period, moving first 25 years from one panel to the next and then 50 years. The red bars show the simulated age-structure of the population, while the blue bars represent a scenario where there is no heritable variation in fertility. After 50 years, the cohort of children is substantially larger if fertility is heritable and after 75 years there is a much larger workforce. The cohort of children continues to increase, approaching a maximum proportion of the

population by year 150. By year 100, the population structure with heritable fertility and the scenario in which fertility is not heritable do not resemble each other.

Figure 7: Population age structure with fertility ratio of 3.0



The dependency ratio for children aged 0 to 14 initially falls, remains low until year 45 and then increases to 32 per cent, while the dependency ratio of those aged over 65 increases for the first 65 years to a peak of 26 per cent and then falls to 11 per cent (Figure 8). The net result of these two effects is a relatively stable but high total dependency ratio of 43 per cent. This contrasts with a long-run dependency ratio of 15 per cent for the young and 28 per cent for the elderly if fertility is not heritable, with a simular total dependency ratio of 43 per cent (Figure 9). This pattern holds for other fertility ratios, with the total dependency ratio approaching 43 per cent but the proportion of young increasing as the fertility ratio increases. Accordingly, the nature of the budget pressures and policy challenges would be different despite similar total dependency ratios. This finding is consistent with other analyses of increases in the fertility rate (for example, Lattimore & Pobke (2008)).

Figure 8: Dependency ratio with fertility ratio of 3.0

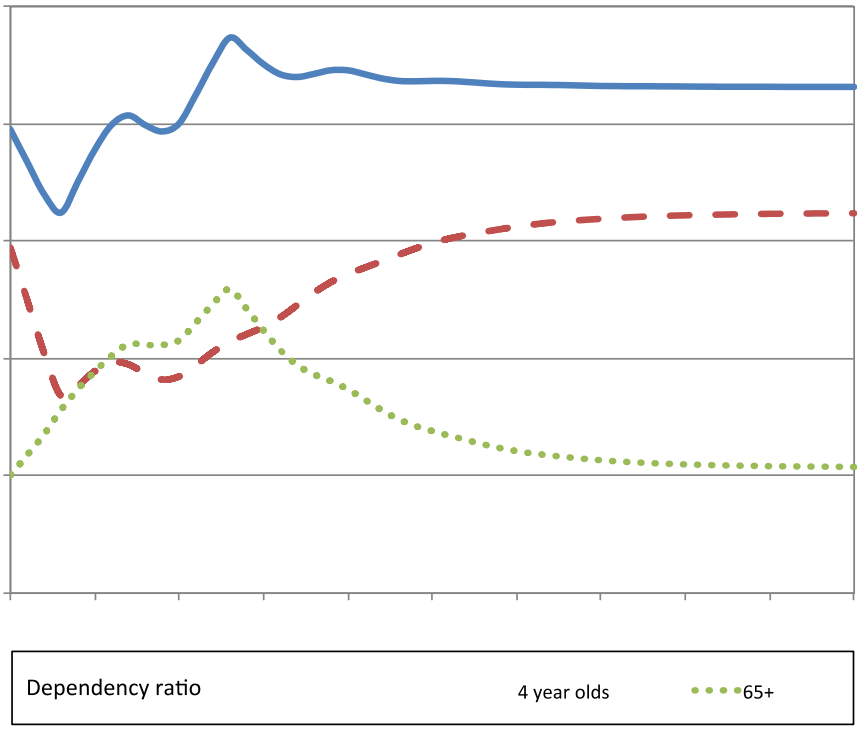


Figure 9: Dependency ratio with no heritability of fertility

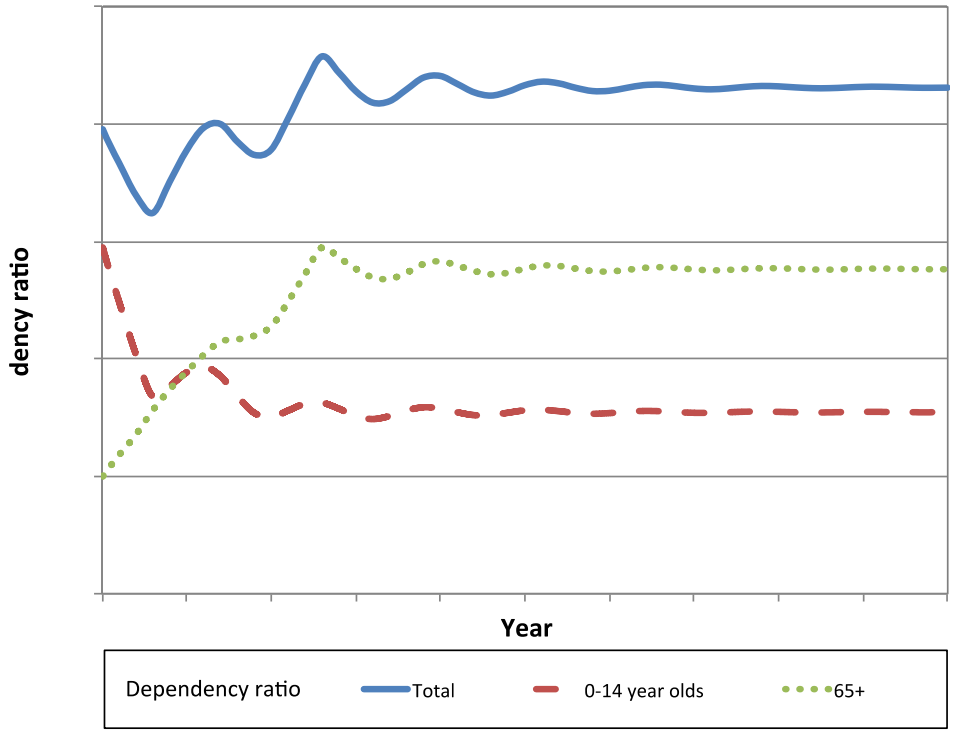


Figure 10 shows the steady increase in the total fertility rate over the 250 years from the start of the simulation. The fertility rate for three other simulations with a fertility ratio of 1.5, 2.0 and 4.0 is also shown. In the 3.0 ratio case, the fertility rate surges above replacement within 30 years and is above three within 75 years. Where the fertility ratio is 1.5, fertility increases above replacement after 100 years from the shock.

Figure 10: Total fertility rate

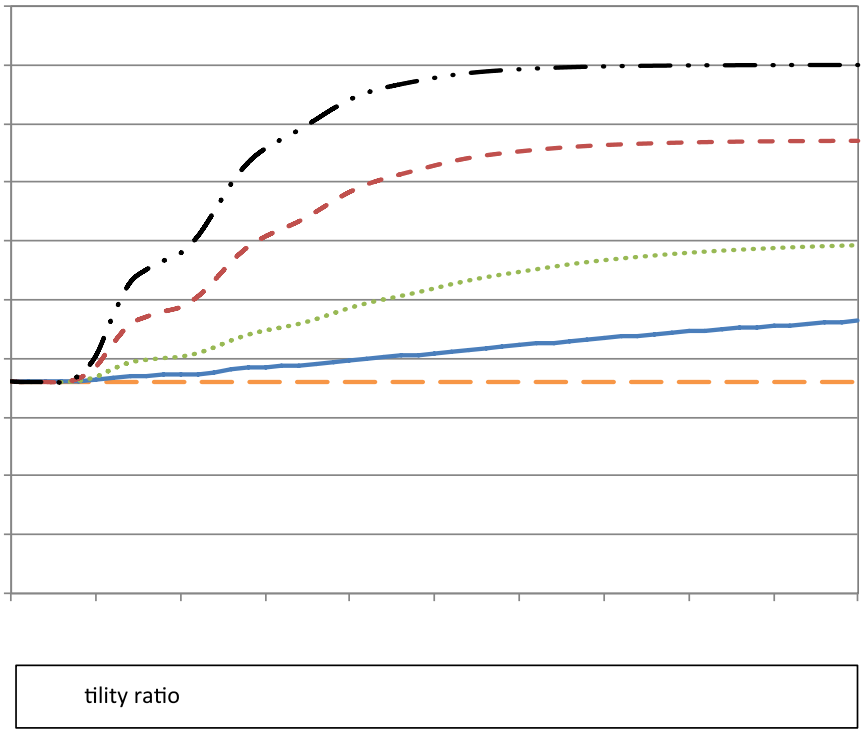
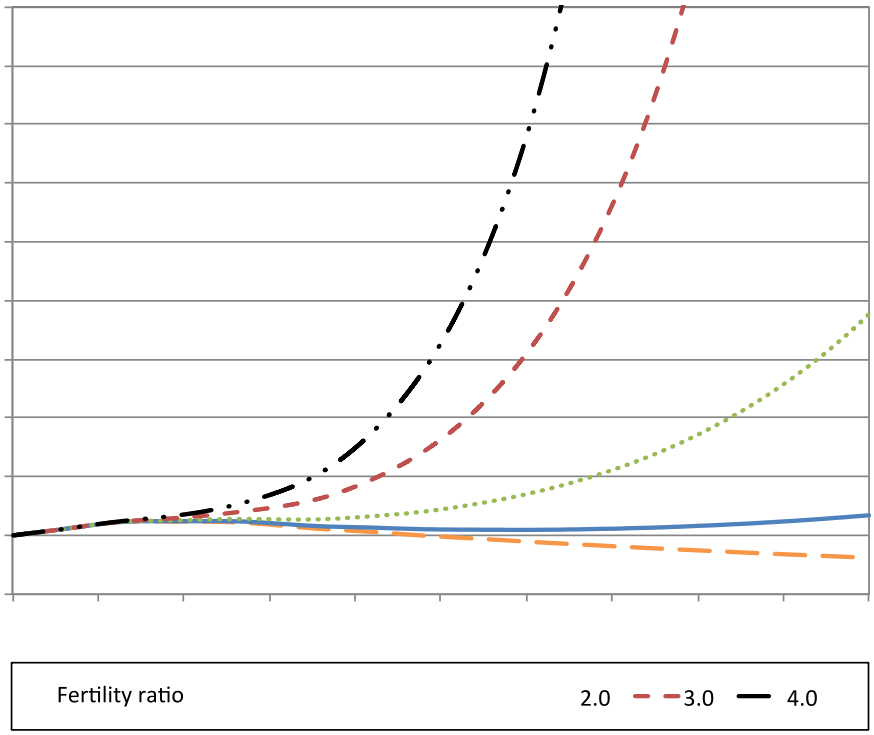


Figure 11 shows that the population response is similarly rapid, increasing monotonically and doubling within 110 years with a 3.0 fertility ratio, rather than declining steadily from year 30 when fertility is not heritable. The population for three other simulations with a fertility ratio of 1.5, 2.0 and 4.0 is also shown.

Figure 11: Population



In these age-structured model simulations with heritable fertility, there is a lag before there is a noticeable change in the age structure of the population. At best, it takes two to three generations before the high-fertility genotype has materially boosted the working population. Whether there will be any amelioration of the issues created by an ageing population over the next 50 years depends on the biological parameters and whether there have been subsequent shocks to fertility. The use of haploid agents and perfect heritability in the age-structured model is likely to increase the rate of spread of the high-fertility allele relative to a diploid model or model with heritability of less than one, but other assumptions lower the rate of change, particularly the restricted variation in family size.

5. Discussion

Most current population projections implicitly assume that the fertility rate is at, or close to, a steady state and fertility shocks are essentially modelled as permanent shocks

(for example, see Lee and Tuljapurkar's (2001) analysis of United States Census Bureau forecasts). For some genotypes a representation that the shock is permanent may be accurate, since certain genotypes may have experienced permanent fertility reductions following the recent changes in the human environment. However, heritable variation in fertility-related traits favours those genotypes with the greatest immunity to the shock, thereby raising the total fertility rate. This result holds in all three models presented in this paper; only the timing of the recovery in fertility is in serious question.

One factor that affects the timing of the recovery in fertility is the nature of the environmental shock. The models in this paper are premised on a one-off negative fertility shock, whereas the historical pattern of decline in fertility is more consistent with multiple shocks, striking different population subgroups at different times. For example, the demographic transition in England occurred first among high-income families, before spreading to the broader population (Clark & Cummins 2010). The persistence of fertility heritability and the failure of the fertility rate to recover is evidence that multiple negative shocks have delayed a return to steady state in the past. The projected recovery in fertility does not, however, require an absence of further environmental change. Even with more environmental shocks, fertility will recover if the population response is small, which may be the case if humans are becoming better adapted to the types of environmental shocks generated by modern living.

Myrskyla et al. (2009) related the increase in fertility to increases in the human development index (HDI), published by the United Nations Development Programme. They proposed that increasing development above a certain level reverses the well-established negative relationship between development and fertility and noted that the recovery in fertility could ameliorate projected socioeconomic challenges. The hypothesis presented in this paper is not inconsistent with their observation, as the HDI

tends to exceed the threshold level in those countries that have been developed for longer and experienced the associated fertility shocks earlier. The earlier that a country experiences a fertility shock, the sooner those immune to the shock will increase in prevalence in the population and drive increases in the total fertility rate.

Other proposed explanations of recent fertility increases, including government policies (for example, Milligan (2005) and Lalive and Zweimüller (2009)), may also be consistent with our models. Government policies may accelerate or mitigate the selection of high fertility genotypes because different genotypes may respond differently to government incentives. In that sense, policy changes are a further environmental shock.

Another factor influencing fertility is the effect of immigration and immigration policy. Migrants tend to increase the total fertility rate in the short-run through their higher fertility levels. However, while their fertility may initially be higher, their fertility may be lower than that of the host population in the long-run if they are less adapted to the new environment, which would make them more susceptible to the environmental fertility shocks of the host country.

For all these reasons, it is possible that the return to a replacement-level fertility rate will not occur as rapidly as we expect. However, even where our predictions prove to be incorrect, our models provide a theoretical framework for thinking about fertility projections and their policy implications. Focusing on the heritability of fertility, our models suggest a biological mechanism by which fertility will recover after a shock. By ignoring the evolutionary underpinnings of fertility, demographers and policy makers risk underestimating future fertility rates and population growth. As a result, governments may prepare for challenges different from those that their populations will actually face.

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Appendix A: Model parameters

Table 1: Diploid model phenotype fertility

Initial frequency high-fertility phenotype	Implied fertility low-fertility phenotype
0	1.80
0.01	1.78
0.02	1.76
0.05	1.71
0.10	1.60
0.20	1.35
0.40	0.60

Table 2: Age-structured model population parameters

Age cohort (τ)	Fertility rate at t_0	Death rate	Population at t_0
0-4	0	0.005	0.10
5-9	0	0.0005	0.10
10-14	0	0.0005	0.095
15-19	0.1	0.002	0.075
20-24	0.3	0.002	0.065
25-29	0.6	0.003	0.060
30-34	0.5	0.004	0.070
35-39	0.2	0.005	0.070
40-44	0.1	0.006	0.065
45-49	0	0.01	0.060
50-54	0	0.01	0.055
55-59	0	0.02	0.045
60-64	0	0.03	0.040
65-69	0	0.05	0.035
70-74	0	0.1	0.025
75-79	0	0.15	0.015
80-84	0	0.25	0.010
85-89	0	0.4	0.010
90-94	0	0.6	0.003
95-99	0	0.8	0.002
100+	0	1	0
Total	1.8		1

Appendix B: Selection pressure

The rate of change in frequency of the high-fertility allele varies by the fertility of the heterozygote phenotype, which has one of each allele. If the ratio of fertility between the high-fertility homozygote (*HH*), heterozygote (*HL*) and low-fertility homozygote (*LL*) is 1:(1—*hs*):(1—*s*), the rate of change of the high-fertility allele is:

$$\Delta\pi_t^H = \frac{s\pi_t^H\left(1-\pi_t^H\right)\left(1-\pi_t^H+h\left(2\pi_t^H-1\right)\right)}{1-s\left(1-\pi_t^H\right)+s\pi_t^H\left(1-2h\right)\left(1-\pi_t^H\right)} \tag{17}$$

s is the selection coefficient, while *h* is the degree of dominance of the high-fertility allele.

Where the high-fertility allele is dominant, the heterozygote has the same fertility as the high-fertility homozygote. Equation (17) simplifies to:

$$\Delta\pi_t^H = \frac{s\pi_t^H\left(1-\pi_t^H\right)^2}{1-s\left(1-\pi_t^H\right)^2} \tag{18}$$

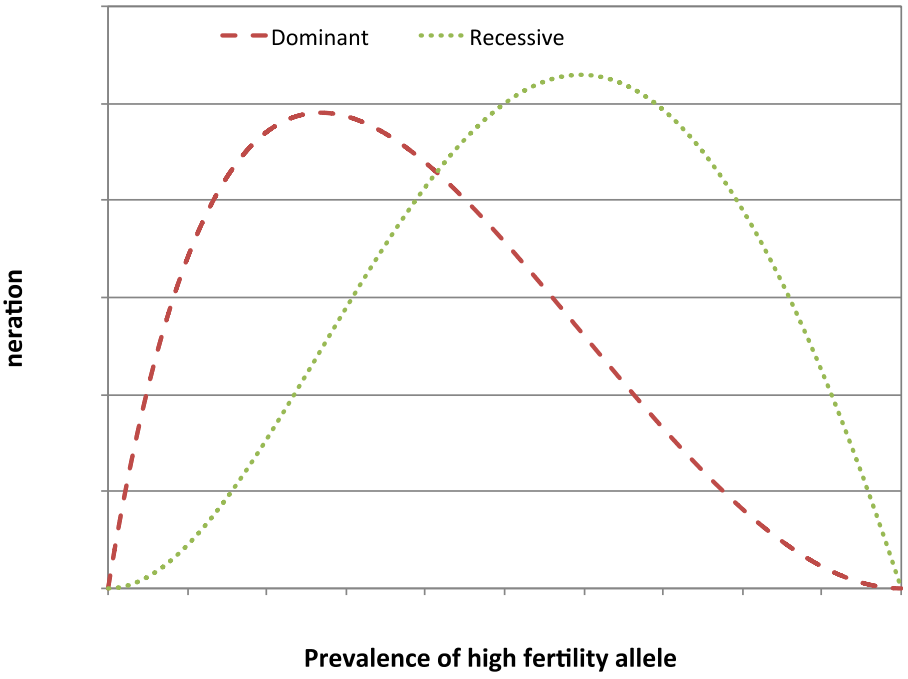
Where the high-fertility allele is recessive, the heterozygote has the same fertility as the low-fertility homozygote. Equation (17) simplifies to:

$$\Delta\pi_t^H = \frac{s\left(\pi_t^H\right)^2\left(1-\pi_t^H\right)}{1-s\left(1-\left(\pi_t^H\right)^2\right)} \tag{19}$$

Equations (18) and (19) show that the high-fertility allele spreads fastest when it is present in proportions at less than 50 per cent when it is dominant and at more than 50 per cent when it is recessive. In each case, it is likely to reach fixation in the population at a similar time.

Figure 12 illustrates the spread of the high fertility allele at different levels of prevalence. The upper axis shows the selection pressure (the percentage point change in allele frequency per generation) and the lower axis indicates the prevalence of the high-fertility allele in the population. The dominant and recessive cases exhibit similar selection pressures over the course of the transition to fixation, but if the allele is dominant, the selection pressure peaks at lower prevalence than if it is recessive. In the dominant case, at low frequencies most high-fertility alleles are in the homozygote and are selected for, which speeds the initial spread. At higher frequencies, the success of the heterozygote prevents elimination of the low-fertility allele. In the recessive case, most high-fertility alleles are eliminated in the heterozygote at low prevalence, while at higher prevalence, selection against the heterozygote assists in the elimination of the now rare low-fertility allele).

Figure 12: Selection pressure



Note: A high-fertility phenotype fertility of 3.6 and a low-fertility phenotype fertility of 1.8 gives a selection coefficient of 0.5.

Appendix C: Spreadsheet model snapshots (highlighted areas for exogenous variables)

C.1 Haploid model

INPUTS	
Fertility gene recessive/dominant	dominant
Proportion of high fertility phenotypes	0.4
Starting population	1
Fertility rate before shock	3.6
Average fertility rate after shock	1.8

OUTPUTS	
Frequency of L gene in population	=IF(C3="recessive",1-C4^0.5,(1-C4)^0.5)
Frequency of H gene in population	=IF(C3="recessive",C4^0.5,1-(1-C4)^0.5)

Type	Initial population	Initial fertility	Post shock fertility
LL (low fertility)	=C10^2*C5	=C6	=IF(C3="recessive",((C7-C16*D16)/(C14+C15)),IF(C3="dominant",((C7-C16*D16-C
HL	=2*C10*C11*C5	=C6	=IF(C3="recessive",E14,IF(C3="dominant",E16,E14+F3*(E16-E14)))
HH (high fertility)	=C11^2*C5	=C6	=C6

	Population				Proportion			
Generation	X(LL)	X(HL)	X(HH)	X(total)	p(LL)	p(HL)	p(HH)	Fertility (average)
-5	=C22/$D$14*2	=D22/$D$15*2	=E22/$D$16*2	=C21+D21+E21	=C21/F21	=D21/F21	=E21/F21	=F22/F21*2
-4	=C23/$D$14*2	=D23/$D$15*2	=E23/$D$16*2	=C22+D22+E22	=C22/F22	=D22/F22	=E22/F22	=F23/F22*2
-3	=C24/$D$14*2	=D24/$D$15*2	=E24/$D$16*2	=C23+D23+E23	=C23/F23	=D23/F23	=E23/F23	=F24/F23*2
-2	=C25/$D$14*2	=D25/$D$15*2	=E25/$D$16*2	=C24+D24+E24	=C24/F24	=D24/F24	=E24/F24	=F25/F24*2
-1	=C26/$D$14*2	=D26/$D$15*2	=E26/$D$16*2	=C25+D25+E25	=C25/F25	=D25/F25	=E25/F25	=F26/F25*2
0	=C14	=C15	=C16	=C26+D26+E26	=C26/F26	=D26/F26	=E26/F26	=F27/F26*2
1	=(G26^2*$E$14+0.5*G26*H26*($E$14+$E$15)+0.25*(H26^2)*$E$15)/2*F26	=(0.5*G26*H26*($E$14+$E$15)+0.5*H26*I26*($E$15+$E$16)+0.5*(H26^2)*$E$15+G26*I26*($E$14+$E$16))/2*F26	=(I26^2*$E$16+0.5*H26*I26*($E$15+$E$16)+0.25*(H26^2)*$E$15)/2*F26	=C27+D27+E27	=C27/F27	=D27/F27	=E27/F27	=F28/F27*2
2	=(G27^2*$E$14+0.5*G27*H27*($E$14+$E$15)+0.25*(H27^2)*$E$15)/2*F27	=(0.5*G27*H27*($E$14+$E$15)+0.5*H27*I27*($E$15+$E$16)+0.5*(H27^2)*$E$15+G27*I27*($E$14+$E$16))/2*F27	=(I27^2*$E$16+0.5*H27*I27*($E$15+$E$16)+0.25*(H27^2)*$E$15)/2*F27	=C28+D28+E28	=C28/F28	=D28/F28	=E28/F28	=F29/F28*2
3	=(G28^2*$E$14+0.5*G28*H28*($E$14+$E$15)+0.25*(H28^2)*$E$15)/2*F28	=(0.5*G28*H28*($E$14+$E$15)+0.5*H28*I28*($E$15+$E$16)+0.5*(H28^2)*$E$15+G28*I28*($E$14+$E$16))/2*F28	=(I28^2*$E$16+0.5*H28*I28*($E$15+$E$16)+0.25*(H28^2)*$E$15)/2*F28	=C29+D29+E29	=C29/F29	=D29/F29	=E29/F29	=F30/F29*2
4	=(G29^2*$E$14+0.5*G29*H29*($E$14+$E$15)+0.25*(H29^2)*$E$15)/2*F29	=(0.5*G29*H29*($E$14+$E$15)+0.5*H29*I29*($E$15+$E$16)+0.5*(H29^2)*$E$15+G29*I29*($E$14+$E$16))/2*F29	=(I29^2*$E$16+0.5*H29*I29*($E$15+$E$16)+0.25*(H29^2)*$E$15)/2*F29	=C30+D30+E30	=C30/F30	=D30/F30	=E30/F30	=F31/F30*2
5	=(G30^2*$E$14+0.5*G30*H30*($E$14+$E$15)+0.25*(H30^2)*$E$15)/2*F30	=(0.5*G30*H30*($E$14+$E$15)+0.5*H30*I30*($E$15+$E$16)+0.5*(H30^2)*$E$15+G30*I30*($E$14+$E$16))/2*F30	=(I30^2*$E$16+0.5*H30*I30*($E$15+$E$16)+0.25*(H30^2)*$E$15)/2*F30	=C31+D31+E31	=C31/F31	=D31/F31	=E31/F31	=F32/F31*2
6	=(G31^2*$E$14+0.5*G31*H31*($E$14+$E$15)+0.25*(H31^2)*$E$15)/2*F31	=(0.5*G31*H31*($E$14+$E$15)+0.5*H31*I31*($E$15+$E$16)+0.5*(H31^2)*$E$15+G31*I31*($E$14+$E$16))/2*F31	=(I31^2*$E$16+0.5*H31*I31*($E$15+$E$16)+0.25*(H31^2)*$E$15)/2*F31	=C32+D32+E32	=C32/F32	=D32/F32	=E32/F32	=F33/F32*2
7	=(G32^2*$E$14+0.5*G32*H32*($E$14+$E$15)+0.25*(H32^2)*$E$15)/2*F32	=(0.5*G32*H32*($E$14+$E$15)+0.5*H32*I32*($E$15+$E$16)+0.5*(H32^2)*$E$15+G32*I32*($E$14+$E$16))/2*F32	=(I32^2*$E$16+0.5*H32*I32*($E$15+$E$16)+0.25*(H32^2)*$E$15)/2*F32	=C33+D33+E33	=C33/F33	=D33/F33	=E33/F33	=F34/F33*2
8	=(G33^2*$E$14+0.5*G33*H33*($E$14+$E$15)+0.25*(H33^2)*$E$15)/2*F33	=(0.5*G33*H33*($E$14+$E$15)+0.5*H33*I33*($E$15+$E$16)+0.5*(H33^2)*$E$15+G33*I33*($E$14+$E$16))/2*F33	=(I33^2*$E$16+0.5*H33*I33*($E$15+$E$16)+0.25*(H33^2)*$E$15)/2*F33	=C34+D34+E34	=C34/F34	=D34/F34	=E34/F34	=F35/F34*2
9	=(G34^2*$E$14+0.5*G34*H34*($E$14+$E$15)+0.25*(H34^2)*$E$15)/2*F34	=(0.5*G34*H34*($E$14+$E$15)+0.5*H34*I34*($E$15+$E$16)+0.5*(H34^2)*$E$15+G34*I34*($E$14+$E$16))/2*F34	=(I34^2*$E$16+0.5*H34*I34*($E$15+$E$16)+0.25*(H34^2)*$E$15)/2*F34	=C35+D35+E35	=C35/F35	=D35/F35	=E35/F35	=F36/F35*2
10	=(G35^2*$E$14+0.5*G35*H35*($E$14+$E$15)+0.25*(H35^2)*$E$15)/2*F35	=(0.5*G35*H35*($E$14+$E$15)+0.5*H35*I35*($E$15+$E$16)+0.5*(H35^2)*$E$15+G35*I35*($E$14+$E$16))/2*F35	=(I35^2*$E$16+0.5*H35*I35*($E$15+$E$16)+0.25*(H35^2)*$E$15)/2*F35	=C36+D36+E36	=C36/F36	=D36/F36	=E36/F36	=F37/F36*2
11	=(G36^2*$E$14+0.5*G36*H36*($E$14+$E$15)+0.25*(H36^2)*$E$15)/2*F36	=(0.5*G36*H36*($E$14+$E$15)+0.5*H36*I36*($E$15+$E$16)+0.5*(H36^2)*$E$15+G36*I36*($E$14+$E$16))/2*F36	=(I36^2*$E$16+0.5*H36*I36*($E$15+$E$16)+0.25*(H36^2)*$E$15)/2*F36	=C37+D37+E37	=C37/F37	=D37/F37	=E37/F37	=F38/F37*2
12	=(G37^2*$E$14+0.5*G37*H37*($E$14+$E$15)+0.25*(H37^2)*$E$15)/2*F37	=(0.5*G37*H37*($E$14+$E$15)+0.5*H37*I37*($E$15+$E$16)+0.5*(H37^2)*$E$15+G37*I37*($E$14+$E$16))/2*F37	=(I37^2*$E$16+0.5*H37*I37*($E$15+$E$16)+0.25*(H37^2)*$E$15)/2*F37	=C38+D38+E38	=C38/F38	=D38/F38	=E38/F38	=F39/F38*2
13	=(G38^2*$E$14+0.5*G38*H38*($E$14+$E$15)+0.25*(H38^2)*$E$15)/2*F38	=(0.5*G38*H38*($E$14+$E$15)+0.5*H38*I38*($E$15+$E$16)+0.5*(H38^2)*$E$15+G38*I38*($E$14+$E$16))/2*F38	=(I38^2*$E$16+0.5*H38*I38*($E$15+$E$16)+0.25*(H38^2)*$E$15)/2*F38	=C39+D39+E39	=C39/F39	=D39/F39	=E39/F39	=F40/F39*2
14	=(G39^2*$E$14+0.5*G39*H39*($E$14+$E$15)+0.25*(H39^2)*$E$15)/2*F39	=(0.5*G39*H39*($E$14+$E$15)+0.5*H39*I39*($E$15+$E$16)+0.5*(H39^2)*$E$15+G39*I39*($E$14+$E$16))/2*F39	=(I39^2*$E$16+0.5*H39*I39*($E$15+$E$16)+0.25*(H39^2)*$E$15)/2*F39	=C40+D40+E40	=C40/F40	=D40/F40	=E40/F40	=F41/F40*2
15	=(G40^2*$E$14+0.5*G40*H40*($E$14+$E$15)+0.25*(H40^2)*$E$15)/2*F40	=(0.5*G40*H40*($E$14+$E$15)+0.5*H40*I40*($E$15+$E$16)+0.5*(H40^2)*$E$15+G40*I40*($E$14+$E$16))/2*F40	=(I40^2*$E$16+0.5*H40*I40*($E$15+$E$16)+0.25*(H40^2)*$E$15)/2*F40	=C41+D41+E41	=C41/F41	=D41/F41	=E41/F41	=F42/F41*2
16	=(G41^2*$E$14+0.5*G41*H41*($E$14+$E$15)+0.25*(H41^2)*$E$15)/2*F41	=(0.5*G41*H41*($E$14+$E$15)+0.5*H41*I41*($E$15+$E$16)+0.5*(H41^2)*$E$15+G41*I41*($E$14+$E$16))/2*F41	=(I41^2*$E$16+0.5*H41*I41*($E$15+$E$16)+0.25*(H41^2)*$E$15)/2*F41	=C42+D42+E42	=C42/F42	=D42/F42	=E42/F42	=F43/F42*2
17	=(G42^2*$E$14+0.5*G42*H42*($E$14+$E$15)+0.25*(H42^2)*$E$15)/2*F42	=(0.5*G42*H42*($E$14+$E$15)+0.5*H42*I42*($E$15+$E$16)+0.5*(H42^2)*$E$15+G42*I42*($E$14+$E$16))/2*F42	=(I42^2*$E$16+0.5*H42*I42*($E$15+$E$16)+0.25*(H42^2)*$E$15)/2*F42	=C43+D43+E43	=C43/F43	=D43/F43	=E43/F43	=F44/F43*2
18	=(G43^2*$E$14+0.5*G43*H43*($E$14+$E$15)+0.25*(H43^2)*$E$15)/2*F43	=(0.5*G43*H43*($E$14+$E$15)+0.5*H43*I43*($E$15+$E$16)+0.5*(H43^2)*$E$15+G43*I43*($E$14+$E$16))/2*F43	=(I43^2*$E$16+0.5*H43*I43*($E$15+$E$16)+0.25*(H43^2)*$E$15)/2*F43	=C44+D44+E44	=C44/F44	=D44/F44	=E44/F44	=F45/F44*2
19	=(G44^2*$E$14+0.5*G44*H44*($E$14+$E$15)+0.25*(H44^2)*$E$15)/2*F44	=(0.5*G44*H44*($E$14+$E$15)+0.5*H44*I44*($E$15+$E$16)+0.5*(H44^2)*$E$15+G44*I44*($E$14+$E$16))/2*F44	=(I44^2*$E$16+0.5*H44*I44*($E$15+$E$16)+0.25*(H44^2)*$E$15)/2*F44	=C45+D45+E45	=C45/F45	=D45/F45	=E45/F45	=F46/F45*2
20	=(G45^2*$E$14+0.5*G45*H45*($E$14+$E$15)+0.25*(H45^2)*$E$15)/2*F45	=(0.5*G45*H45*($E$14+$E$15)+0.5*H45*I45*($E$15+$E$16)+0.5*(H45^2)*$E$15+G45*I45*($E$14+$E$16))/2*F45	=(I45^2*$E$16+0.5*H45*I45*($E$15+$E$16)+0.25*(H45^2)*$E$15)/2*F45	=C46+D46+E46	=C46/F46	=D46/F46	=E46/F46	=F47/F46*2
21	=(G46^2*$E$14+0.5*G46*H46*($E$14+$E$15)+0.25*(H46^2)*$E$15)/2*F46	=(0.5*G46*H46*($E$14+$E$15)+0.5*H46*I46*($E$15+$E$16)+0.5*(H46^2)*$E$15+G46*I46*($E$14+$E$16))/2*F46	=(I46^2*$E$16+0.5*H46*I46*($E$15+$E$16)+0.25*(H46^2)*$E$15)/2*F46	=C47+D47+E47	=C47/F47	=D47/F47	=E47/F47	

C.2 Model of heritability of fertility

INPUTS

Heritability [h^2]	0.2
Maximum family size [n]	10
Initial mean family size	1.8
Initial population	1

Proportion of families with this many children

Generation	Mean	p	Variance	0	1	2	3	4	5	6	7	8	9	10
0	=C5	=C10/$C$4	=C10*(1-D10)	=BINOMDIST($S9,10,$D10,FALSE)	=BINOMDIST($S9,10,$D10,FALSE)	=BINOMDIST($S9,10,$D10,FALSE)	=BINOMDIST($S9,10,$D10,FALSE)	=BINOMDIST($S9,10,$D10,FALSE)	=BINOMDIST($S9,10,$D10,FALSE)	=BINOMDIST($S9,10,$D10,FALSE)	=BINOMDIST($S9,10,$D10,FALSE)	=BINOMDIST($S9,10,$D10,FALSE)	=BINOMDIST($S9,10,$D10,FALSE)	=BINOMDIST($S9,10,$D10,FALSE)
1	=(C61-C10)*$C$3+C10	=C11/$C$4	=C11*(1-D11)	=BINOMDIST($S9,10,$D11,FALSE)	=BINOMDIST($S9,10,$D11,FALSE)	=BINOMDIST($S9,10,$D11,FALSE)	=BINOMDIST($S9,10,$D11,FALSE)	=BINOMDIST($S9,10,$D11,FALSE)	=BINOMDIST($S9,10,$D11,FALSE)	=BINOMDIST($S9,10,$D11,FALSE)	=BINOMDIST($S9,10,$D11,FALSE)	=BINOMDIST($S9,10,$D11,FALSE)	=BINOMDIST($S9,10,$D11,FALSE)	=BINOMDIST($S9,10,$D11,FALSE)
2	=(C62-C11)*$C$3+C11	=C12/$C$4	=C12*(1-D12)	=BINOMDIST($S9,10,$D12,FALSE)	=BINOMDIST($S9,10,$D12,FALSE)	=BINOMDIST($S9,10,$D12,FALSE)	=BINOMDIST($S9,10,$D12,FALSE)	=BINOMDIST($S9,10,$D12,FALSE)	=BINOMDIST($S9,10,$D12,FALSE)	=BINOMDIST($S9,10,$D12,FALSE)	=BINOMDIST($S9,10,$D12,FALSE)	=BINOMDIST($S9,10,$D12,FALSE)	=BINOMDIST($S9,10,$D12,FALSE)	=BINOMDIST($S9,10,$D12,FALSE)
3	=(C63-C12)*$C$3+C12	=C13/$C$4	=C13*(1-D13)	=BINOMDIST($S9,10,$D13,FALSE)	=BINOMDIST($S9,10,$D13,FALSE)	=BINOMDIST($S9,10,$D13,FALSE)	=BINOMDIST($S9,10,$D13,FALSE)	=BINOMDIST($S9,10,$D13,FALSE)	=BINOMDIST($S9,10,$D13,FALSE)	=BINOMDIST($S9,10,$D13,FALSE)	=BINOMDIST($S9,10,$D13,FALSE)	=BINOMDIST($S9,10,$D13,FALSE)	=BINOMDIST($S9,10,$D13,FALSE)	=BINOMDIST($S9,10,$D13,FALSE)
4	=(C64-C13)*$C$3+C13	=C14/$C$4	=C14*(1-D14)	=BINOMDIST($S9,10,$D14,FALSE)	=BINOMDIST($S9,10,$D14,FALSE)	=BINOMDIST($S9,10,$D14,FALSE)	=BINOMDIST($S9,10,$D14,FALSE)	=BINOMDIST($S9,10,$D14,FALSE)	=BINOMDIST($S9,10,$D14,FALSE)	=BINOMDIST($S9,10,$D14,FALSE)	=BINOMDIST($S9,10,$D14,FALSE)	=BINOMDIST($S9,10,$D14,FALSE)	=BINOMDIST($S9,10,$D14,FALSE)	=BINOMDIST($S9,10,$D14,FALSE)
5	=(C65-C14)*$C$3+C14	=C15/$C$4	=C15*(1-D15)	=BINOMDIST($S9,10,$D15,FALSE)	=BINOMDIST($S9,10,$D15,FALSE)	=BINOMDIST($S9,10,$D15,FALSE)	=BINOMDIST($S9,10,$D15,FALSE)	=BINOMDIST($S9,10,$D15,FALSE)	=BINOMDIST($S9,10,$D15,FALSE)	=BINOMDIST($S9,10,$D15,FALSE)	=BINOMDIST($S9,10,$D15,FALSE)	=BINOMDIST($S9,10,$D15,FALSE)	=BINOMDIST($S9,10,$D15,FALSE)	=BINOMDIST($S9,10,$D15,FALSE)
6	=(C66-C15)*$C$3+C15	=C16/$C$4	=C16*(1-D16)	=BINOMDIST($S9,10,$D16,FALSE)	=BINOMDIST($S9,10,$D16,FALSE)	=BINOMDIST($S9,10,$D16,FALSE)	=BINOMDIST($S9,10,$D16,FALSE)	=BINOMDIST($S9,10,$D16,FALSE)	=BINOMDIST($S9,10,$D16,FALSE)	=BINOMDIST($S9,10,$D16,FALSE)	=BINOMDIST($S9,10,$D16,FALSE)	=BINOMDIST($S9,10,$D16,FALSE)	=BINOMDIST($S9,10,$D16,FALSE)	=BINOMDIST($S9,10,$D16,FALSE)
7	=(C67-C16)*$C$3+C16	=C17/$C$4	=C17*(1-D17)	=BINOMDIST($S9,10,$D17,FALSE)	=BINOMDIST($S9,10,$D17,FALSE)	=BINOMDIST($S9,10,$D17,FALSE)	=BINOMDIST($S9,10,$D17,FALSE)	=BINOMDIST($S9,10,$D17,FALSE)	=BINOMDIST($S9,10,$D17,FALSE)	=BINOMDIST($S9,10,$D17,FALSE)	=BINOMDIST($S9,10,$D17,FALSE)	=BINOMDIST($S9,10,$D17,FALSE)	=BINOMDIST($S9,10,$D17,FALSE)	=BINOMDIST($S9,10,$D17,FALSE)
8	=(C68-C17)*$C$3+C17	=C18/$C$4	=C18*(1-D18)	=BINOMDIST($S9,10,$D18,FALSE)	=BINOMDIST($S9,10,$D18,FALSE)	=BINOMDIST($S9,10,$D18,FALSE)	=BINOMDIST($S9,10,$D18,FALSE)	=BINOMDIST($S9,10,$D18,FALSE)	=BINOMDIST($S9,10,$D18,FALSE)	=BINOMDIST($S9,10,$D18,FALSE)	=BINOMDIST($S9,10,$D18,FALSE)	=BINOMDIST($S9,10,$D18,FALSE)	=BINOMDIST($S9,10,$D18,FALSE)	=BINOMDIST($S9,10,$D18,FALSE)
9	=(C69-C18)*$C$3+C18	=C19/$C$4	=C19*(1-D19)	=BINOMDIST($S9,10,$D19,FALSE)	=BINOMDIST($S9,10,$D19,FALSE)	=BINOMDIST($S9,10,$D19,FALSE)	=BINOMDIST($S9,10,$D19,FALSE)	=BINOMDIST($S9,10,$D19,FALSE)	=BINOMDIST($S9,10,$D19,FALSE)	=BINOMDIST($S9,10,$D19,FALSE)	=BINOMDIST($S9,10,$D19,FALSE)	=BINOMDIST($S9,10,$D19,FALSE)	=BINOMDIST($S9,10,$D19,FALSE)	=BINOMDIST($S9,10,$D19,FALSE)
10	=(C70-C19)*$C$3+C19	=C20/$C$4	=C20*(1-D20)	=BINOMDIST($S9,10,$D20,FALSE)	=BINOMDIST($S9,10,$D20,FALSE)	=BINOMDIST($S9,10,$D20,FALSE)	=BINOMDIST($S9,10,$D20,FALSE)	=BINOMDIST($S9,10,$D20,FALSE)	=BINOMDIST($S9,10,$D20,FALSE)	=BINOMDIST($S9,10,$D20,FALSE)	=BINOMDIST($S9,10,$D20,FALSE)	=BINOMDIST($S9,10,$D20,FALSE)	=BINOMDIST($S9,10,$D20,FALSE)	=BINOMDIST($S9,10,$D20,FALSE)
11	=(C71-C20)*$C$3+C20	=C21/$C$4	=C21*(1-D21)	=BINOMDIST($S9,10,$D21,FALSE)	=BINOMDIST($S9,10,$D21,FALSE)	=BINOMDIST($S9,10,$D21,FALSE)	=BINOMDIST($S9,10,$D21,FALSE)	=BINOMDIST($S9,10,$D21,FALSE)	=BINOMDIST($S9,10,$D21,FALSE)	=BINOMDIST($S9,10,$D21,FALSE)	=BINOMDIST($S9,10,$D21,FALSE)	=BINOMDIST($S9,10,$D21,FALSE)	=BINOMDIST($S9,10,$D21,FALSE)	=BINOMDIST($S9,10,$D21,FALSE)
12	=(C72-C21)*$C$3+C21	=C22/$C$4	=C22*(1-D22)	=BINOMDIST($S9,10,$D22,FALSE)	=BINOMDIST($S9,10,$D22,FALSE)	=BINOMDIST($S9,10,$D22,FALSE)	=BINOMDIST($S9,10,$D22,FALSE)	=BINOMDIST($S9,10,$D22,FALSE)	=BINOMDIST($S9,10,$D22,FALSE)	=BINOMDIST($S9,10,$D22,FALSE)	=BINOMDIST($S9,10,$D22,FALSE)	=BINOMDIST($S9,10,$D22,FALSE)	=BINOMDIST($S9,10,$D22,FALSE)	=BINOMDIST($S9,10,$D22,FALSE)
13	=(C73-C22)*$C$3+C22	=C23/$C$4	=C23*(1-D23)	=BINOMDIST($S9,10,$D23,FALSE)	=BINOMDIST($S9,10,$D23,FALSE)	=BINOMDIST($S9,10,$D23,FALSE)	=BINOMDIST($S9,10,$D23,FALSE)	=BINOMDIST($S9,10,$D23,FALSE)	=BINOMDIST($S9,10,$D23,FALSE)	=BINOMDIST($S9,10,$D23,FALSE)	=BINOMDIST($S9,10,$D23,FALSE)	=BINOMDIST($S9,10,$D23,FALSE)	=BINOMDIST($S9,10,$D23,FALSE)	=BINOMDIST($S9,10,$D23,FALSE)
14	=(C74-C23)*$C$3+C23	=C24/$C$4	=C24*(1-D24)	=BINOMDIST($S9,10,$D24,FALSE)	=BINOMDIST($S9,10,$D24,FALSE)	=BINOMDIST($S9,10,$D24,FALSE)	=BINOMDIST($S9,10,$D24,FALSE)	=BINOMDIST($S9,10,$D24,FALSE)	=BINOMDIST($S9,10,$D24,FALSE)	=BINOMDIST($S9,10,$D24,FALSE)	=BINOMDIST($S9,10,$D24,FALSE)	=BINOMDIST($S9,10,$D24,FALSE)	=BINOMDIST($S9,10,$D24,FALSE)	=BINOMDIST($S9,10,$D24,FALSE)
15	=(C75-C24)*$C$3+C24	=C25/$C$4	=C25*(1-D25)	=BINOMDIST($S9,10,$D25,FALSE)	=BINOMDIST($S9,10,$D25,FALSE)	=BINOMDIST($S9,10,$D25,FALSE)	=BINOMDIST($S9,10,$D25,FALSE)	=BINOMDIST($S9,10,$D25,FALSE)	=BINOMDIST($S9,10,$D25,FALSE)	=BINOMDIST($S9,10,$D25,FALSE)	=BINOMDIST($S9,10,$D25,FALSE)	=BINOMDIST($S9,10,$D25,FALSE)	=BINOMDIST($S9,10,$D25,FALSE)	=BINOMDIST($S9,10,$D25,FALSE)
16	=(C76-C25)*$C$3+C25	=C26/$C$4	=C26*(1-D26)	=BINOMDIST($S9,10,$D26,FALSE)	=BINOMDIST($S9,10,$D26,FALSE)	=BINOMDIST($S9,10,$D26,FALSE)	=BINOMDIST($S9,10,$D26,FALSE)	=BINOMDIST($S9,10,$D26,FALSE)	=BINOMDIST($S9,10,$D26,FALSE)	=BINOMDIST($S9,10,$D26,FALSE)	=BINOMDIST($S9,10,$D26,FALSE)	=BINOMDIST($S9,10,$D26,FALSE)	=BINOMDIST($S9,10,$D26,FALSE)	=BINOMDIST($S9,10,$D26,FALSE)
17	=(C77-C26)*$C$3+C26	=C27/$C$4	=C27*(1-D27)	=BINOMDIST($S9,10,$D27,FALSE)	=BINOMDIST($S9,10,$D27,FALSE)	=BINOMDIST($S9,10,$D27,FALSE)	=BINOMDIST($S9,10,$D27,FALSE)	=BINOMDIST($S9,10,$D27,FALSE)	=BINOMDIST($S9,10,$D27,FALSE)	=BINOMDIST($S9,10,$D27,FALSE)	=BINOMDIST($S9,10,$D27,FALSE)	=BINOMDIST($S9,10,$D27,FALSE)	=BINOMDIST($S9,10,$D27,FALSE)	=BINOMDIST($S9,10,$D27,FALSE)
18	=(C78-C27)*$C$3+C27	=C28/$C$4	=C28*(1-D28)	=BINOMDIST($S9,10,$D28,FALSE)	=BINOMDIST($S9,10,$D28,FALSE)	=BINOMDIST($S9,10,$D28,FALSE)	=BINOMDIST($S9,10,$D28,FALSE)	=BINOMDIST($S9,10,$D28,FALSE)	=BINOMDIST($S9,10,$D28,FALSE)	=BINOMDIST($S9,10,$D28,FALSE)	=BINOMDIST($S9,10,$D28,FALSE)	=BINOMDIST($S9,10,$D28,FALSE)	=BINOMDIST($S9,10,$D28,FALSE)	=BINOMDIST($S9,10,$D28,FALSE)
19	=(C79-C28)*$C$3+C28	=C29/$C$4	=C29*(1-D29)	=BINOMDIST($S9,10,$D29,FALSE)	=BINOMDIST($S9,10,$D29,FALSE)	=BINOMDIST($S9,10,$D29,FALSE)	=BINOMDIST($S9,10,$D29,FALSE)	=BINOMDIST($S9,10,$D29,FALSE)	=BINOMDIST($S9,10,$D29,FALSE)	=BINOMDIST($S9,10,$D29,FALSE)	=BINOMDIST($S9,10,$D29,FALSE)	=BINOMDIST($S9,10,$D29,FALSE)	=BINOMDIST($S9,10,$D29,FALSE)	=BINOMDIST($S9,10,$D29,FALSE)
20	=(C80-C29)*$C$3+C29	=C30/$C$4	=C30*(1-D30)	=BINOMDIST($S9,10,$D30,FALSE)	=BINOMDIST($S9,10,$D30,FALSE)	=BINOMDIST($S9,10,$D30,FALSE)	=BINOMDIST($S9,10,$D30,FALSE)	=BINOMDIST($S9,10,$D30,FALSE)	=BINOMDIST($S9,10,$D30,FALSE)	=BINOMDIST($S9,10,$D30,FALSE)	=BINOMDIST($S9,10,$D30,FALSE)	=BINOMDIST($S9,10,$D30,FALSE)	=BINOMDIST($S9,10,$D30,FALSE)	=BINOMDIST($S9,10,$D30,FALSE)

Generation	Population
0	=C6
1	=C36*Q36/2
2	=C37*Q37/2
3	=C38*Q38/2
4	=C39*Q39/2
5	=C40*Q40/2
6	=C41*Q41/2
7	=C42*Q42/2
8	=C43*Q43/2
9	=C44*Q44/2
10	=C45*Q45/2
11	=C46*Q46/2
12	=C47*Q47/2
13	=C48*Q48/2
14	=C49*Q49/2
15	=C50*Q50/2
16	=C51*Q51/2
17	=C52*Q52/2
18	=C53*Q53/2
19	=C54*Q54/2
20	=C55*Q55/2

Number of children in each family

Generation	0	1	2	3	4	5	6	7	8	9	10	Check total [=mean]
0	=F10*FS35	=G10*GS35	=H10*HS35	=I10*IS35	=J10*JS35	=K10*KS35	=L10*LS35	=M10*MS35	=N10*NS35	=O10*OS35	=P10*PS35	=SUM(F36:F36)
1	=F11*FS35	=G11*GS35	=H11*HS35	=I11*IS35	=J11*JS35	=K11*KS35	=L11*LS35	=M11*MS35	=N11*NS35	=O11*OS35	=P11*PS35	=SUM(F37:F37)
2	=F12*FS35	=G12*GS35	=H12*HS35	=I12*IS35	=J12*JS35	=K12*KS35	=L12*LS35	=M12*MS35	=N12*NS35	=O12*OS35	=P12*PS35	=SUM(F38:F38)
3	=F13*FS35	=G13*GS35	=H13*HS35	=I13*IS35	=J13*JS35	=K13*KS35	=L13*LS35	=M13*MS35	=N13*NS35	=O13*OS35	=P13*PS35	=SUM(F39:F39)
4	=F14*FS35	=G14*GS35	=H14*HS35	=I14*IS35	=J14*JS35	=K14*KS35	=L14*LS35	=M14*MS35	=N14*NS35	=O14*OS35	=P14*PS35	=SUM(F40:F40)
5	=F15*FS35	=G15*GS35	=H15*HS35	=I15*IS35	=J15*JS35	=K15*KS35	=L15*LS35	=M15*MS35	=N15*NS35	=O15*OS35	=P15*PS35	=SUM(F41:F41)
6	=F16*FS35	=G16*GS35	=H16*HS35	=I16*IS35	=J16*JS35	=K16*KS35	=L16*LS35	=M16*MS35	=N16*NS35	=O16*OS35	=P16*PS35	=SUM(F42:F42)
7	=F17*FS35	=G17*GS35	=H17*HS35	=I17*IS35	=J17*JS35	=K17*KS35	=L17*LS35	=M17*MS35	=N17*NS35	=O17*OS35	=P17*PS35	=SUM(F43:F43)
8	=F18*FS35	=G18*GS35	=H18*HS35	=I18*IS35	=J18*JS35	=K18*KS35	=L18*LS35	=M18*MS35	=N18*NS35	=O18*OS35	=P18*PS35	=SUM(F44:F44)
9	=F19*FS35	=G19*GS35	=H19*HS35	=I19*IS35	=J19*JS35	=K19*KS35	=L19*LS35	=M19*MS35	=N19*NS35	=O19*OS35	=P19*PS35	=SUM(F45:F45)
10	=F20*FS35	=G20*GS35	=H20*HS35	=I20*IS35	=J20*JS35	=K20*KS35	=L20*LS35	=M20*MS35	=N20*NS35	=O20*OS35	=P20*PS35	=SUM(F46:F46)
11	=F21*FS35	=G21*GS35	=H21*HS35	=I21*IS35	=J21*JS35	=K21*KS35	=L21*LS35	=M21*MS35	=N21*NS35	=O21*OS35	=P21*PS35	=SUM(F47:F47)
12	=F22*FS35	=G22*GS35	=H22*HS35	=I22*IS35	=J22*JS35	=K22*KS35	=L22*LS35	=M22*MS35	=N22*NS35	=O22*OS35	=P22*PS35	=SUM(F48:F48)
13	=F23*FS35	=G23*GS35	=H23*HS35	=I23*IS35	=J23*JS35	=K23*KS35	=L23*LS35	=M23*MS35	=N23*NS35	=O23*OS35	=P23*PS35	=SUM(F49:F49)
14	=F24*FS35	=G24*GS35	=H24*HS35	=I24*IS35	=J24*JS35	=K24*KS35	=L24*LS35	=M24*MS35	=N24*NS35	=O24*OS35	=P24*PS35	=SUM(F50:F50)
15	=F25*FS35	=G25*GS35	=H25*HS35	=I25*IS35	=J25*JS35	=K25*KS35	=L25*LS35	=M25*MS35	=N25*NS35	=O25*OS35	=P25*PS35	=SUM(F51:F51)
16	=F26*FS35	=G26*GS35	=H26*HS35	=I26*IS35	=J26*JS35	=K26*KS35	=L26*LS35	=M26*MS35	=N26*NS35	=O26*OS35	=P26*PS35	=SUM(F52:F52)
17	=F27*FS35	=G27*GS35	=H27*HS35	=I27*IS35	=J27*JS35	=K27*KS35	=L27*LS35	=M27*MS35	=N27*NS35	=O27*OS35	=P27*PS35	=SUM(F53:F53)
18	=F28*FS35	=G28*GS35	=H28*HS35	=I28*IS35	=J28*JS35	=K28*KS35	=L28*LS35	=M28*MS35	=N28*NS35	=O28*OS35	=P28*PS35	=SUM(F54:F54)
19	=F29*FS35	=G29*GS35	=H29*HS35	=I29*IS35	=J29*JS35	=K29*KS35	=L29*LS35	=M29*MS35	=N29*NS35	=O29*OS35	=P29*PS35	=SUM(F55:F55)
20	=F30*FS35	=G30*GS35	=H30*HS35	=I30*IS35	=J30*JS35	=K30*KS35	=L30*LS35	=M30*MS35	=N30*NS35	=O30*OS35	=P30*PS35	=SUM(F56:F56)

Number of children in families of this size

Generation	0	1	2	3	4	5	6	7	8	9	10	Mean family size t+1
0	=F36/SQ36*FS60	=G36/SQ36*GS60	=H36/SQ36*HS60	=I36/SQ36*IS60	=J36/SQ36*JS60	=K36/SQ36*KS60	=L36/SQ36*LS60	=M36/SQ36*MS60	=N36/SQ36*NS60	=O36/SQ36*OS60	=P36/SQ36*PS60	=SUM(F63:P63)
1	=F37/SQ37*FS60	=G37/SQ37*GS60	=H37/SQ37*HS60	=I37/SQ37*IS60	=J37/SQ37*JS60	=K37/SQ37*KS60	=L37/SQ37*LS60	=M37/SQ37*MS60	=N37/SQ37*NS60	=O37/SQ37*OS60	=P37/SQ37*PS60	=SUM(F62:P62)
2	=F38/SQ38*FS60	=G38/SQ38*GS60	=H38/SQ38*HS60	=I38/SQ38*IS60	=J38/SQ38*JS60	=K38/SQ38*KS60	=L38/SQ38*LS60	=M38/SQ38*MS60	=N38/SQ38*NS60	=O38/SQ38*OS60	=P38/SQ38*PS60	=SUM(F63:P63)
3	=F39/SQ39*FS60	=G39/SQ39*GS60	=H39/SQ39*HS60	=I39/SQ39*IS60	=J39/SQ39*JS60	=K39/SQ39*KS60	=L39/SQ39*LS60	=M39/SQ39*MS60	=N39/SQ39*NS60	=O39/SQ39*OS60	=P39/SQ39*PS60	=SUM(F64:P64)
4	=F40/SQ40*FS60	=G40/SQ40*GS60	=H40/SQ40*HS60	=I40/SQ40*IS60	=J40/SQ40*JS60	=K40/SQ40*KS60	=L40/SQ40*LS60	=M40/SQ40*MS60	=N40/SQ40*NS60	=O40/SQ40*OS60	=P40/SQ40*PS60	=SUM(F65:P65)
5	=F41/SQ41*FS60	=G41/SQ41*GS60	=H41/SQ41*HS60	=I41/SQ41*IS60	=J41/SQ41*JS60	=K41/SQ41*KS60	=L41/SQ41*LS60	=M41/SQ41*MS60	=N41/SQ41*NS60	=O41/SQ41*OS60	=P41/SQ41*PS60	=SUM(F66:P66)
6	=F42/SQ42*FS60	=G42/SQ42*GS60	=H42/SQ42*HS60	=I42/SQ42*IS60	=J42/SQ42*JS60	=K42/SQ42*KS60	=L42/SQ42*LS60	=M42/SQ42*MS60	=N42/SQ42*NS60	=O42/SQ42*OS60	=P42/SQ42*PS60	=SUM(F67:P67)
7	=F43/SQ43*FS60	=G43/SQ43*GS60	=H43/SQ43*HS60	=I43/SQ43*IS60	=J43/SQ43*JS60	=K43/SQ43*KS60	=L43/SQ43*LS60	=M43/SQ43*MS60	=N43/SQ43*NS60	=O43/SQ43*OS60	=P43/SQ43*PS60	=SUM(F68:P68)
8	=F44/SQ44*FS60	=G44/SQ44*GS60	=H44/SQ44*HS60	=I44/SQ44*IS60	=J44/SQ44*JS60	=K44/SQ44*KS60	=L44/SQ44*LS60	=M44/SQ44*MS60	=N44/SQ44*NS60	=O44/SQ44*OS60	=P44/SQ44*PS60	=SUM(F69:P69)
9	=F45/SQ45*FS60	=G45/SQ45*GS60	=H45/SQ45*HS60	=I45/SQ45*IS60	=J45/SQ45*JS60	=K45/SQ45*KS60	=L45/SQ45*LS60	=M45/SQ45*MS60	=N45/SQ45*NS60	=O45/SQ45*OS60	=P45/SQ45*PS60	=SUM(F70:P70)
10	=F46/SQ46*FS60	=G46/SQ46*GS60	=H46/SQ46*HS60	=I46/SQ46*IS60	=J46/SQ46*JS60	=K46/SQ46*KS60	=L46/SQ46*LS60	=M46/SQ46*MS60	=N46/SQ46*NS60	=O46/SQ46*OS60	=P46/SQ46*PS60	=SUM(F71:P71)
11	=F47/SQ47*FS60	=G47/SQ47*GS60	=H47/SQ47*HS60	=I47/SQ47*IS60	=J47/SQ47*JS60	=K47/SQ47*KS60	=L47/SQ47*LS60	=M47/SQ47*MS60	=N47/SQ47*NS60	=O47/SQ47*OS60	=P47/SQ47*PS60	=SUM(F72:P72)
12	=F48/SQ48*FS60	=G48/SQ48*GS60	=H48/SQ48*HS60	=I48/SQ48*IS60	=J48/SQ48*JS60	=K48/SQ48*KS60	=L48/SQ48*LS60	=M48/SQ48*MS60	=N48/SQ48*NS60	=O48/SQ48*OS60	=P48/SQ48*PS60	=SUM(F73:P73)
13	=F49/SQ49*FS60	=G49/SQ49*GS60	=H49/SQ49*HS60	=I49/SQ49*IS60	=J49/SQ49*JS60	=K49/SQ49*KS60	=L49/SQ49*LS60	=M49/SQ49*MS60	=N49/SQ49*NS60	=O49/SQ49*OS60	=P49/SQ49*PS60	=SUM(F74:P74)
14	=F50/SQ50*FS60	=G50/SQ50*GS60	=H50/SQ50*HS60	=I50/SQ50*IS60	=J50/SQ50*JS60	=K50/SQ50*KS60	=L50/SQ50*LS60	=M50/SQ50*MS60	=N50/SQ50*NS60	=O50/SQ50*OS60	=P50/SQ50*PS60	=SUM(F75:P75)
15	=F51/SQ51*FS60	=G51/SQ51*GS60	=H51/SQ51*HS60	=I51/SQ51*IS60	=J51/SQ51*JS60	=K51/SQ51*KS60	=L51/SQ51*LS60	=M51/SQ51*MS60	=N51/SQ51*NS60	=O51/SQ51*OS60	=P51/SQ51*PS60	=SUM(F76:P76)
16	=F52/SQ52*FS60	=G52/SQ52*GS60	=H52/SQ52*HS60	=I52/SQ52*IS60	=J52/SQ52*JS60	=K52/SQ52*KS60	=L52/SQ52*LS60	=M52/SQ52*MS60	=N52/SQ52*NS60	=O52/SQ52*OS60	=P52/SQ52*PS60	=SUM(F77:P77)
17	=F53/SQ53*FS60	=G53/SQ53*GS60	=H53/SQ53*HS60	=I53/SQ53*IS60	=J53/SQ53*JS60	=K53/SQ53*KS60	=L53/SQ53*LS60	=M53/SQ53*MS60	=N53/SQ53*NS60	=O53/SQ53*OS60	=P53/SQ53*PS60	=SUM(F78:P78)
18	=F54/SQ54*FS60	=G54/SQ54*GS60	=H54/SQ54*HS60	=I54/SQ54*IS60	=J54/SQ54*JS60	=K54/SQ54*KS60	=L54/SQ54*LS60	=M54/SQ54*MS60	=N54/SQ54*NS60	=O54/SQ54*OS60	=P54/SQ54*PS60	=SUM(F79:P79)
19	=F55/SQ55*FS60	=G55/SQ55*GS60	=H55/SQ55*HS60	=I55/SQ55*IS60	=J55/SQ55*JS60	=K55/SQ55*KS60	=L55/SQ55*LS60	=M55/SQ55*MS60	=N55/SQ55*NS60	=O55/SQ55*OS60	=P55/SQ55*PS60	=SUM(F80:P80)
20	=F56/SQ56*FS60	=G56/SQ56*GS60	=H56/SQ56*HS60	=I56/SQ56*IS60	=J56/SQ56*JS60	=K56/SQ56*KS60	=L56/SQ56*LS60	=M56/SQ56*MS60	=N56/SQ56*NS60	=O56/SQ56*OS60	=P56/SQ56*PS60	=SUM(F81:P81)

C.3 Age-structured model (Snapshot of parameters, year 0 and year 5. Further years are iterations of year 5)

INPUTS

Fertility ratio	3
Total fertility rate	=W13
High fertility	=B3*B6
Low fertility	=B4/(B3*B7+B8)
Proportion high fertility	0.2
Proportion low fertility	=1-B7

Birth schedules

Average fertility at 0 — **Total**

Age	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100+	
Fertility/year	0	0	0	0.1	0.3	0.6	0.5	0.2	0.1	0	0	0	0	0	0	0	0	0	0	0	0	=SUM(B13:V13)

Fertility low fertility type

Age	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100+	
Fertility/year	=($B$6/$B$4)*B13	=($B$6/$B$4)*C13	=($B$6/$B$4)*D13	=($B$6/$B$4)*E13	=($B$6/$B$4)*F13	=($B$6/$B$4)*G13	=($B$6/$B$4)*H13	=($B$6/$B$4)*I13	=($B$6/$B$4)*J13	=($B$6/$B$4)*K13	=($B$6/$B$4)*L13	=($B$6/$B$4)*M13	=($B$6/$B$4)*N13	=($B$6/$B$4)*O13	=($B$6/$B$4)*P13	=($B$6/$B$4)*Q13	=($B$6/$B$4)*R13	=($B$6/$B$4)*S13	=($B$6/$B$4)*T13	=($B$6/$B$4)*U13	=($B$6/$B$4)*V13	=SUM(B17:V17)

Fertility high fertility type

Age	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100+	
Fertility/year	=($B$5/$B$4)*B13	=($B$5/$B$4)*C13	=($B$5/$B$4)*D13	=($B$6/$B$4)*E13	=($B$5/$B$4)*F13	=($B$5/$B$4)*G13	=($B$5/$B$4)*H13	=($B$5/$B$4)*I13	=($B$5/$B$4)*J13	=($B$5/$B$4)*K13	=($B$5/$B$4)*L13	=($B$5/$B$4)*M13	=($B$6/$B$4)*N13	=($B$6/$B$4)*O13	=($B$5/$B$4)*P13	=($B$5/$B$4)*Q13	=($B$6/$B$4)*R13	=($B$5/$B$4)*S13	=($B$5/$B$4)*T13	=($B$6/$B$4)*U13	=($B$5/$B$4)*V13	=SUM(B21:V21)

Death schedule

Age	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100+
Percent deaths	0.005	0.0005	0.0005	0.002	0.002	0.003	0.004	0.005	0.006	0.01	0.01	0.02	0.03	0.05	0.09	0.15	0.26	0.42	0.62	0.77	1

Starting population

Age	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100+	
Total	0.1	0.1	0.095	0.075	0.065	0.06	0.07	0.07	0.065	0.06	0.055	0.045	0.04	0.035	0.025	0.015	0.01	0.01	0.003	0.002	0	=SUM(B29:V29)

Year 0

Low fertility type

Age	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100+	
Total	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Births	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Deaths	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

High fertility type

Age	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100+	
Total	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Births	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Deaths	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Total

Age	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100+	
Total	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Births	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Deaths	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Average fertility by age [illegible] — **Average fertility** [illegible]

Base case no heritability

Age	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100+	
Total	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Births	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Deaths	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Heritable case
Proportion of 0-14 years olds [illegible]
Proportion of 65+ [illegible]

Base case
Proportion of 0-14 years olds [illegible]
Proportion of 65+ [illegible]

Year 5

Low fertility type

Age	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100+	
Total	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Births	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Deaths	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

High fertility type

Age	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100+	
Total	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Births	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Deaths	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Total

Age	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100+	
Total	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Births	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Deaths	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Average fertility by age [illegible] — **Average fertility** [illegible]

Base case no heritability

Age	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100+	
Total	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Births	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Deaths	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Heritable case
Proportion of 0-14 years olds [illegible]
Proportion of 65+ [illegible]

Base case
Proportion of 0-14 years olds [illegible]
Proportion of 65+ [illegible]

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