



# ong term stationary phase in Escherichia coli and Pseudomonas fluorescens

Jenna Gallie, <sup>1</sup> Saul Pierotti, <sup>1</sup>

#### Abstract

Recent analyses suggest that a few major shifts in diversification rate may be enough to explain most of the disparity in diversity among vertebrate lineages. At least one significant increase in diversification rate appears to have occurred within the birds; however, several nested lineages within birds have been identified as hyperdiverse by different studies. A clade containing the finches and relatives (within the avian order Passeriformes), including a large radiation endemic to the New World that comprises  $\sim 8\%$  of all bird species, may be the true driver of this rate increase. Understanding the patterns and processes of diversification of this diverse lineage may go a long way toward explaining the apparently rapid diversification rates of both passerines and of birds as a whole.

Key words: Concatenation, concordance, congruence, diversification, gene tree, New World, Passeriformes.

# Introduction

This paper considers an overlapping generations model without external effects or a social security system. Nonetheless, we show that a population decline can worsen the welfare of agents if it is caused by a change in the timing of childbirth or, more specifically, when many people decide to delay childbearing to older ages.

Delayed childbearing has been broadly observed in developed countries. Between 1975 and 2005,

the fraction of Japanese children who were born to mothers in their 20s decreased from 75% to 45%, whereas those born to mothers in their 30s increased from 20% to 52%. A similar trend is observed in the United States and advanced European countries (Gustafsson and

© The Author 2013. Published by Oxford University Press on behalf of the Society for Molecular Biology and Evolution. All rights reserved. For permissions, please email: journals.permissions@oup.com





<sup>&</sup>lt;sup>1</sup>Department of Ecology, Evolution and Behavior

<sup>&</sup>lt;sup>2</sup>Bell Museum of Natural History, University of V<br/>Minnesota, 100 Ecology, 1987 Upper Buford Circle, St Paul, MN 55108

 $<sup>^3\</sup>mathrm{Department}$ of Biology, San Diego State University, San Diego, CA 92182

<sup>&</sup>lt;sup>4</sup>Marjorie Barrick Museum of Natural History, Box 454012, University of Nevada, Las Vegas, 4505 Maryland Parkway, Las Vegas, NV 89154

<sup>&</sup>lt;sup>5</sup>Fuller Evolutionary Biology Program, Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA

<sup>\*</sup>Corresponding author: E-mail:gallie@evolbio.mpg.de Associate Editor:





Gallie et al.  $\cdot$  doi:10.1093/molbev/sys000

Kalwij, 2006), and also in Canada, Australia, and New Zealand?. Interestingly, as pointed out by (??), even when the cohort's lifetime fertility rate (the number of children a mother has in her lifetime) does not fall, the delayed childbearing alone leads to a decline in the number of childbirths, measured by the total period fertility rates (TPFRs). ?, ?, and Sobotka (2004) confirmed that, to a certain extent, the delay of marriage and motherhood is responsible for the observed period fertility rate decline (now known as the 'tempo effect'). This paper considers an overlapping generations model without external effects or a social security system.

As the variation in the age composition of workers affects the distribution of income among different cohorts (Berger, 1989), demographic cycles lead to cycles in the aggregate saving rate, which drive fluctuations in the capitallabor ratio. We will show that the fluctuations in the capital-labor ratio have differential effective labor produces a fixed welfare effects on agents depending on their positions in the demographic cycles. This point was not found by earlier studies. For instance, ? considered a small open economy with a fixed capital-labor ratio, savings were not allowed in ?, and (?) and d'Albis et al. (2010) assumed a linear technology where one unit of effective labor produces a fixed amount of output. The remainder of the paper is structured as follows. Section introduces the theoretical model. Section analytically examines the impact

of delayed childbearing on capital accumulation and welfare. Section numerically examines the general case where only a fraction of agents delay their childbearing. Section considers extensions of the model with a lower lifetime fertility rate and technological progress. Section concludes the paper. Appendices A and B provide the proofs of the lemmas.

Delayed childbearing has been broadly observed in developed countries. Between 1975 and 2005, the fraction of Japanese children who were born to mothers in their 20s decreased from 75% to 45%, whereas those born to mothers in their 30s increased from 20% to 52%. A similar trend is observed in the United States and advanced European countries ?, and also in Canada, Australia, and New Zealand (?).

# Demographic structure

Delayed childbearing has been broadly observed in developed countries. Between 1975 and 2005, the fraction of Japanese children who were born to mothers in their 20s decreased from 75% to 45%, whereas those born to mothers in their 30s increased from 20% to 52%. A similar trend is observed in the United States and advanced European countries (Gustafsson and Kalwij, 2006), and also in Canada, Australia, and New Zealand (?).

# Demographic structure

Interestingly, as pointed out by (??), even when the cohort's lifetime fertility rate (the number of









LTSP in E. coli and P. fluorescens  $\cdot$  doi:10.1093/molbev/sys000

children a mother has in her lifetime) does not fall, the delayed childbearing alone leads to a decline in the number of childbirths, measured by the total period fertility rates (TPFRs).

#### $Demographic\ structure$

Ogawa and Retherford (1993), Kohler et al. (2002), and (?) confirmed that, to a certain extent, the delay of marriage and motherhood is responsible for the observed period fertility rate decline (now known as the 'tempo effect'). This paper considers an overlapping generations model without external effects or a social security system. Nonetheless, we show that a population decline can worsen the welfare of agents if it is caused by a change in the timing of childbirth or, more specifically, when many people decide to delay child bearing to older ages. Iyigun (2000) built a growth model where women face a tradeoff between childbearing and human capital accumulation when young, and derived multiple steady state equilibria. ? illustrated the mechanism where an increase in longevity delays the timing of childbearing. ? constructed an endogenous childbirth timing model where the solution is obtained as a closed form. d'Albis et al. (2010) proved the existence of a monetary equilibrium in a model where the age of childbearing is determined endogenously.

Demographic structure. Of course, the declining birth rate can cause welfare problems when the population size has some positive externality, or when social security systems are explicitly considered. To support a pay-as-you-go pension system, the economy must have enough children. Apart from these issues, it has been generally perceived that the population decline is favorable to economic welfare. A notable exception is (?), which showed that when agents are uncertain about the length of their life and there is a perfect annuity market, the capital—labor ratio may respond nonmonotonically to the population growth rate.

This paper considers an overlapping generations model without external effects or a social security system. Nonetheless, we show that a population decline can worsen the welfare of agents if it is caused by a change in the timing of childbirth or, more specifically, when many people decide to delay childbearing to older ages.

As the variation in the age composition of workers affects the distribution of income among different cohorts (?), demographic cycles lead to cycles in the aggregate saving rate, which drive fluctuations in the capital—labor ratio. We will show that the fluctuations in the capital—labor ratio have differential welfare effects on agents depending on their positions in the demographic cycles. This point was not found by earlier studies. For instance, Iyigun (2000) considered a small open economy with a fixed capital—labor ratio, savings were not allowed in (?), and Mullin and Wang (2002) and d'Albis et al. (2010) assumed a linear technology where one









Gallie et al. · doi:10.1093/molbev/sys000

unit of effective labor produces a fixed amount of output. The remainder of the paper is structured as follows. Section introduces the theoretical model. Section analytically examines the impact of delayed childbearing on capital accumulation and welfare. Section numerically examines the general case where only a fraction of agents delay their childbearing. Section considers extensions of the model with a lower lifetime fertility rate and technological progress. Section concludes the paper. Appendices A and B provide the proofs of the lemmas.

Delayed childbearing has been broadly observed in developed countries. Between 1975 and 2005, the fraction of Japanese children who were born to mothers in their 20s decreased from 75% to 45%, whereas those born to mothers in their 30s increased from 20% to 52%. A similar trend is observed in the United States and advanced European countries (Gustafsson and Kalwij, 2006), and also in Canada, Australia, and New Zealand?. Interestingly, as pointed out by Bongaarts and Feeney (1998), even when the cohort's lifetime fertility rate (the number of children a mother has in her lifetime) does not fall, the delayed childbearing alone leads to a decline in the number of childbirths, measured by the total period fertility rates (TPFRs). Ogawa and Retherford (1993), Kohler et al. (2002), and Sobotka (2004) confirmed that, to a certain extent, the delay of marriage and motherhood is responsible for the observed period fertility rate

decline (now known as the 'tempo effect'). This paper considers an overlapping generations model without external effects or a social security system. Nonetheless, we show that a population decline can worsen the welfare of agents if it is caused by a change in the timing of childbirth or, more specifically, when many people decide to delay childbearing to older ages.

The seminal studies that incorporated the tempo effect into economic theory are Happel et al. (1984) and (?). These studies constructed models where women endogenously choose their career paths or the accumulation of human capital. For empirical studies on this issue, see (?), which employed the National Longitudinal Survey of Youth to investigate the return to delayed childbearing in the US. Using Japanese panel data, Higuchi (2001) investigated the effects of labor market changes on the timing of marriage, childbirth, and employment. Incorporating this idea into the theory of economic growth, Iyigun (2000), ?, Mullin and Wang (2002), and d'Albis et al. (2010) constructed dynamic general equilibrium models where the timing of childbirth is endogenous.

 Consider a fall in population induced by a decline in the number of births in the economy, taking as given mortality and migration.









- 2) It is well known that a lower population growth raises the capital–labor ratio in the Solow–Swan growth model.
- 3) The same property holds in Diamond's (1965) overlapping generations model, and it enhances welfare as long as the economy is dynamically efficient; i.e., when the interest rate exceeds the population growth rate.

Complementary to these preceding studies, this paper focuses on the aspect that delayed childbearing changes the age structure of the labor force. When a considerable fraction of mothers begin to delay childbearing, it causes a temporary baby bust in the economy, and the echoes of the initial baby bust create long-lasting demographic cycles.

- Consider a fall in population induced by a decline in the number of births in the economy, taking as given mortality and migration.
- It is well known that a lower population growth raises the capital—labor ratio in the Solow—Swan growth model.
- The same property holds in Diamond's (1965) overlapping generations model, and it enhances welfare as long as the economy is dynamically efficient; i.e., when the interest rate exceeds the population growth rate.

A similar trend is observed in the United States and advanced European countries (Gustafsson and Kalwij, 2006), and also in Canada, Australia, and New Zealand (Sardon, 2006). Interestingly,

as pointed out by Bongaarts and Feeney (1998), even when the cohort's lifetime fertility rate (the number of children a mother has in her lifetime) does not fall, the delayed childbearing alone leads to a decline in the number of childbirths, measured by the total period fertility rates (TPFRs).

# Model

#### Demographic structure

Let us consider an overlapping generations model where each agent lives for four periods, referred to as child, young, middle-aged, and old. A group of young agents in period t (i.e., those who are born in period t-1) is called generation t, and its cohort size is denoted by  $N_t$ . Each agent has one child during her lifetime (the gender of the agents is not considered), and she is able to bear a child either in her youth or middle age. In this paper, we say that an agent 'delays childbearing' if she bears her (only) child in her middle age.

# $Demographic\ structure$

Let us denote by  $\lambda_t \in [0,1]$  the fraction of agents among generation-t agents who delay childbearing. This means that among the generation-t agents with population  $N_t$ , the fraction  $\lambda_t$  bear their children in their middle age (period t+1), and the remaining fraction  $1-\lambda_t$  bear their children in their youth (period t). The cohort size of generation t+1, born in period t, is thus determined by:

$$N_{t+1} = (1 - \lambda_t) N_t + \lambda_{t-1} N_{t-1}. \tag{1}$$









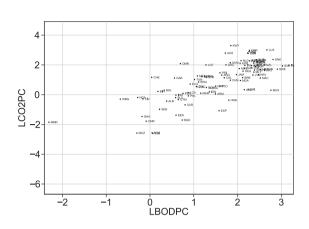
Gallie et al. · doi:10.1093/molbev/sys000

To highlight the effect of age distribution on capital accumulation and welfare as simply as possible, the timing of childbearing is assumed to be exogenous throughout the analysis. Doepke (2005) showed that the timing of childbirth is affected by the child mortality rate in a sequential fertility choice model. A decline in child mortality also reduces the uncertainty about the number of surviving children, which lowers the fertility rate and raises educational investment, causing the demographic transition (Kalemli-Ozcan, 2002, 2003; Tamura, 2006). We consider the situation where all agents until generation -1bear their children when they are young, and from generation 0 a constant fraction  $\lambda$  of agents bear their children when they are middle-aged, i.e.:

$$\lambda_t = \begin{cases} 0, \ t < 0, \\ \lambda, \ t \ge 0. \end{cases} \tag{2}$$

We normalize the cohort size so that  $N_0=1$  holds. As equations (1) and (2) imply that the cohort size is constant until period 0,  $N_t=1$  holds for all  $t \le 0$ . When delayed childbearing begins, the period fertility rate temporarily falls. In period 0, only fraction  $1-\lambda$  of generation-0 young agents bear children, while the generation-(-1) middleaged agents do not bear children because they completed childbearing in the previous period (i.e.,  $\lambda_{-1}=0$ ). Thus, the cohort size of generation 1, who are born in period 0, is given by:

$$N_1 = 1 - \lambda. \tag{3}$$



**FIG. 1.** Fluctuations in Cohort Size  $N_t$  over Generations.

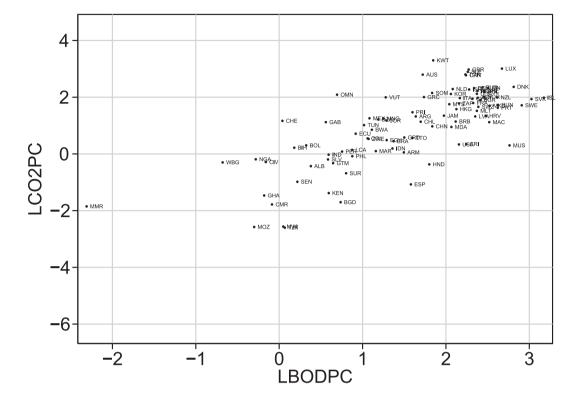
From period 1 on, not only a fraction  $1-\lambda$  of young agents, but also a fraction  $\lambda$  of middle-aged agents bear children. Hence, the period fertility rate recovers to some extent, which is consistent with Bongaarts and Feeney (1998). Substituting  $N_0=1, N_1=1-\lambda$ , and equation (2) into (1), the cohort size after generation 0 is solved as  $N_t$ =  $\frac{1}{1+\lambda} \left( 1 + (-1)^t \lambda^{t+1} \right)$  for  $t \ge 0$ . Figure 1 depicts the sequences of  $N_t$  for various levels of  $\lambda$ . It shows that the cohort size  $N_t$  fluctuates after delayed childbearing begins (i.e., after period 0), and that the amplitude of oscillation is larger when  $\lambda$  is higher. This indicates that the initial fluctuation of age structure (i.e., the fall in the fertility rate in period 0 and a recovery in period 1) has recurrent 'echo effects' over many generations. If  $\lambda \in (0,1)$ , the fluctuation decays and  $N_t$  converges to a stationary level at  $\lim_{t\to\infty} N_t = 1/(1+\lambda)$ , This is consistent with Lotka's stable population theory, which states that in a closed economy where there is no migration, a long-run age distribution becomes time invariant when age-specific fertility and mortality rates are constant (see Keyfitz and







LTSP in  $E.\ coli$  and  $P.\ fluorescens$  · doi:10.1093/molbev/sys000



**FIG. 2.** Fluctuations in Cohort Size  $N_t$  over Generations.

Caswell, 2005). although  $N_t$  fluctuates forever in the polar case of  $\lambda = 1$ .

#### Economic environment

Agents undertake no economic activity in their childhood, supply one unit of labor inelastically in their youth and middle age, respectively, and retire when old. The total labor force in period t is thus expressed as:

$$L_t = N_t + N_{t-1}, (4)$$

which is depicted in Fig. 1 for various levels of  $\lambda$ . This figure shows that the delayed childbearing decreases the labor force permanently even when the lifetime fertility rate is held constant, and the level of  $L_t$  is lower when a larger fraction of agents decide to delay childbearing (i.e., when  $\lambda$  is higher). Using  $N_t = \frac{1}{1+\lambda} \left(1 + (-1)^t \lambda^{t+1}\right)$ ,

the total labor force is expressed as  $L_t = \frac{1}{1+\lambda} \left(2+(-1)^{t-1}\lambda^t(1-\lambda)\right)$  for  $t \ge 1$ . In period 0, it is given by  $2-\lambda$ . It can be shown analytically that  $L_t$  is a decreasing function with respect to  $\lambda$  when  $0 \le \lambda \le 1$ . Similarly, the total population,  $\sum_{j=-1}^2 N_{t-j}$ , also decreases as  $\lambda$  increases. Observe also that the labor force  $L_t$  has much smaller oscillations than the cohort size  $N_t$  (in fact, there is no oscillation when  $\lambda = 1$ ). We will show that the fluctuations in the age composition of the labor force, rather than in the size of the labor force itself, drive the economic dynamics in this model.

There is a single final good in each period that can be used for either consumption or investment. Consumption takes place when agents are middleaged and old. For simplicity, we do not explicitly consider consumption in childhood and youth as









the main results are not qualitatively affected. We also ignore the utility from and the costs of having children. See, for example, Tamura (2006) for the fertility decision through utility maximization. The utility of a generation-t agent is given by:

$$U_t = \log c_{m,t+1} + \beta \log c_{o,t+2}, \tag{5}$$

where  $c_{m,t+1}$  and  $c_{o,t+2}$  represent generation-t consumption in their middle age (period t+1) and old age (period t+2), respectively.

Let  $w_t$  and  $r_t$  denote the wage rate and the gross interest rate (i.e., including the principal) in period t. Then, the budget constraint of a generation-t agent is:

$$a_{y,t} = w_t, (6)$$

$$c_{m,t+1} + a_{m,t+1} = w_{t+1} + r_{t+1}a_{y,t}, (7)$$

$$c_{o,t+2} = r_{t+2} a_{m,t+1}, (8)$$

where  $a_{y,t}$  and  $a_{m,t+1}$  denote the amounts of assets held by a generation-t agent when she is young and middle-aged, respectively. Maximizing (5) subject to (6)-(8) yields:

$$c_{m,t+1} = (1-z)(r_{t+1}w_t + w_{t+1}), (9)$$

$$a_{m,t+1} = z(r_{t+1}w_t + w_{t+1}), (10)$$

where  $z \equiv \beta/(1+\beta)$  denotes the propensity to save by the middle-aged, which is a key parameter in the following analysis.

Observe that in period t, aggregate savings consist of the asset holdings of young agents,  $a_{y,t}N_t$ , and the assets held by the middle-aged,  $a_{m,t}N_{t-1}$ . These aggregate savings, denoted by  $S_t$ ,

become the capital stock in the next period. From (6) and (10), this means that the capital stock in period t+1, denoted by  $K_{t+1}$ , is determined as:

$$K_{t+1} = S_t = a_{y,t} N_t + a_{m,t} N_{t-1} = w_t N_t + z(r_t w_{t-1} + w_t) N_{t-1}.$$
(11)

Goods are produced competitively by a representative firm using labor and the capital stock. The aggregate amount of production is given by a standard Cobb-Douglas production function  $Y_t = AK_t^{\alpha}L_t^{1-\alpha}$ , where parameter A > 0 is total factor productivity, whereas parameter  $\alpha \in (0,1)$  represents the share of capital. The production function can be expressed in terms of per-worker values as  $y_t = Ak_t^{\alpha}$ , where  $y_t \equiv Y_t/L_t$  is output per worker and  $k_t \equiv K_t/L_t$  is the capital-labor ratio. Denoting the capital depreciation rate by  $\delta \in [0,1]$ , the profit-maximizing condition for the firm implies that the factor prices in equilibrium are:

$$r_t = A\alpha k_t^{\alpha - 1} + 1 - \delta \equiv r(k_t), \tag{12}$$

$$w_t = A(1 - \alpha)k_t^{\alpha} \equiv w(k_t). \tag{13}$$

Substituting these factor prices into (11) gives the evolution of per-worker capital over generations:

$$k_{t+1} = A(1-\alpha) \frac{N_t k_t^{\alpha} + z N_{t-1}}{N_{t+1} + N_t}, \qquad (14)$$

where we used the fact that  $k_{t+1} = K_{t+1}/L_{t+1} = K_{t+1}/(N_{t+1}+N_t)$ . Recalling that the timing of childbirth  $\lambda_t$  for all t is given by (2), equation (1) and initial condition  $N_{-1} = N_0 = 1$  determine the demographic dynamics  $N_t$  for all t. Then, given









LTSP in E. coli and P. fluorescens  $\cdot$  doi:10.1093/molbev/sys000

Table 1. Evolution of Demographic Structure When  $\lambda=1$ . Numbers in Italic Indicate the Cohorts in the Labor Force

	Period −1	Period 0	Period 1	Even periods $t=2,4,\ldots$	Odd periods $t = 3,5,$
Old	1	1	1	1	0
Middle-Aged (worker)	1	1	1	0	1
Young (worker)	1	1	0	1	0
Child	1	0	1	0	1

NOTE.—Therefore, they earn the entire output  $Y_t$ . The middle-aged are the sole savers in odd periods, and they save fraction z of their income. Throughout this section, we focus on the polar case of  $\lambda = 1$ , where all agents beginning from generation 0 bear children in middle age.

the path of  $N_t$  and the initial two values of capital,  $k_0$  and  $k_{-1}$ , (14) determines the dynamic path of the capital–labor ratio  $k_t$  for all t.

# **Dynamic Effects of Delayed Childbearing**

In the following, we investigate the dynamic effects of delayed childbearing on capital accumulation and welfare. Throughout this section, we focus on the polar case of  $\lambda=1$ , where all agents beginning from generation 0 bear children in middle age. Although this case is not very plausible, it allows us to analytically explain the effect of delaying childbearing in a simple way. We also assume full capital deprecation  $(\delta=1)$  in this section. The general case with  $\lambda, \delta \in (0,1)$  will be numerically investigated in the next section.

Equilibrium path when all agents delay childbearing

When  $\lambda=1$ , the demographic dynamics (1) simplify to  $N_{t+1}=N_{t-1}$  for all  $t\geq 1$ . Substituting  $N_0=1$  and  $N_1=0$  from (3) into this equation, it turns out that  $N_t=1$  for all even t and  $N_t=0$  for all odd t. Table 1 describes the implied demographic structure at each point in time. Note that the whole labor force consists only of young workers in even periods, and only of

middle-aged workers in odd periods. Of course, this is an extreme possibility: young and middle-aged workers would coexist if  $\lambda \in (0,1)$ . However, the important point is that the composition of young and middle-aged workers in the labor force fluctuates, which is still true for  $\lambda \in (0,1)$ . Observe from the demographic dynamics illustrated by Fig. 2 that the young workers are the majority (i.e.,  $N_t > N_{t-1}$ ) in the even periods, whereas the middle-aged workers are the majority (i.e.,  $N_t < N_{t-1}$ ) in the odd periods.

With the path of  $N_t$ , we can derive the equilibrium path of the capital–labor ratio  $k_t$ , given the initial  $k_0$  and  $k_{-1}$  values. Substituting  $N_0 = N_{-1} = 1$  and  $N_1 = 0$  into (14) for t = 0, we obtain the capital–labor ratio in period 1: Recall also that we have assumed  $\delta = 1$  for this section.

$$k_1 = A(1-\alpha) \left[ (1+z)k_0^{\alpha} + zA\alpha k_0^{\alpha-1} k_{-1}^{\alpha} \right].$$
 (15)

This pattern of dynamics can be intuitively interpreted in terms of the aggregate saving rate (adjusted for labor force growth), defined by:

$$v_t \equiv \frac{S_t}{Y_t} / \frac{L_{t+1}}{L_t} = \frac{K_{t+1}/L_{t+1}}{Y_t/L_t} = \frac{k_{t+1}}{Ak_t^{\alpha}}.$$
 (16)

As labor force  $L_t$  is constant at 1 for all  $t \ge 1$  (see Fig. 1),  $v_t$  simply represents the aggregate saving rate for  $t \ge 1$ .





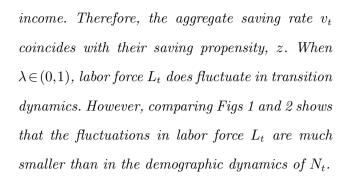


Using this definition, the first line of equation (??) can be restated as  $v_t = 1 - \alpha$ . In even periods, young agents are the sole workers, and thus they earn the labor share of output,  $(1-\alpha)Y_t$ . At the same time, they are also the sole savers in even periods, and because they save their income entirely, aggregate savings coincide with their income,  $(1-\alpha)Y_t$ . Therefore, in even periods, the aggregate saving rate  $v_t$  is determined by the labor share of the production,  $1-\alpha$ .

**Theorem 1** The middle-aged are the sole savers in odd periods, and they save fraction z of their income. Therefore, the aggregate saving rate  $v_t$  coincides with their saving propensity, z. When  $\lambda \in (0,1)$ , labor force  $L_t$  does fluctuate in transition dynamics. However, comparing Figs 1 and 2 shows that the fluctuations in labor force  $L_t$  are much smaller than in the demographic dynamics of  $N_t$ .

For odd periods, the second line of equation (??) can be restated as  $v_t = (1-\alpha)z(1+\alpha/v_{t-1})$ . Note that  $v_{t-1}$  in this equation refers to the aggregate saving rate in even periods, which is  $1-\alpha$  as shown above. By substituting  $v_{t-1}=1-\alpha$  into the above equation, it simplifies to  $v_t=z$ . In odd periods  $(t \geq 3)$ , the middle-aged are the only workers. In addition, the capital used in odd periods is owned solely by the middle-aged, because they are the only savers in the previous period (when they were young in even periods). Therefore, they earn the entire output  $Y_t$ .

**Lemma 1.** The middle-aged are the sole savers in odd periods, and they save fraction z of their 10



To summarize, the aggregate saving rate  $v_t$  exhibits a two-period cycle after period 2: There is no cycle in the knife-edge case of  $1-\alpha=z$ . For completeness,  $v_0$  is obtained by  $v_0=k_1/(Ak_0^\alpha)$ , where  $k_0$  is a part of the initial condition and  $k_1$  is given by (1). The level of  $v_1$  is then obtained by  $v_1=(1-\alpha)z(1+\alpha/v_0)$ .

for 
$$t \ge 2$$
,  $v_t = \begin{cases} 1 - \alpha \text{ if } t \text{ is even,} \\ z \text{ if } t \text{ is odd.} \end{cases}$  (17)

Note that either the saving rate in even periods  $1-\alpha$ , or that in odd periods z, could be larger. On one hand, young workers have a high saving propensity (unity), but they save only out of labor income  $(w_t)$ . On the other hand, middleaged workers earn both labor and capital income  $(w_t + r_t w_{t-1})$ , but their saving propensity is lower (z<1). From the Family Income and Expenditure Survey for wage-earning households with two or more persons in Japan, we confirmed that the average saving rate (1- the average propensity to consume) tends to fall with the age of the household head, from 32.0% (thirties) to 28.8% (forties) to 25.4% (fifties) and then to 11.3%(sixties) using 2000–2010 data. While some other reports find flat or rising age-saving profiles







LTSP in E. coli and P. fluorescens · doi:10.1093/molbev/sys000

(even after the retirement age), Jappelli and Modigliani (2005) pointed out that these are because contributions to pension funds (including employers' contribution) are not regarded as savings, and also because pension incomes are treated as income although they should be regarded as dissavings. They estimated the effects of social security on the age-saving profile in Italy, which showed that actual savings are highest when

Using the values of  $v_t$  in (17), we can derive the sequence of  $k_t$ . Note that (16) implies a simple relationship between the aggregate saving rate  $v_t$ and the evolution of the capital-labor ratio  $k_t$ :

the household head is in his/her late thirties and

then falls to zero around age 60.

$$k_{t+1} = v_t A k_t^{\alpha}. \tag{18}$$

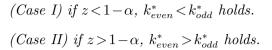
Taking the logs of (18) and applying this recursively, we obtain:

$$\log k_t = \left(\sum_{j=0}^{t-3} \alpha^j\right) \log A + \left(\sum_{j=0}^{t-3} \alpha^j \log v_{t-1-j}\right) + \alpha^{t-2} \log k_2, \text{ which converges to } (1-\alpha)^{-1} \log V_{odd}(z), \text{ where:}$$

$$(19) \qquad \qquad V_{odd}(z) = \left[(1-z)^{-1} \log V_{odd}(z)\right]$$

where  $k_2 = A(1-\alpha)z\{k_1^{\alpha} + A\alpha k_0^{\alpha} k_1^{\alpha-1}\}$  from (??),  $k_1$  is given by (1), and  $k_0$  (and  $k_{-1}$ ) is given as the initial value. This equilibrium path has the following property.

**Lemma 2.** In the equilibrium with  $\lambda = 1$ ,  $\left\{k_{t}\right\}_{t=0}^{\infty}$  converges to a two-period limit cycle regardless of the initial values. Define  $k_{even}^* \equiv$  $\lim_{s\to+\infty} k_{2s}$  and  $k_{odd}^* \equiv \lim_{s\to+\infty} k_{2s+1}$ , where s is an integer. Depending on  $z \equiv \beta/(1+\beta)$ , the relative magnitude of  $k_{even}^*$  and  $k_{odd}^*$  is:



*Proof.* As  $t \to \infty$ , the first term of (19) converges to  $(1-\alpha)^{-1}\log A$ , whereas the third term vanishes because  $\alpha \in (0,1)$ . When t is even (i.e., when t=2s for some integer s), from (17), the second term is expanded as  $\log z + \alpha \log(1 - z)$  $\alpha$ ) +  $\alpha^2 \log z + \alpha^3 \log(1-\alpha) + \cdots$ , which converges to  $(1-\alpha)^{-1}\log V_{even}(z)$ , where:

$$V_{even}(z) \equiv \left[ (1 - \alpha)^{\alpha} z \right]^{\frac{1}{1 + \alpha}} \tag{20}$$

is a geometric weighted average of the aggregate saving rate  $v_t$ . Observe that  $V_{even}(z)$  in (20) puts a higher weight on z than on  $(1-\alpha)$  because in even periods the most recent aggregate saving rate is  $v_{2s-1} = z$ . Similarly,  $V_{odd}(z)$  in (21) puts a higher weight on  $(1-\alpha)$ . Similarly, when t is odd (i.e., when t=2s+1), the second term is expanded as  $\log(1-\alpha) + \alpha \log z + \alpha^2 \log(1-\alpha) + \alpha^3 \log z + \cdots$ ,

$$V_{odd}(z) \equiv \left[ (1 - \alpha) z^{\alpha} \right]^{\frac{1}{1 + \alpha}}.$$
 (21)

From these, we conclude that the values of  $k_t$  in even and odd periods, respectively, converge to:

$$\lim_{s \to \infty} \log k_{2s} = \log k_{even}^* = \frac{1}{1 - \alpha} [\log V_{even}(z) + \log A],$$

(22)

(23)

$$\lim_{s \to \infty} \log k_{2s+1} = \log k_{odd}^* = \frac{1}{1 - \alpha} [\log V_{odd}(z) + \log A].$$

Note that  $V_{even}(z) < V_{odd}(z)$  holds if  $z < 1 - \alpha$ (Case I), whereas the opposite holds if  $z > 1 - \alpha$ 









(Case II). Therefore,  $k_{even}^* < k_{odd}^*$  holds if and only if  $z < 1 - \alpha$ . 

Proposition 1 states that if all agents from period 0 delay childbearing, the capital-labor ratio  $k_t$  eventually converges to a two-period limit cycle. This fluctuation is driven not by the size of the labor force (which is constant), but by the age distribution within it, through the fluctuations in the aggregate saving rate  $v_t$ . Figure 1 illustrates the limit cycles for the two cases, where the two loci are drawn by substituting  $1-\alpha$  (even periods) and z (odd periods) for  $v_t$  in the capital accumulation equation (18). Panel (i) shows that in Case I  $(z < 1 - \alpha)$ , the aggregate saving rate is higher in even periods, which results in a higher capital stock in odd periods. Conversely, panel (ii) depicts that the higher saving rate in odd periods results in the higher capital stock in even periods in Case II  $(z>1-\alpha)$ .

# Effects on capital accumulation

As we have seen in Fig. 1, delayed childbearing lowers the labor force permanently. This subsection examines how this affects capital accumulation in the economy by comparing the capital-labor ratio in the limit cycles to the economy without delayed childbearing.

Note that without delayed childbearing (i.e., when  $\lambda = 0$ ),  $N_t = 1$  holds for all t from (1) and the initial condition  $N_0=1$ . By substituting  $N_{t-1} = N_t = N_{t+1} = 1$  and  $\delta = 1$  into the capital accumulation equation (14), and rewriting the

resulting equation using  $v_t \equiv k_{t+1}/(Ak_t^{\alpha})$ , we obtain the evolution of the aggregate saving rate  $v_t$  for the case of  $\lambda = 0$ . From it, we find that the steady state level of  $v_t$  is a (positive) solution to a quadratic equation  $\xi(v) \equiv 2v^2 - (1-\alpha)(1+z)v \alpha(1-\alpha)z=0$ , which we obtain as:

$$v^*(z) \equiv \frac{1}{4} \{ (1-\alpha)(1+z) \}.$$
 (24)

Solving  $k^*/(A(k^*)^{\alpha}) = v^*(z)$  for  $k^*$ , the steady state capital–labor ratio for  $\lambda = 0$  is obtained as:

$$\log k^* = \frac{1}{1 - \alpha} [\log v^*(z) + \log A]. \tag{25}$$

It is apparent from (22), (23) and (25) that the relative magnitudes of the capital-labor ratios,  $k_{odd}^*$ ,  $k_{even}^*$ , and  $k^*$ , can be obtained by comparing  $V_{odd}(z)$ ,  $V_{even}(z)$ , and  $v^*(z)$ . To focus on the relevant situation, we assume that the share of capital is not too high:  $\alpha < (\sqrt{5} - 1)/2 \approx 0.618$ . With this assumption, we can show the following property.

Lemma 3. (i) At  $z=1-\alpha$ ,  $V_{odd}(z)=V_{even}(z)=$  $v^*(z) = 1 - \alpha \ holds.$ 

(ii) There exist  $\widehat{z} \in (0,1-\alpha)$  such that  $V_{odd}(\widehat{z}) =$  $v^*(\widehat{z})$  holds.  $V_{odd}(z) > v^*(z)$  holds if and only if  $z \in$ 

(iii) 
$$V_{even}(z) > v^*(z)$$
 holds if and only if  $z > 1 - \alpha$ .

*Proof.* Property (i) is immediately confirmed by comparing (20), (21), and (24) at  $z=1-\alpha$ . The proofs of (ii) and (iii) are given in Appendix 1.  $\square$ 

As summarized in Table 1, Proposition 1 and Lemma 1 imply three possibilities regarding the relative magnitudes of  $k_{odd}^*$ ,  $k_{even}^*$ , and  $k^*$ : It







LTSP in E. coli and P. fluorescens  $\cdot$  doi:10.1093/molbev/sys000

can also be shown that if  $z=1-\alpha$  (i.e., when capital does not fluctuate),  $k_{even}^*=k_{odd}^*=k^*$  holds. In addition, if  $z=\widehat{z},\ k_{even}^*< k_{odd}^*=k^*$  holds. We ignore these border cases because they do not occur except for a (measure 0) coincidence.

Observe that the lower end of the limit cycle  $(\min\{k_{odd}^*, k_{even}^*\})$  is always smaller than the steady state level  $k^*$  in the economy without delayed childbearing (which we call the benchmark economy). In addition, if z is sufficiently small  $(z < \hat{z})$ , the upper end of the limit cycle can also be smaller than  $k^*$ . This means that the long-term levels of the capital-labor ratio  $k_t$ in the delayed childbearing economy are always smaller than the steady state capital-labor ratio  $k^*$  in the benchmark economy. This might seem paradoxical, given that in the delayed childbearing economy, the labor force remains low compared with the benchmark economy (compare  $\lambda=1$  to  $\lambda = 0$  in Fig. 1). This paradoxical result can be explained by the alternating age composition in the labor force. Recall from (17) that the aggregate saving rate alternates between  $1-\alpha$  and z. In Case Ia, the saving propensity of the middleaged agents,  $z \equiv \beta/(1+\beta)$ , is small. Thus, in odd periods, when the labor force is entirely composed of middle-aged agents, the aggregate saving rate  $v_t = z$  is low. This makes capital per worker in the next period  $(k_{even}^*)$  considerably smaller than in the benchmark  $(k^*)$ , and therefore also the wage rate. As a result, workers in even periods, who are composed of young agents, receive substantially

lower incomes than in the benchmark economy. Thus, even though the aggregate saving rate in even periods  $v_t = 1 - \alpha$  is higher than that in the benchmark economy  $(v^*(z))$ , the amount of aggregate savings can be lower, which explains the possibility of  $k^*_{even} < k^*_{odd} < k^*$ . One may then wonder why  $k^* < k^*_{odd} < k^*_{even}$  never occurs in Case II. As we assumed  $\alpha$  to be lower than  $\left(\sqrt{5}-1\right)/2$ , the wage equation  $w_t = A(1-\alpha)k^{\alpha}_t$  has a certain degree of concavity with respect to  $k_t$ . This concavity implies that, while a negative deviation  $k^*_{even}$  from  $k^*$  in Case I results in a substantial drop in the wage income, a positive deviation of  $k^*_{even}$  from  $k^*$  in Case II results in a relatively small

#### Welfare effects

in Case II.

We now examine how the cycles in the capital—labor ratio in the delayed childbearing economy affect the welfare of agents. Note that, by substituting (8), (9), and (10) into (5), the utility of generation-t agents (those who are born in period t-1) is written as:

wage increase. Therefore,  $k_{odd}^*$  does not exceed  $k^*$ 

$$U_{t} = \beta \log z + \log(1-z) + (1+\beta)\log(r_{t+1}w_{t} + w_{t+1}).$$
(26)

Let us call those agents born in odd periods and thus young in even periods the 'even-period generations.' In the delayed childbearing economy ( $\lambda=1$ ), the whole population is composed only of the even-period generations ( $N_t=0$  for all odd t). Therefore, the long-term welfare of agents







in the limit cycle can be measured by  $U_{even}^* \equiv \lim_{s \to +\infty} U_{2s}$ . Using the limit-cycle values of the capital–labor ratio, we can write long-term welfare with  $\lambda = 1$  as:

$$U_{even}^* = (1+\beta)\log[A\alpha(k_{odd}^*)^{\alpha-1}(k_{even}^*)^{\alpha} + (k_{odd}^*)^{\alpha}],$$
(27)

where C is a constant term defined as  $C \equiv \beta \log \beta - (1+\beta)\log(1+\beta) + \beta \log A\alpha + (1+\beta)\log A(1-\alpha)$ . Similarly, long-term welfare in the benchmark economy  $(\lambda=0)$  can be written as:

$$U^* = (1+\beta)\log[A\alpha(k^*)^{2\alpha-1} + (k^*)^{\alpha}] - \beta(1-\alpha)\log k^* + C$$
(28)

Comparing (27) with (28), we have the following property.

As function  $\Omega(z)$  is continuous, Lemma 2 implies that when z is sufficiently close to 0,  $\Omega(z)$  must be negative, and hence  $U_{even}^* < U^*$  holds. The next proposition states this result.

As long as the saving propensity of the middle-aged,  $z \equiv \beta/(1+\beta)$ , is sufficiently small, or equivalently when the agents discount the future significantly (i.e.,  $\beta$  is small), the delayed childbearing ( $\lambda=1$ ) causes the long-run welfare of agents to fall compared with the case where delayed childbearing does not occur ( $\lambda=0$ ). This again seems paradoxical, because when the population falls from the initial level, it is usually anticipated that each agent enjoys a higher perworker capital and hence higher consumption. This does not hold true in this case, similar to the

discussion in the previous subsection, because of the fluctuations in the age composition of workers.

# Numerical Analysis

This section considers a general case where only a fraction of agents delay childbearing. When  $\lambda \in (0,1)$ , the fluctuations in  $N_t$  gradually settle to a long-term value (see Fig. 2). Nonetheless, the fluctuations in  $N_t$  continue for an extended number of generations, especially when  $\lambda$  is relatively large. For example, if 80% of agents delay childbearing ( $\lambda$ =0.8), it can be seen that substantial fluctuations in  $N_t$  remain even after 10 generations (around 200 years). This section examines their effects on capital accumulation and welfare in the transitional dynamics. We also relax the assumption of complete capital depreciation.

# Equilibrium dynamics under

For a given value of  $\lambda$ , the path of  $N_t$  is readily calculated as depicted in Fig. 2 using (1) and (2) along with initial condition  $N_0=1$ . As  $N_t=1$  for all  $t \leq 0$ , we reasonably assume that the economy has reached the steady state under  $N_t=1$  by period -1, and also remains at the same steady state at period 0. Note that, even though  $\lambda_t$  jumps up from 0 to  $\lambda > 0$  in period 0, the labor force is not immediately affected, nor is the capital–labor ratio, because the fertility in period 0 determines the amount of labor supplied in period 1 and beyond. We previously calculated this steady state in Subsection as the benchmark case, where the steady state level of the capital–labor ratio  $k^*$  is









LTSP in  $E.\ coli$  and  $P.\ fluorescens$  · doi:10.1093/molbev/sys000

given by (25). Thus, we use  $k_{-1}=k_0=k^*$  as the initial condition to calculate the path of  $k_t$  using (14).

We specify the parameters as follows. As an agent lives for four periods, one period in the model can be considered as approximately 20 years. If agents discount future consumption by 1% per quarter, as is often assumed in the literature, the discount factor  $\beta$  will be (1+  $0.01)^{-4\times20}\approx0.45$ . Therefore, we take  $\beta=0.45$  as the reference value, and also examine the low-beta  $(\beta=0.1)$  and the high-beta  $(\beta=0.9)$  cases. For the depreciation parameter  $\delta$ , Nadiri and Prucha (1996) estimated a yearly depreciation rate for the physical capital stock of 5.9%, and 1.2% for the R&D capital stock. The capital stock  $K_t$ in our model includes both physical and R&D capital stocks, but these estimates suggest that a good fraction of the aggregate capital stock that remains after 20 years would be R&D capital. Therefore we use a yearly depreciation rate of 2% as a reference (which means  $\delta = 0.33$  for a period of 20 years), and also examine the case of a higher depreciation rate of 5% per year ( $\delta = 0.64$ ). The share of capital  $\alpha$  is set to 0.4. As we do not distinguish between physical and human capital, the share of  $K_t$ ,  $\alpha$ , should be higher than the conventionally measured share of physical capital. Thus, we choose  $\alpha = 0.4$ , although the value of  $\alpha$ does not substantially change the pattern of the dynamics. The scaling parameter A is set to 1.5. Under these parameter values, we confirmed that

dynamic efficiency  $r_t > 1$  is always satisfied at the steady state.

Figure 2 shows the equilibrium paths of  $k_t$  for  $\beta = 0.1, 0.45, \text{ and } 0.9, \text{ respectively, and also for }$  $\delta = 0.33$  and 0.64. Each panel depicts 10 paths of  $k_t$ , where each path corresponds to the cases of  $\lambda = 0.1, 0.2, ..., 0.9, \text{ and } 1.$  In period 1, the labor force falls from 2 to  $2-\lambda$  because fraction  $\lambda$  of parents in the previous period decided to delay childbearing, and hence there are only 1- $\lambda$  young workers in this period. Note also that the aggregate capital stock is the same as in the initial steady state, because it is determined by the aggregate savings in the previous period. This result depends on the logarithmic period utility function, which implies that the savings of agents do not depend on the interest rate. If the agents are more risk averse (i.e., if the intertemporal elasticity of substitution is because they know that the interest rate in period lower than unity), the middle-aged agents in period 0 would somewhat increase savings, because they know that the interest rate in period 1 will be lower because of the reduced labor supply, and would want to supplement old-age consumption by saving more. Therefore, the magnitude of the initial fluctuations will be larger than shown in this paper. Therefore, the initial response of the capital-labor ratio is always positive, and  $k_1$  $(2/(2-\lambda))k^*$  is higher when  $\lambda$  is higher.

Observe from Fig. 1 that the labor force falls further in period 2 (except for the case of  $\lambda=1$ ,









Gallie et al. · doi:10.1093/molbev/sys000

steady state value  $k^*$ , whereas in odd periods they are barely above  $k^*$  (except for the case of  $\lambda = 1$ , where  $k_t$  in odd periods is also smaller than  $k^*$ , as we mentioned in Case Ia in Proposition 1). This asymmetry can be understood in terms of the reason why both  $k^*_{even}$  and  $k^*_{odd}$  can be lower than  $k^*$  when z is small, which we discussed in Subsection .

Figure 2(iii) shows that the pattern of the cycle is opposite when  $\beta$  is large. The capital–labor ratio is larger in even periods than in odd periods, similar to Case II in Proposition 2. When  $\beta$  is at an intermediate value ( $\beta$ =0.45), Fig. 3(ii) suggests that the pattern is similar to Case I if  $\lambda$  is large, whereas it is similar to Case II if  $\lambda$  is intermediate (and no cycle if  $\lambda$  is small). Finally, Fig. 3(iv) illustrates that a higher  $\delta$  shifts the entire path of the capital–labor ratio  $k_t$  downwards, but the effect of  $\delta$  on the pattern of the fluctuations is not clear from this figure.

To show the dependence of the pattern of cycles on parameter values more explicitly, we experimented with 40000 combinations of  $\lambda$  and  $\beta$  by varying each of them from 0.005 to 1.00 in 200 steps, and we repeated this for two values of  $\delta$ . We calculated the dynamic path of  $k_t$  for each combination of parameters until period 10, and then classified the result according to the pattern of movements, based on that in Proposition 3. The phase diagrams depicted in Fig. 2 summarize the result. When the combination of  $\lambda$  and  $\beta$  belongs to the area labeled as Case Ib, we find  $[k_t$  in even

where  $L_t$  falls to the bottom only in one period). At the same time, however, the aggregate capital stock is also lower than the initial steady state, because there were fewer young workers in the previous period  $(N_1=1-\lambda)$  who contributed to aggregate savings. Figure 2 shows that the second effect dominates, and the size of the fall in  $k_t$  at t=2 is larger when  $\lambda$  is larger. In addition, when  $\beta$  is small (i.e., when the saving propensity of the middle-aged  $z = \beta/(1+\beta)$  is small), the major portion of the aggregate savings depends on the savings by the young workers. Therefore, with large  $\lambda$  and small  $\beta$ , the fall in aggregate savings in t=2 is so large that  $k_2$  falls below (or 'overshoots') the initial capital-labor ratio  $k^*$ . For example, in Fig. 3, it can be observed that  $k_2 < k^*$  occurs when  $\beta = 0.1$  and  $\lambda \ge 0.6$ .

The pattern of dynamics after period 3 depends both on  $\lambda$  and  $\beta$ . When only a small fraction of parents delay childbearing, the fluctuations in cohort size  $N_t$  disappear in a relatively short period of time. Therefore, with small  $\lambda$ ,  $k_t$  settles to the steady state value  $k^*$  relatively quickly, without cycles. If  $\lambda$  is relatively large, two-period cycles in  $k_t$  are present, which last for many generations. The pattern of the cycles is comparable to the results we obtained in Proposition 1. Figure 2(i) shows that when  $\beta$  is small, the capital–labor ratio  $k_t$  is smaller in even periods than in odd periods, which corresponds to Case I (a and b) in Proposition 1. In particular, the values of  $k_t$  in even periods are far below the









LTSP in  $E.\ coli$  and  $P.\ fluorescens$  · doi:10.1093/molbev/sys000

periods]  $\langle k^* \langle [k_t \text{ in odd periods}] \text{ holds for all }$ t>3, whereas we find  $[k_t \text{ in even periods}] < [k_t]$ in odd periods]  $\langle k^* \rangle$  in the small area labeled as Case Ia. As explained in the text, we classify the pattern of the dynamics according to the level of  $k_t$  relative to the steady state value  $k^*$ . An alternative method of classification is to focus on the first difference of the capital-labor ratio,  $k_t - k_{t-1}$ , and examine if it is greater (or less) than zero. This calculation shows that the resulting phase diagram is almost identical to Fig. 2. The sign of  $k_t - k_{t-1}$  is positive only in odd periods in the area labeled as Case Ia and Ib, and the opposite holds in Case II. The sign of  $k_t - k_{t-1}$  is negative for all t > 3 in the 'No cycle' area because  $k_t$  monotonically falls to the steady state level. Similarly, in the area labeled as Case II,  $[k_t]$  in odd periods]  $\langle k^* \langle [k_t \text{ in even periods}] \text{ holds. In}$ the area 'No cycle,'  $k_t > k^*$  holds for all t > 3. The remaining white areas correspond to the border cases where the movements of  $k_t$  do not fit exactly any of the above patterns (e.g., when cycles are present until a certain period but disappear before period t=10).

Figure 3 confirms that cycles in the capital–labor ratio emerge when a certain fraction (around 0.4) of agents delay childbearing. When cycles emerge, the capital–labor ratio is higher in odd periods if the discount factor  $\beta$  (or equivalently the propensity to save z) is small, and vice versa. Observe also that the border between Case Ib and Case II bends toward the right as  $\lambda$  increases.

Thus, for a given intermediate  $\beta$ , the pattern of cycles can be reversed depending on the fraction of agents who delay childbearing  $(\lambda)$ . In addition, comparing panels (i) and (ii) in Fig. 2 shows that a higher depreciation rate  $\delta$  shifts the border to the right. Intuitively, when  $\delta$  is higher, the gross interest rate falls, which reduces the income of the middle-aged agents. This lowers aggregate savings in odd periods (when the middle-aged workers are the majority in the labor force), and in turn reduces the capital stock in even periods, making Case Ib more likely. In Proposition 2, we have shown that the border between Cases Ib and Case II is at  $z=1-\alpha$ , given  $\lambda=1$  and  $\delta = 1$ . As  $z \equiv \beta/(1+\beta)$ , this implies that the border would be at  $\beta = (1-\alpha)/\alpha$ , which is 1.5 if  $\alpha = 0.4$ . Therefore, it is almost impossible to obtain Case II under the assumption of  $\lambda = 1$  and  $\delta = 1$  (see footnote 2). However, the discussion in the text suggests that this is only because the highest combination of  $\lambda$  and  $\delta$  pushes the border too far away in the direction of the higher  $\beta$ . Under realistic values of  $\delta$ , Fig. 2 shows that both Case I and Case II are possible with a plausible range of  $\beta$ . Finally, observe that Case Ia is obtained under a reasonable depreciation rate, although it occurs only when  $\beta$  is very small (i.e., when agents discount the future quite significantly) and  $\lambda$  is close to one (i.e., when almost everyone delays childbearing).

It is intuitive that when  $k_t$  converges monotonically to  $k^*$ , the welfare of generations









Gallie et al. · doi:10.1093/molbev/sys000

 $U_t$  also converges to the steady state value  $U^*$ . Therefore, the region of 'No cycle' in Fig. 2 naturally corresponds to the same region in Fig. 3. The correspondence of the other regions can be understood in terms of the incomes that agents earn throughout their lives. Consider the case where the combination of  $\beta$  and  $\lambda$  belongs to the 'Case Ib' region of Fig. 2. This means that, after the initial response, the capital-labor ratio  $k_t$  is higher than the steady state value  $k^*$ in odd periods, whereas  $k_t < k^*$  in even periods. This pattern of movement in  $k_t$  affects the income profiles of agents differently depending on whether they belong to odd- or even-period generations. The odd-period generations (i.e., those who are young in an odd period t) enjoy high wage incomes in their youth because  $k_t > k^*$ , and also high interest incomes in their middle age because  $k_{t+1} < k^*$ . Although they suffer from low wage incomes in their middle age (because  $k_{t+1} < k^*$ ) and low interest incomes in their old age (because  $k_{t+2} > k^*$ ), the high incomes in the earlier part of their life affect their welfare more significantly because of discounting, and hence  $U_t$  tends to be higher than the steady state level,  $U^*$ . On the contrary, as summarized by the bottom row in Table 2, even-period generations (i.e., those who are young in an even period) lose income in the earlier part of their lives. Thus, their lifetime welfare  $U_t$  tends to be lower than  $U^*$ . As a result, [the welfare of the even-period generations]  $\langle U^* \langle$  [the welfare of odd-period generations] holds in the region labeled 'Case I' in Fig. 3.

Welfare analysis under

While we examined  $U_t$  only for even-period generations in Subsection , here we examine  $U_t$ for both even- and odd-period generations because  $\lambda \in (0,1)$  implies that  $N_t > 0$  for all generations t. By substituting the path of  $k_t$  into (12) and (13), we obtain factor prices,  $r_t$  and  $w_t$ , on the equilibrium path. Then, substituting these into (26) gives the welfare  $U_t$  for all generations. Similar to Fig. 2, we calculated 80000 paths of  $U_t$ by varying  $\beta$ ,  $\lambda$ , and  $\delta$ , and classified the pattern of evolution of  $U_t$  according to when  $U_t$  is above (or below) the welfare of agents in the initial steady state,  $U^*$ , as given by (28). Figure 3 shows that the resulting phase diagrams are basically similar to Fig. 2. Strictly speaking, there is a slight difference in the upper-right corner of Fig. 3(ii), where the pattern becomes ambiguous. Note that  $\beta$  is close to 1 in this region, which means that the agents do not care about the timing of consumption. We guess that this is one reason why cycles in  $U_t$  are less evident in this region (see Tables 1 and 2). Another slight difference is that there is no 'Case Ia' region in Fig. 3(i), while there was a small region of 'Case Ia' in Fig. 2(i).

Recall from Fig. 2 that even-period generations have larger cohort sizes than odd-period generations, and the difference is more significant when  $\lambda$  is higher. Therefore, the result in Table 2 suggests that the majority of agents









LTSP in E. coli and P. fluorescens  $\cdot$  doi:10.1093/molbev/sys000

in the economy suffer from welfare loss when the economy lies in Case I (i.e., when  $\beta$ , or equivalently z, is small). This can be viewed as a generalized result of Proposition 2, which has shown that the welfare of all agents falls if z is sufficiently small in the case where only even-period generations exist  $(\lambda=1)$ .

#### **Extensions and Robustness**

#### Declining population

Prior to the previous section, we examined the effect of delayed childbearing by assuming that each agent has exactly one child in her lifetime. This is equivalent to assuming that the lifetime fertility rate (LFR) is exactly at the replacement level. However, in most developed countries where delayed childbirth is observed, the lifetime fertility rate is far below the replacement level (with a possible exception of the United States, where the LFR is around the replacement level). This means that the population is declining in the long run, even without delayed childbearing. Here, we briefly examine the effect of delayed childbearing in the economy where each agent has, on average, less than one child in her lifetime.

Combining (1) with (2), we obtain the pattern of evolution of  $N_t$ . With the initial condition of  $N_0 = 1$  and  $N_1 = n(1-\lambda)$ , equation  $N_{t+1} = n(1-\lambda)N_t + n\lambda N_{t-1}$  for  $t \ge 1$  can be solved as  $N_t = c_1\sigma_1^t + c_2\sigma_2^t$ , where  $\sigma_1 = (n/2)\left\{1-\lambda+\sqrt{(1-\lambda)^2+(4\lambda/n)}\right\} > n$  and  $\sigma_2 = n(1-\lambda)-\sigma_1 < 0$ , given  $\lambda$ ,  $n \in (0,1)$ . As  $|\sigma_2| < |\sigma_1| < 1$ , the evolution of  $N_t$  in the long run is dominated by the  $c_1\sigma_1^t$  term, which means that

delayed childbearing increases the long-term rate of population growth from n to  $\sigma_1 > n$ . Figure 3(i) depicts the path of  $N_t$  for the case of n=0.8, which roughly corresponds to the lifetime fertility rate of 1.68 = 2.1 (replacement rate)  $\times 0.8$ . When  $\lambda > 0$ , the initial fall in the cohort population  $(N_1 = n(1-\lambda) < N_0 = 1)$  is more significant than the benchmark case ( $\lambda = 0$ ), not only because each agent has fewer children in their life, but also because a fraction  $\lambda$  of young agents in period 0 postpone childbearing until the next period. However, in the long run, the delay of motherhood slows the pace of depopulation compared with the case of  $\lambda = 0$ . As a result, for larger t, the the delay of population is actually higher when a larger fraction of agents delay childbearing.

In a similar way to that in Subsection , substituting the path of  $N_t$  into (14) gives the equilibrium dynamics for  $k_t$ , as shown by Fig. 2(ii). When compared with Fig. 3(ii), we observe that, although the pattern of the fluctuations are similar, the long-run capital—labor ratio  $k_t$  is lower than in the initial steady state, and the difference is larger when  $\lambda$  is higher. Intuitively, delayed childbearing in this economy (with n < 1) raises the long-run rate of population growth, which naturally leads to a lower capital—labor ratio through a capital-dilution effect. See Blanchet (1988) and Brander and Dowrick (1994) for more discussion on the capital-dilution effect by demographic growth.









**Table 2.** SH test results on nuclear and mitochondrial phylogenetic trees

Sequence data	Tree	$-\ln L$	SH test $P$ -value
mtDNA	mtDNA	-109219.5	0.5
mtDNA	Nuclear	-61720.8	< 0.00001
Nuclear	mtDNA	-113033.1	< 0.00001
Nuclear	Nuclear	-60699.9	0.5

As the capital-dilution effect has already been well studied, we examine whether there are cycles in the paths of  $k_t$  and  $U_t$  after removing this effect. Using the long-term rate of population growth with delayed childbearing  $\sigma_1$ =  $(n/2)\left\{1-\lambda+\sqrt{(1-\lambda)^2+(4\lambda/n)}\right\}$ , we calculate the long-term levels of  $k_t$  and  $U_t$ , which depend on  $\lambda$  because of the capital-dilution effect (see footnote). Then, we examine if there are cycles in the paths of  $k_t$  (and  $U_t$ ) relative to their respective long-term levels. The results are shown in Fig. 2. By comparing Fig. 2(i) with Fig. 2(i), we observe that the border between Case Ib and Case II shifts to the left because of a lower n. In addition to the effect of overall population decline, a lower nalso has an effect on the composition of the labor force: if agents have fewer children, the fraction of younger workers ceteris paribus will fall compared with older (middle-aged) workers. This increases the aggregate savings in odd periods raises the capital (when the middle-aged workers are the majority in the labor force), and in turn raises the capital stock in even periods, making Case II more likely.

The pattern of cycles in  $U_t$ , shown in Fig. 2(ii), generally matches the pattern in  $k_t$ , although in the upper-right corner we find that the welfare is

higher than the long-term level both for the oddand even-period generations, at least until t=10. However, note that this gain in welfare exists only after controlling for the capital-dilution effect. The overall effect of delayed childbearing on the capital-labor ratio and welfare is certainly more negative than analysed in the previous section because of the capital-dilution effect that shifts the entire paths of  $k_t$  and  $U_t$  downward.

# Technological progress

To ensure the robustness of the results obtained so far, here we confirm that the inclusion of technological progress does not significantly change the pattern of cycles induced by delayed childbearing. Assume that in every period there is exogenous technological progress that increases labor productivity by a factor of  $\gamma > 1$ . When labor productivity at period 0 is normalized to unity, production per worker can be represented as  $y_t =$  $A\gamma^t k_t^{\alpha}$ , where  $k_t \equiv K_t/(\gamma^t L_t)$  now represents the amount of capital per efficiency unit of labor. Note that the amount of labor income for each worker (not efficiency unit) should be modified from (13) to  $w_t = A(1-\alpha)\gamma^t k_t^{\alpha}$ , whereas the expression for  $r_t$  is the same as (12). Then, instead of (14), we obtain the evolution of  $k_t \equiv K_t/(\gamma^t L_t)$  as:

$$k_{t+1} = \frac{A(1-\alpha)}{\gamma} \frac{N_t k_t^{\alpha} + z N_{t-1} \left[ \left( A \alpha k_t^{\alpha-1} + 1 - \delta \right) k_{t-1}^{\alpha} \right]}{N_{t+1} + N_t}$$
(29)

Figure 1 shows the path of  $k_t$  in the presence of yearly labor productivity growth of 2%, i.e., when labor productivity is multiplied by  $\gamma =$ 









LTSP in E. coli and P. fluorescens  $\cdot$  doi:10.1093/molbev/sys000

 $1.49 \approx (1+0.02)^{20}$  in each period. It looks almost the same as the reference case of Fig. 3(ii), but the level of the whole path is lower than the equilibrium without technological progress. This is because technological progress expands the labor force measured in efficiency units, and thus dilutes capital per efficiency unit of labor.

Figure 1(i) depicts the pattern of cycles in  $k_t$ for various  $\beta$  and  $\lambda$ , under  $\gamma = 1.49$  and  $\delta = 0.33$ . When it is compared with the two panels in Fig. 2, this phase diagram matches more closely the high-depreciation case of Fig. 2(ii), where  $\delta = 0.64$  (5% annum), rather than the reference case with the same depreciation rate ( $\delta = 0.33$ ). This result suggests that technological progress affects the pattern of cycles in  $k_t$  in a similar way to a higher depreciation rate. Note that while technological progress in a given period enhances total output  $Y_t$  in that period, the amount of remaining capital after depreciation  $(1-\delta)K_t$  is unaffected because the latter is determined by the savings in the previous period. Therefore, technological progress reduces  $(1-\delta)K_t/Y_t$ , and hence lowers the proportion of income received by the middle-aged agents (who have claims on the remaining capital).

We also examined the pattern of cycles in the utility of generations,  $U_t$ . Note that, even in the steady state, labor income  $w_t$  increases by a factor of  $\gamma$  in each period. By substituting  $w_t = A(1-\alpha)\gamma^t k_t^{\alpha}$  into (26), it can be observed that the utility of generations has a trend term (1+

 $\beta$ )(log $\gamma$ )t. Therefore, after calculating the path of  $U_t$  for each  $\beta$  and  $\lambda$  by substituting the path of  $k_t$  into (26), we removed the trend by subtracting  $(1+\beta)(\log\gamma)t$  from it, and then examined the pattern of the cycles in the detrended path of  $U_t$ . Figure 2(ii) shows that the result is similar to Fig. 3(ii). This confirms that the effects of technological progress on the cycles of  $k_t$  and  $U_t$  are similar to the effects of a higher depreciation rate.

### **Concluding Remarks**

In a simple overlapping generations model, we examined the effects of delayed childbearing on capital accumulation and the welfare of generations. A notable feature of the delayed childbearing economy is that it causes fluctuations in the age composition of workers for a long period of time. As workers at different life stages have different sources of income and also different saving propensities, fluctuations in the age composition affect the aggregate saving rate, causing cycles in the capital-labor ratio. The cycles in the capital-labor ratio cause the lifetime welfare of agents to change generation by generation in an alternating fashion. Depending on the parameters, the majority of agents can experience lower lifetime welfare when the cycles in the capital-labor ratio affect the factor prices in such a way that their income in the early stage of their life falls. We also examined extensions of the model with declining population and technological progress, and confirmed the









Gallie et al. · doi:10.1093/molbev/sys000

robustness of our results. Our analysis suggests that delayed childbearing can also generate fluctuations in the age distribution of workers, which have differential welfare effects on cohorts.

Although our model is very stylized, it gives insights into a possible cause and effects of fluctuations in the age distribution of the labor force, which have been examined in different contexts in the literature. For example, Lee (1997) pointed out that baby booms and busts can cause fluctuations in the age structure. Mankiw and Weil (1989) investigated their effects on the US housing market. Our analysis suggests that delayed childbearing can also generate fluctuations in the age distribution of workers, which have differential welfare effects on cohorts.

This paper attempted to analyse the effects of the age distribution on capital accumulation and economic welfare as intuitively as possible. For this reason, our model treated the timing of childbirth and the number of children as exogenous. However, in analyzing the implications of policies that aim to cope with delayed childbearing and the low fertility rate, it will be necessary to clarify how agents endogenously choose the timing of their childbearing and the number of children. It will also be interesting to investigate the endogenous relationship between delayed childbearing and declining lifetime fertility rate, which in this study we assumed are independent. The exploration of these issues is left for future research. For example, Lee (1997)

pointed out that baby booms and busts can cause fluctuations in the age structure. Mankiw and Weil (1989) investigated their effects on the US housing market.

#### **Supplementary Material**

Supplementary tables S1?S7 and figures S1?S11 are available at Molecular Biology and Evolution online (http://www.mbe.oxfordjournals.org/).

# Acknowledgments

The authors gratefully acknowledge the help of John Novembre for providing ms scripts for the simulations of the isolation-by-distance model. The authors thank Abigail Bigham and Marc Bauchet for providing their compiled data set, Olivier Franc?ois for stimulating discussions, and Carina Schlebusch for providing information about the history of the Xhosa people. This work was supported by a grant from the Swedish Foundation for International Cooperation in Research and Higher Education (STINT) provided to M.J. and M.G.B.B. A grant of the French national research agency awarded to M.G.G.B. (DATGEN project, ANR-2010- JCJC-1607-01) provided a salary to F.J. during part of the work.



