Life history Theory Predicts Age of First Reproduction with Economic and Longevity Factors

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2013 Population Association of American Annual Meeting

Abstract

The age of first reproduction is known to correlate with economic- and longevity-related factors and a general pattern emerges in which reproduction timing is advanced when expected lifespan is shorter and timing is delayed with increased wealth and education. While these patterns have been considered with economic models, quantitative models based on life history theory are rare. In this paper I demonstrate that a simple life history model can generate the observed patterns. Moreover, the model contains only two parameters, one representing the rate of wealth accumulation and a second representing the rate at which reproductive capacity declines with age. The model is applied to data and illuminates implicit assumptions in life history theory that may not typically be considered in demography.

Introduction

The age of reproduction is a fundamental life history trait of great interest in both ecology and demography. Cross-species studies in animals reveal age of reproduction and expect life span (ELS) exhibit regular relationships with body mass and evolutionary theory explains these relationships in animal in terms of optimal strategies balancing a tradeoff between growth, fecundity and survival. The tradeoff expresses a population's fitness and is a cornerstone of natural selection theory. The timing of first child birth in human populations is a fundamental demographic variable that exhibits complex social-economic and historical patterns. Two separate approaches have evolved in considering the underlying causes of age of reproduction in humans; one based on optimizing wealth and one based on optimizing life time reproduction.

The economic theories have focused on the increasing age of first births (Cigno and Ermisch 1989, Gustafsson 2001), which exhibits a significant pattern with social-economic status. The first birth age has been considered in terms of maximizing family lifetime wealth. Models suggest that the husband's income is positively correlated with the time of first birth while the wife's pattern of wages is negatively correlated with the timing while education is positively correlated timing (Kravdal 1994). Happel et al. (1984) noted that for woman, assuming that wages increase with age and that child rearing removes them from the workforce, then earlier births reduce the income loss and so promotes earlier births in general. Studies have demonstrated that the age of reproduction depends on family income, which during the reproductive years increases with the age of the parents e.g. Klevmarken (2004). Additionally, the education level has a positive effect on birth timing (Ní Bhrolcháin and Beaujouan 2012) and in turn education is positively correlated with income (Griliches and Mason 1972). Thus, income and life time wage trajectories correlate with life style decisions that tend to correlate positively with birth timing, i.e. delaying the timing of the first child.

A second school of theory bases reproduction timing on patterns of mortality. For example, Wilson and Daly (1997) found parents in Chicago neighborhoods with shorter life expectancy tend to have their first child at earlier ages than parents in neighborhoods with longer life expectancy. However median household income did not correlate with life expectancy. In Caribbean societies reproductive timing exhibits complex relationships with infant and adult mortality. Similar patterns have also been observed in other communities and the age of birth timing correlates with the infant mortality rate (Quinlan 2010). Groups with moderately high levels of infant mortality tend to reproduce earlier than those with low or very high levels. Higher adult mortality rates also correlate with earlier birth timing, except in groups with very high infant mortality. Earlier birth timing also correlates with poor health of the mother in her childhood (Waynforth 2012). Nettle (2010) found a well-defined asymptotic positive relationship between neighborhood social-economic quality and age of reproduction in England. These studies are qualitatively based on life history theory in which fertility is higher when perceived life expectancy is lower (Anderson 2010).

Thus, we see two relatively distinct theories for the age of reproduction, one based on economic considerations maximizes wealth and one based life history considerations maximizes reproduction. While the economic theories tend to be highly quantitative, theories based on life history tend to be qualitative. Also, to some degree each approach does not consider the pattern that is the focal point of the other. In this paper I explore a model that combines economic and longevity factors in a quantitative life history framework.

The economic and life history theories address different levels of detail. Economic theory tends to consider in great detail the life-time economic consequences of birth timing. Life history theory tends to explain broader patterns that exist across species. Thus, the two approaches are somewhat incompatible. My immediate goal is to explore a model that addresses the effects of income on delaying reproduction timing and the effects of mortality in advancing the timing. Because, life history theory involves subtle and implicit assumptions that are not necessarily evident when the theory is discussed in a qualitative sense, I first present the basic elements of the theory and then demonstrate its application with a classical model of the reproductive timing of fish.

Life history Theory

In life history theory reproductive timing is explained in terms of a tradeoff of two general processes, age-increasing potential fecundity m against age-decreasing probability of survival l. Optimal age for reproduction is the age that maximizes the product of the two processes. For illustrative purposes consider a semelparous species. The expected total reproductive output is the product $m_x l_x$ and the age x* that maximizes reproduction occurs when the derivative is zero

$$\frac{dm_x l_x}{dx} = 0 \quad at \quad x = x^* . \tag{1}$$

Furthermore, the criteria for the optimum depends on the rates of change of the two processes balancing such that the specific rate of increase in fecundity with age just balances the specific rate of decline in survival with age giving

$$\frac{1}{m}\frac{dm}{dx} = -\frac{1}{l}\frac{dl}{dx} . \tag{2}$$

Implicit in this theory is that the decision to reproduce depends on the conditions at the moment. In applying the theory to animal populations we assume animals have evolved maturation systems that functionally meet the criteria of equation (2) and therefore animals optimize reproduction as a result of their genetics. Ecologists tend not to consider how an animal actually perceives the balance implied by equation (2), only that evolution has worked out the problem. However, in applying the theory to humans it is a fair question to ask – how an individual knows the best time to reproduce. Of course in practice, an individual need not reproduce at the optimum time but over a population it is implicitly assumed the criterion is achieved. It seems that for economic theories it is possible that individuals can project lifetime expectations of income and therefore use income changes from one year to the next to make a reproduction decision and thus effectively use the expected rate of yearly income change as the decision variable. However, if timing is based on life expectancy, it is interesting to consider how reproductive decisions would be based on changes in a sense of one's personal chance of survival. The point here is that applying life history theory to human reproduction implicitly assumes that humans make decision based on the instantaneous rates of change of their wellbeing. This assumption is not evident when qualitatively applying the theory.

Fish Model

To illustrate how life history theory has been applied in ecology consider the classical work by Roff (1984) that explained the age of reproduction across 30 stocks of fish. The model is based on age-dependent rates of survival and fecundity. Survival of fish was assumed to decline exponentially with age, $l \sim e^{-kx}$ where k is a mortality rate. Fecundity was assumed to be proportional to fish mass which was taken to increase according to the standard a von Bertalanffy growth function giving $m \sim (1-\mathrm{e}^{-gx})^3$ where g is a growth rate in terms of fish length. From equation (1) the optimum age of reproduction is simply

$$x* = \frac{1}{g}\ln\left(\frac{3g}{k}+1\right) . \tag{3}$$

The relationship of the variables is illustrated in Figure 1. The optimum time of reproduction occurs when the specific rate of decline of survival *l* with age equals the negative of the specific rate of increase of fecundity *m*. Note that increases in growth rate and mortality rate both decrease the reproduction time (Figure 2) and have about equal impacts on the age of reproduction as expressed by the slopes of the lines at *x**.

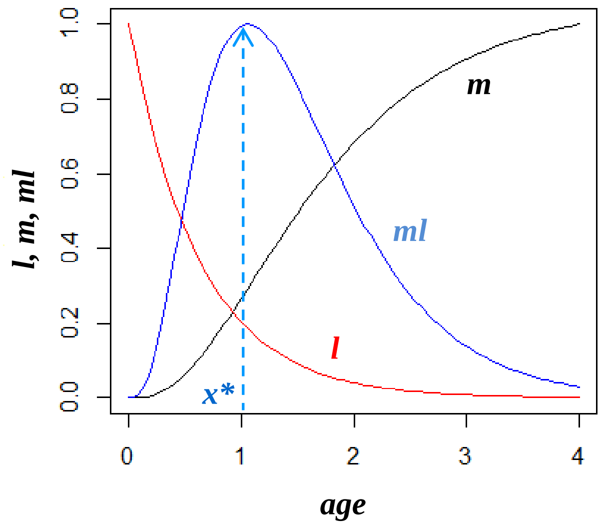

Figure 1. Example of life history parameters for stickleback fish from (Roff 1984). Survival *l*, fecundity *m* and reproduction potential *ml* as a function of age *x* in years. Optimal age of reproduction is *x determined from equation (3). Variables are normalized to unity. Model parameters: *g* = 1, *k* = 1.6.**

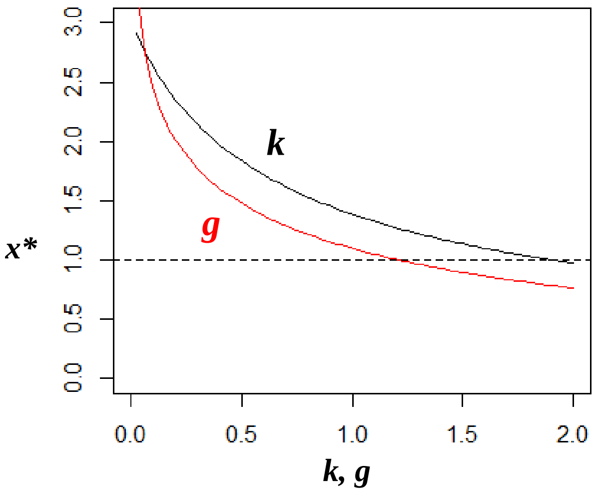

Figure 2. Effect of growth rate *g* and mortality rate *k* on optimal age of reproduction *x is determined from equation (3) based on stickleback fish from (Roff 1984). Dashed line is *x**.**

Human Model

Based on the literature of reproduction timing in humans we express the tradeoff in equation (2) in terms of a measure of income accumulation m and a measure of physiological status l. If we take life history theory at its face value, the reproduction decision depends on a balance in the rates of change of the positive and negative factors that contribute to the decision. We may postulate several categories of factors that contribute to these two general measures.

First consider the physiological measure. We require an equation that generally declines with age and therefore promote births at earlier ages. Factors may involve the individual's sense of longevity as it affects the number of years available to raise a child. Clearly, early reproduction timing allows more years of a parent's overlap with the child and so the force of this factor declines with increasing age of reproduction. A second category includes the intrinsic vitality or energy that a parent is able to devote to child care. This factor also declines with age. A third category encompasses birth defects which increase with parent age. Finally, we require a lower limit on the age of reproduction. Therefore, a physiological measure involves both expectations of future sharing and child health as well as the immediate assessments of the current capacity of the parents, the probability of birth defects and physiological maturation schedules, i.e. menarche.

Following the tradition of models in life history theory, consider a simple continuous function that contains the desired properties for a physiological measure, i.e., zero at the parent's birth, climbing to a peak at after puberty and then declining. A simple function with these properties is $l = xe^{-rx}$. Notably, the function is 0 at $x = 0$ increases to a maximum value at $x_0 = 1/r$ and then declines in an exponential-like manner with x. The peak x_0 is a fundamental property of the model and represents a measure of the optimum physiological age of reproduction based on the tradeoff of linearly increasing reproductive capacity expressed by the x and the exponentially declined reproductive capacity expressed by e^{-rx}.

In considering the economic measure of reproduction timing first note that economic theories generally assume that child rearing is a lifelong undertaking requiring a lifetime perspective in the economic variables (Gustafsson 2001). Lifelong considerations may at first seen to contradict life history theory, which as expressed by equation (2) considers the instantaneous rates of change of competing factors. Thus, in life history theory the rate of wealth accumulation is important, not the life time accumulation of wealth. From this perspective the detailed characteristic of economic models might be ignored and we focus on the overall rate of wealth accumulation.

To develop the economic component, assume wealth accumulates as a sub-exponential growth function $dm/dx = \alpha m^{\beta}$ where α is a wealth scale factor and β is the wealth accumulation shape factor. We might also consider that β is a life-time expectation of an individual and therefor may vary with social economic status. For example, educated individuals expect to accumulate more wealth than less educated people. In this manner β does express a lifetime measure but it plausibly would adjust according to economic conditions. The rate is bounded, $0 < \beta < 1$, where if $\beta = 0$ wealth accumulates linearly over life and as $\beta \to 1$ accumulation approaches an exponential rate. Since β is assumed to reflect social-economic status this factor takes on added significance in contributing to reproduction timing. The resulting life time wealth then is described $m = \left(\alpha(1-\beta)\right)^{\frac{1}{1-\beta}} x^{1/(1-\beta)}$ or simplifying the coefficients as $m = ax^b$.

Now combining these physiological and economic functional forms into m_x and l_x in equation (2) the human reproduction time becomes

$$x^* = \frac{1}{r}\left(\frac{1}{1-\beta} + 1\right) \tag{4}$$

where again β is the economic factor expressing the rate of wealth accumulation and r is the physiological factor expressing the rate at which reproductive capacity declines with age. The properties of the model illustrated in Figure 3 and the relationship of the model parameters to age of reproduction is illustrated in Figure 4. Note that age of reproduction increases as the wealth accumulation rate increases and declines as the rate of physiological decline increases.

The wealth rate parameter was derived by fitting $m = ax^b$ to data on the median family wealth in Sweden in 1998 (Klevmarken 2004). The physiological rate r was then adjusted to fit the mean age of first births in Sweden in 1997 (Gustafsson 2001). Thus, the model was completely fit with independent economic and demographic information.

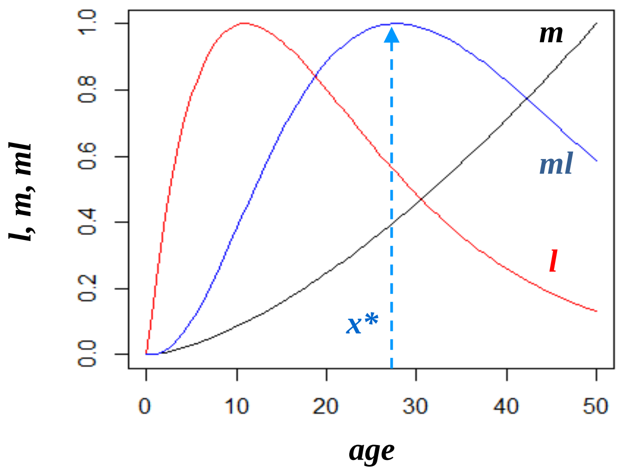

Figure 3. Example of life history variables for Swedish population. Reproductive capacity *l*, wealth *m* and reproductive potential *ml* are functions of age in years. Optimal age of reproduction is x^* from equation (4). Variables are normalized to unity. Model parameters: $\beta = 0.34$, $r = 0.09$, $\alpha = 1$.

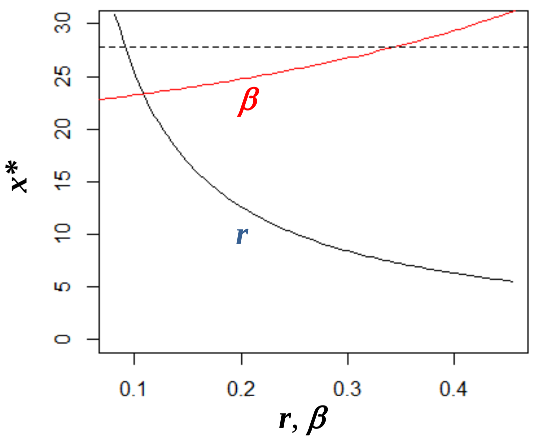

Figure 4. Effect of wealth accumulation rate β and physiological capacity rate *r* on optimal age of reproduction is x^* determined from equation (4). Data based on Swedish wealth accumulation rate (Klevmarken 2004). Dashed line is age of reproduction from base parameters.

Discussion

Life history theory is well established as an approach to understand and predict life history traits in animal populations and it reduces the reproductive decisions to a tradeoff between survival and fecundity. In this paper I apply the principles of the theory to model the effects of economic and physiological processes on the age of first reproduction in human populations. Although this results in an extreme distillation of the factors involving human reproductive decisions, the approach may have value from a heuristic perspective, in particular for illuminating implicit assumptions in such models. In humans the implicit assumption of this simple model is that two opposing groups of processes determine the age of reproduction. The optimal reproduction age occurs when rate change of factors promoting later birth times, e.g. wealth, balances the rate of change of favoring promoting earlier birth times, e.g. health. In this interpretation that decision of when to reproduce does not depend on the absolute values of the competing processes, but on how they change with age.

What factors and how they contribute to reproductive decisions is not captured by a simple life history approach but he literature on reproductive timing indicates that social-economic and health factors are important. This exploratory paper demonstrates that simplistic representations of how these measured might change with age does generate realistic reproductive timing. It remains to be determined if this approach has utility. However, two points emerge. First, in this model the reproductive timing is strongly affected by the physiology factor *r* and weakly affected by the economic factor β. This comports with general observations that within social-economic groups the age of reproduction has increased only slightly over time (one or two years over a half century) (Gustafsson 2001) while across social-economic groups the timing varies by a decade (Nettle 2010). Perhaps the most interesting concept that emerges is the reproductive decisions might be formed by the rate of change of opposing processes not their absolute levels. Such a rate-drive perspective might suggest that forces shaping demographic patterns might also be considered in terms of the immediate states of individuals.

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