ELSEVIER

Evolution and Human Behavior 32 (2011) 433 – 443

Evolution and Human Behavior

Theoretical Contribution

Age at first reproduction and probability of reproductive failure in women

Jianghua Liu*, Virpi Lummaa

Department of Animal and Plant Sciences, University of Sheffield, United Kingdom

Initial receipt 3 February 2010; final revision received 23 October 2010

Abstract

Life history theory predicts a trade-off between fitness benefits and costs of delaying age at first reproduction (AFR). In many human populations, maternal AFR has been increasingly delayed beyond sexual maturity over the past decades, raising a question of whether any fitness benefits accrued outweigh costs incurred. To investigate the cost–benefit trade-off concerning AFR in women, we construct a theoretical model and test its predictions using pedigree data from historical Finnish mothers. The model predicts that the probability of reproductive failure (no offspring produced reaching breeding) will increase with AFR if the benefit with delaying in terms of improvement to offspring quality (i.e., breeding probability) cannot offset the cost from decline in offspring quantity. The data show that offspring quantity declined significantly with delayed reproduction, while offspring quality remained initially constant before declining when AFR was delayed beyond 30. Consistent with the theoretical model's predictions, reproductive failure probability increased markedly with delaying AFR after 30, independently of maternal socioeconomic status. Our study is the first to investigate the associations between delay in AFR after sexual maturity and changes in not only offspring quantity but also offspring quality and suggest a significant evolutionary disadvantage of delayed AFR beyond 30 for lineage persistence in a predemographic transition society.

Keywords: Delayed reproduction; Sexual maturity; Life history; Lineage persistence

1. Introduction

Reproduction is fundamental for evolutionary success, and reproductive scheduling is central for the evolution of life histories (Roff, 1992). Among the components of reproductive scheduling, age at first reproduction (AFR) is particularly important, having a pivotal effect on reproductive success or fitness (Roff, 1992; Stearns, 1992). For females, AFR should evolve to maximize fitness subject to the benefits and costs of delayed reproduction (Stearns, 1992). The costs of delaying reproduction may include increased accumulated mortality hazard before reproduction, reduced reproductive span, reduced reproductive output, and longer generation time, while the benefits may include larger body size/weight, higher initial fecundity, and lower offspring mortality brought by longer growth (Kawecki, 1993; Kozlowski, 1992; Migliano, Vinicius & Lahr, 2007; Stearns, 1992; Stearns & Hoekstra, 2005).

In human females, AFR is among the most important life-history traits affecting between-female variation in fitness (Käär, Jokela, Helle, & Kojola, 1996; Migliano et al., 2007; Pettay, Helle, Jokela & Lummaa, 2007) as a result of the costs and benefits mentioned above. By considering the trade-off between such costs and benefits, Hill and Hurtado (1996) were the first to combine theoretical analysis and testing this with empirical data on the optimality of female AFR in humans using Malthusian parameter or instantaneous rate of increase as the fitness measure. Here, the costs of delayed AFR included longer generation time and higher chance of dying before reproducing, whereas the major benefit included higher initial fecundity brought by increased body weight with delay in AFR. Hill and Hurtado (1996) predicted the optimal maternal AFR to be 18 years, close to the observed mean AFR (17.5 years) in Ache, their studied traditional hunter–gatherer tribe of Paraguay. A similar study was carried out on Gambian females by Allal, Sear, Prentice and Mace (2004), who found that female height could be a better indicator than weight in predicting optimal AFR. However, as noted by Hill and Hurtado (1996), such

* Corresponding author. Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, United Kingdom.

E-mail address: jianghua.liu@sheffield.ac.uk (J. Liu).

1090-5138/$ – see front matter © 2011 Elsevier Inc. All rights reserved.
doi:10.1016/j.evolhumbehav.2010.10.007

analyses apply to human populations where AFR is tightly linked with age at sexual maturity (with a short lag; e.g., in the case of Ache females, this lag was 1 year used for pregnancy), but not to an increasing number of populations where AFR varies independently of age at sexual maturity (Hill & Hurtado, 1996; Wood, 1994). Maternal AFR has become increasingly delayed beyond sexual maturity in postdemographic transition Western societies, especially during recent decades (Frejka & Sardon, 2006; Sobotka, 2004). Similar delays in AFR were also common in 18th and 19th European countries, such as Finland (Lutz, 1987). For such cases, the evolutionary benefits of delays in first reproduction remain currently unclear. Firstly, clinic data indicate that female fecundity remains constant from age at sexual maturity to age 30 and then declines significantly from 30 onwards (Schwartz & Mayaux, 1982; van Noord-Zaadstra et al., 1991). Secondly, after controlling for confounding factors, later maternal age is associated with higher risk of producing offspring with low birth weight (<2500 g) (Geronimus, 1996; Lee, Ferguson, Corpuz & Gartner, 1988), possibly leading to increased infant mortality (Vanlandingham, Buehler, Hogue & Strauss, 1988). Finally, reproduction at advanced maternal age (beyond 35) is also associated with higher risk of stillbirth (Raymond, Cnattingius & Kiely, 1994).

Given the disadvantages of delaying AFR, it seems that women should begin to reproduce when reaching sexual maturity (Fisher, 1999), but this is increasingly not observed worldwide. One emerging evolutionary hypothesis for the increasing delay in female AFR beyond age at sexual maturity is socioeconomic benefits. These benefits have been suggested to include the opportunity to accumulate more social resources so as to improve offspring performance or, in other words, "favorable eventual placement of children in the mating market" (Kaplan, Lancaster, Tucker & Anderson, 2002). Thus, mothers who delay reproduction may be trading off a rise in socioeconomic status against a fall in reproductive physiology. Such a rise is assumed to be able to compensate for the costs of delayed reproduction by improving the quality of offspring in order to pay off in terms of long-term likelihood of spreading genes into future generations, i.e., maximizing lineage persistence likelihood.

Investigating empirically whether this is true is difficult because it requires, by definition, individual-based lifelong records on survival and fecundity for whole lineages across several generations, and such data are difficult to obtain for any species, let alone for humans with exceptionally long lifespan. Two previous studies shed some light on this issue. First, Kaplan et al. (2002) used a sample of men and women from the National Survey of Families and Households in the USA and another sample of interviewed men in Albuquerque, NM, USA, to show that delayed reproduction in both men and women was associated with lower fertility. For the Albuquerque men, lower fertility was not compensated by income level to increase numbers of grandchildren born (Kaplan, Lancaster, Bock & Johnson, 1995). There were two important limitations, however: the direct link between AFR and numbers of grandchildren was not investigated to address how a delay in reproductive onset is associated with both offspring quantity and quality, and the analysis of grandchildren numbers concerned only men whose reproductive physiology is less constrained by age than that of women and whose fitness may be limited by trade-offs different to women (Lahdenperä, Russell & Lummaa, 2007). It is thus unknown how the conclusion on grandchildren applies to women. Second, using simulations based on data on education, income, AFR, and lifetime fertility of modern American women, Low, Simon and Anderson (2002) showed that despite of socioeconomic benefits brought by delayed AFR, mothers with later AFR were predicted to have reduced fertility and longer generation time and, consequently, increasingly lower proportion of descendants in the future population. Another simulation indicated that even longer generation time itself as the result of delayed AFR could lead to the same result (Low, Simon & Anderson, 2003). However, these simulations by Low et al. (2002) and (2003) considered only offspring survival rate but not their breeding success, which might be fundamentally affected by the suggested benefits of delayed maternal AFR.

In summary, at present, no empirical studies exist on women to show how delays in AFR relate to offspring quality, depicted not only by their survival to breeding age but also by their recruitment to the breeding population. Such information is crucial for determining whether delays in AFR could improve offspring quality, for example, through socioeconomic benefits and, despite reduced offspring quantity, thus lead to evolutionary benefits in the long-run, i.e., lineage persistence. We thus know currently little about whether and how the relationship between delayed reproduction, socioeconomic factors, and offspring quality can influence a woman's lineage persistence over time.

Here, we focus on investigating the association for females between delaying AFR and change in the vulnerability of their lineages to extinction, the opposite of lineage persistence likelihood. First, we introduce a quantitative index to assess this vulnerability and construct a generalized mathematical model to identify the association between delaying AFR and change in lineage extinction vulnerability. Secondly, we evaluate the predictions of the model using data from a multigenerational, individual-based dataset of preindustrial Finns from the 18th and 19th centuries where the average AFR, similarly as modern societies, was significantly beyond maturity. Specifically, we investigate the associations between maternal AFR and (i) offspring quantity (lifetime number of children), (ii) offspring quality (measured by their probability of being recruited to breeding population) and its major component (survival rate at reproductive age 15), and (iii) the probability of maternal reproductive failure (lineage extinction or no breeding children). Additionally, we represent environmental conditions by socioeconomic status and investigate how this influenced the above associations.