PROCEEDINGS OF THE ROYAL SOCIETY B

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**Cite this article:** Nenko I, Hayward AD, Lummaa V. 2014 The effect of socio-economic status and food availability on first birth interval in a pre-industrial human population. *Proc. R. Soc. B* **281**: 20132319.
http://dx.doi.org/10.1098/rspb.2013.2319

Received: 6 September 2013
Accepted: 30 October 2013

**Subject Areas:**
evolution, ecology

**Keywords:**
nutritional status, reproduction, environmental variation, first childbirth

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2013.2319 or via http://rspb.royalsocietypublishing.org.

Royal Society Publishing

# The effect of socio-economic status and food availability on first birth interval in a pre-industrial human population

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Individual variation in nutritional status has direct implications for fitness and thus is crucial in shaping patterns of life-history variation. Nevertheless, it is difficult to measure in natural populations, especially in humans. Here, we used longitudinal data on individual life-histories and annual crop yield variation collected from pre-industrial Finnish populations experiencing natural mortality and fertility to test the validity of first birth interval (FBI; time between marriage and first birth) as a surrogate measure of nutritional status. We evaluated whether women with different socio-economic groups differ in length of FBI, whether women of poorer socio-economic status and experiencing lower crop yields conceive slower following marriage, and whether shorter FBI is associated with higher lifetime breeding success. We found that poorer women had longer FBI and reduced probability of giving birth in months with low food availability, while the FBI of richer women was not affected by variation in food availability. Women with shorter FBI achieved higher lifetime breeding success and a faster reproductive rate. This is, to our knowledge, the first study to show a direct relationship between environmental conditions and speed of childbirth following marriage, highlighting the value of FBI as an indicator of nutritional status when direct data are lacking.

## 1. Introduction

It is well established that nutritional status in adulthood affects female fertility [1]. Females in better condition have a higher chance of successful reproduction and achieve greater lifetime reproductive success [2], and favourable environmental conditions reduce the costs of breeding [2,3]. Linking variation in ecological conditions and availability of resources with measures of individual growth, body maintenance and reproduction is a cornerstone of evolutionary ecological studies ranging from epigenetics to adaptive plasticity and life-history trade-offs [4]. However, it is difficult to reliably measure individual variation in food availability or body condition in many natural populations of animals. Often only larger scale comparisons, such as those between birth cohorts with differing climatic conditions, are possible [5].

The analysis of human life-history patterns and evolutionary ecology requires detailed longitudinal information over the entire lifespan of a large number of individuals. Datasets obtained from epidemiological and cohort studies as well as some long-term anthropological field projects typically have detailed longitudinal information on individuals and are thus a valuable tool in addressing many mechanistic and behavioural underpinnings of life-history patterns (e.g. [6,7]). However, they often do not cover the entire lifespan of a sufficient number of individuals living without access to modern medical care and birth control methods to allow meaningful analyses of lifetime fitness. In addition, few of them have the entire reproductive histories of several generations of individuals, which is required to distinguish, for example, genetic and environmental effects on life-history traits ([8], but see, e.g. [9]). By contrast, parish records have detailed individual-level data on lifetime measures of fitness and lifespan and have been extensively used to study human life-history patterns and evolutionary ecological questions [10]. Unfortunately, however, they have limited information on individual condition and environmental variation. To overcome this problem, information on social class has been used as a proxy of access to resources and nutritional status [11,12]. For example, previous studies have shown that women from different socio-economic classes differ in age at first reproduction, and that this has implications for their fitness [13–16]. However, such an approach neglects year-to-year variation in environmental conditions which may affect nutritional status. In addition, information on social status is not available for many otherwise well-documented historical populations. Consequently, there is a need to find an indicator of nutritional status independent of social class that could be easily derived for large numbers of individuals.

One possibility for an indicator of individual nutritional status in historical populations with no birth control is the first birth interval (FBI) of females [17]. FBI is the time between marriage and first birth and is distinct from age at first reproduction (AFR; age at which a female first gives birth), which varies not only owing to nutritional differences but also owing to cultural constraints on marriage or sexual behaviour. In many societies, marriage gives the official right to start childbearing [18], and even if women may wish to limit their family size at later ages, at the beginning of marriage children are often desired and expected. The ability to conceive rapidly following marriage may thus truly reflect female condition, whereas AFR is a composite measure of both how early women get married and how early in marriage they conceive. Consistent with this idea, pre-industrial Polish women with shorter FBI, and thus presumably better nutritional status, have been reported to have more children born over their entire lifespan, more children who survived to adulthood, more sons and shorter mean inter-birth intervals [17]. However, it remains to be confirmed whether food availability indeed affects the length of FBI.

We analysed data on a pre-industrial Finnish population using demographic data combined with historical harvest success records [19,20]. Finland is one of the few countries worldwide for which there are complete population registers dating from the pre-industrial era [21]. The whole population was Lutheran and from 1749 onwards, local clergymen were by law required to submit to the state accurate censuses of all births, movements, marriages and deaths for individuals of each parish in the country. The transformation from an agrarian to an industrial country began in Finland in the 1880s and it was only from that decade onwards that significant changes appeared in food supply, healthcare, life expectancy at birth and female education level that eventually led to decreased fertility rates [22]. These data thus provide a reliable source of historical demographic data on pre-industrial human populations, and information on natural individual-level variation in survival and reproduction.

In this study, we test: (i) whether pre-industrial women from different socio-economic groups and thus of differing wealth and access to food differ in their length of FBI, (ii) whether annual variation in food availability measured by crop yields modifies the monthly probability that women conceive their first child since marriage, and (iii) whether FBI is associated with other reproductive traits, indicating that it predicts reproductive performance across lifetime. We predict that: (i) women of poor socio-economic status should have a longer FBI than women from the wealthier classes, (ii) annual food availability should be positively associated with the cumulative probability of giving birth to first child, particularly in the poorest group with the most limited access to food, and (iii) shorter FBI is positively associated with measures of lifetime reproductive performance. Our results show that FBI can be used as surrogate measure of nutritional status with implications for researchers who lack direct information on nutritional status.

## 2. Material and methods

### (a) Study population and data collection

We used demographic data collected by the Lutheran church in Finland from the seventeenth century onwards. Our database was compiled using church registers of births, movements, marriages and deaths in eight Finnish parishes: Hiittinen, Kustavi, Rymättylä, Ikaalinen, Pulkkila, Tyrvää, Rautu and Jaakkima (e.g. [19,23]). We used data collected between 1649 and 1900, a period which largely predates industrialization, healthcare improvements and modern birth control methods in Finland [22]. The populations were strictly monogamous, with divorce forbidden by the church and adultery punishable, both of which mean that the extra-marital paternity rate is likely to have been very low [24]. Women may have remarried if their husband died, but here we include only data from women who married once in their lifetime (approx. 90% of all married women) to avoid unusually long FBI values caused by an infertile first marriage followed by reproduction with the second husband. In addition, to avoid including premarital conceptions, we excluded women who gave birth to a child before the marriage date and less than nine months after marriage.

Individuals were classified into three socio-economic classes based on husband's occupation: the wealthy class included farm-owners and merchants; the middle class, craftsmen and tenant farmers; the poor, crofters and labourers [14]. The studied populations were subsistence farmers, who were dependent largely on the cultivation of rye and barley [25,26]. Around 60% of the energy consumed by working people was contributed by rye alone, 20% came from potatoes and barley [27], and this was supplemented by meat, fish and dairy products from domesticated and wild sources [28].

#### (i) Social status and first birth interval

First, we tested for differences in FBI between women from the three socio-economic groups in eight parishes. In this analysis, we included all women for whom at least the month (and year) of marriage and month (and year) of first birth were known; for 99.6% of this sample, the exact dates of both of these events were known. The sample comprised 3036 women who married only once in their lifetime, produced their first child a minimum of nine months after marriage, and had their entire reproductive history and their husband's occupation recorded. These women were born in 1649–1880 and married in 1668–1899 at an average age of 24.06 years (s.d. = 4.80). Their first babies were born in 1681–1900 at an average age of 26.15 years (s.d. = 5.27).

#### (ii) Rye yield and probability of giving first birth

Second, we analysed associations between food availability and the probability of giving birth to the first child in each month following marriage. Quantifying variation in food availability in pre-industrial populations is challenging. For example, climate proxies reconstructed from historical data [29] may be associated with harvest success, but such large-scale measures are unlikely to predict local conditions, which vary considerably across space [30]. Here, we use two long-term series of local crop yield data, available for two of our eight parishes (Ikaalinen and Tyrvää) for the years 1804–1874. These grain-yield data on the main crop species (rye) were collected from the Spåre family archive from the estate of Valkila, located within 35 and 40 km of the centres of Ikaalinen and Tyrvää, respectively. Grain-yield data collected across such distances have a correlation of 0.65–0.80 [31], suggesting that they accurately reflect the conditions experienced by our study individuals. Annual harvest success was quantified as the amount of grain harvested as a multiple of the quantity sown ('yield' from herein), a measure which is unbiased by variation in planting effort and population size. Although grain yields do not directly reflect individual food availability, this measure is relative to the success compared to other years and reflects year-to-year variation in harvest quality, which varied considerably during the study period [20]. In addition, low grain yields have been found to be associated with documented famines [32], and birth year grain figures in the study population predict later-life survival [19], later-life reproduction [33] and immediate mortality risk [20]. Following the selection criteria described above (see §2a(i)), 578 women born in Ikaalinen and Tyrvää during 1769–1857 and married 1804–1873 were included in this analysis.

#### (iii) First birth interval and measures of reproductive performance

Third, we tested whether FBI was associated with lifetime measures of reproductive performance. In this analysis, we included 884 women from eight parishes, who married once in their lifetime and produced at least one child a minimum of nine months after marriage. For both marriage and first birth at least the month and year were known; for 99.7% of this sample, the exact dates of both of these events were known. In addition, women had to survive until 50 years of age and their husband had to be alive at the woman's 50th birthday. These women were born between 1665 and 1850, and died between 1716 and 1900. Their first babies were born between 1695 and 1884, they had on average 5.28 children (s.d. = 3.12) and 3.45 (s.d. = 2.08) who survived to adulthood. Mean inter-birth interval was 43.13 months (s.d. = 25.92) and was calculated only for children who survived at least until 2 years of age in order to avoid short inter-birth intervals which could result from high infant mortality (i.e. reversed causality with short inter-birth interval reflecting poor rather than good reproductive performance). Women gave birth to their last child at the age of 39.29 years (s.d. = 5.26) and lived on average 67.26 years (s.d. = 9.98).

### (b) Statistical analysis

#### (i) Social status and first birth interval

Differences in the length of FBI among social groups (three levels, see above) were analysed using generalized linear models (GLMs) with negative binomial errors and a log link function. FBI was quantified as the number of months between a female marrying and delivering her first child. To control for possible confounding terms affecting fertility patterns, we included the following variables in the model: parish (categorical variable with eight levels [34]), female and husband's age at marriage (both linear and quadratic terms [35]), year of birth (as a continuous covariate [16]) and month of marriage (as a categorical variable with 12 levels [36]). Non-significant terms were removed in sequential order of least significance from the maximal model, as assessed by $p$-values derived from $z$ statistics, on the appropriate number of degrees of freedom.

#### (ii) Rye yield and probability of giving first birth

We next investigated associations between annual rye yield and the probability of giving birth in each month following marriage using binomial GLMs with a logit link function (8566 records from 578 women). We initially fitted birth year as a random effect in generalized linear mixed-effects models, but it was not statistically significant and so was omitted from all analysis. For each female, we analysed the probability of giving birth in each month following their marriage, up until the month when the first baby was born (0 = did not give birth to the first child; 1 = gave birth to the first child). This corresponds to an event-history analysis, where the response variable is scored as 0 until the time of the event (first child's birth), at which point the response variable is scored as 1 and the female leaves the analysis. This approach allows us to statistically control for changes in crop yields and women's ages over time between marriage and first birth, and is directly related to FBI through an interaction with time—a faster birth following marriage is a lower FBI. All females included in the sample had complete monthly records from their month of marriage until the month of their first child's birth. We analysed associations with the rye yield nine months previous to the month being analysed, so that for the month of birth, the rye yield would reflect conditions around time of conception. Rye was harvested in the autumn [26] and so for the months of January–August, the rye yield from the previous year was used as the proxy for current food availability, whereas in the months September–December, the rye-yield value of the current year was used. To allow meaningful assessment of interactions between the crop yield and other factors and to avoid the results being biased by a few extreme crop yield values, rye yield was divided into two groups based on the median value: a yield of below or equal to 6.45 was 'low', whereas a yield of above 6.45 was 'high'. We also accounted for a number of variables that could potentially affect the probability of giving birth. The initial model included: time since marriage in months, woman's age in the month that was being analysed and husband's age at marriage (all three as both linear and quadratic terms), month of marriage (as a categorical variable with 12 levels), parish (as a categorical variable with two levels), social class (as categorical variable with three levels) and rye yield (as a categorical variable with two levels).

We included an interaction between time (months since marriage) and rye yield to test the prediction that high rye yield would increase the probability of giving birth earlier in marriage, and an interaction between social class and rye yield to test the prediction that individuals of the lowest social class would be most positively affected by high rye yield. In addition, an interaction between time since marriage and social class was used to test the prediction that individuals of the highest social class would have a higher probability of reproduction earlier in marriage, such that a faster birth following marriage would translate to a lower FBI. Finally, a three-way interaction between social class, time and rye yield was used to test the prediction that the poorest social class experiencing the lowest crop yields would be the slowest to reproduce following marriage. We tested the significance of these variables by dropping terms from the maximal model as described above. In the analysis, the probability of giving birth in each month was tested; however, for graphical representation, cumulative probability of giving birth with time since marriage was calculated for each wealth and rye-yield group.

#### (iii) First birth interval and measures of reproductive performance

The associations between FBI and measures of reproductive performance over lifetime were tested in separate models. We analysed the following reproductive traits as response variables: the total number of children born across the woman's lifespan (lifetime breeding success), the time between first and last reproduction (reproductive lifespan), the proportion of children who survived to adulthood at 15 years (lifetime reproductive success), the rate at which women produced their children (mean inter-birth interval).

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**Table 1.** Parameter estimates for the minimal adequate GLM with negative binomial errors showing differences in length of FBI between women from different social groups in 3036 females born 1649–1882.

| fixed terms | estimate | s.e. | *z*-value | *p*-value |
|---|---|---|---|---|
| intercept | 8.6117 | 0.7052 | 12.212 | <0.001 |
| parish (Hiittinen) | 0.0000 | | | |
| parish (Ikaalinen) | 0.0613 | 0.0469 | 1.306 | 0.192 |
| parish (Jaakkima) | 0.1198 | 0.0595 | 2.013 | 0.044 |
| parish (Kustavi) | 0.2242 | 0.0533 | 4.207 | <0.001 |
| parish (Pulkkila) | −0.1329 | 0.0657 | −2.024 | 0.043 |
| parish (Rautu) | 0.3177 | 0.0609 | 5.219 | <0.001 |
| parish (Rymättylä) | 0.2453 | 0.0839 | 2.924 | 0.003 |
| parish (Tyrvää) | 0.8433 | 0.0501 | 16.831 | <0.001 |
| social class (wealthy) | 0.0000 | | | |
| social class (middle) | −0.0223 | 0.0302 | −0.738 | 0.460 |
| social class (poor) | 0.1345 | 0.0386 | 3.487 | <0.001 |
| age at marriage | −0.0115 | 0.0030 | −3.850 | <0.001 |
| husband's age at marriage | −0.0316 | 0.0109 | −2.904 | 0.004 |
| husband's age at marriage$^2$ | 0.0006 | 0.0002 | 3.403 | <0.001 |
| birth year | −0.0027 | 0.0004 | −7.197 | <0.001 |

Lifetime breeding success and reproductive lifespan were natural log transformed and analysed using GLMs with a Gaussian error structure. The proportion of children surviving to adulthood was analysed as a matched pair variable, with number of children who survived to adulthood (number of successes) and number of children who did not survive to adulthood (number of fails), in a GLM with binomial errors. Finally, mean inter-birth interval was analysed using a GLM with negative binomial errors and a log link function. To control for possible confounding terms affecting fertility patterns, we included the following variables in the model: parish (categorical variable with eight levels), female and husband's age at marriage (both linear and quadratic terms), year of birth (as a continuous covariate), and social status (as a categorical variable with three levels). The minimal model was obtained as in §2b(i). All analyses were performed with R v. 2.15.2 (http://www.R-project.org) using the function glm.nb from the MASS package [37].

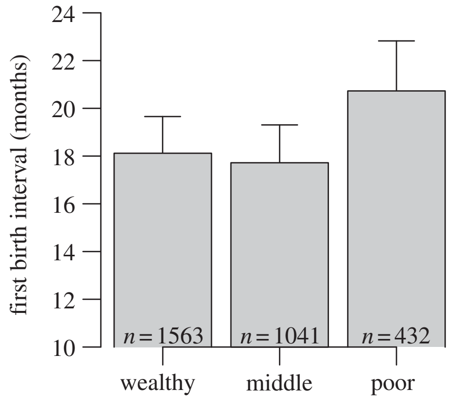


**Figure 1.** Differences in FBI among women from three socio-economic groups. The figure shows back-transformed predicted mean values ± 95% confidence intervals that were generated using parameter estimates from a GLM with negative binomial errors (table 1).

## 3. Results

### (a) Social status and first birth interval

The mean FBI across our study individuals was 25.9 months (s.d. = 30.35), but there were significant differences in the FBI of women from the three socio-economic classes. Women from the poor group had, on average, significantly (2.6 months) longer FBI than women from the wealthy group ($p < 0.001$; table 1 and figure 1), and the parameter estimates and associated standard errors suggest that the poor also had significantly (on average 3.0 months) longer FBI than women in the middle class. The difference between the middle and the wealthy group was not statistically significant (on average 0.4 months). The differences between the socio-economic classes remained qualitatively unchanged when women with probable fertility problems (those with FBI longer than 10 years, 2.4% of all women) were excluded from the analysis.

The observed differences were not an artefact of variation between the social status groups in, for example, age at marriage, husband's age at marriage or geographical variation, since our models controlled for such confounding factors (table 1). For example, there was a significant linear negative relationship between age at marriage and FBI, such that women who married at older ages had a shorter FBI. In addition, there was a significant negative association between FBI and husband's age at marriage which showed that women with older husbands had a shorter FBI. Finally, the mean FBI differed significantly among the studied parishes. Of the terms included in our original model, only month of marriage was not significantly associated with the length of FBI.

### (b) Rye yield and probability of giving first birth

The monthly probability of giving birth to the first offspring following marriage varied with time since marriage (table 2),

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**Table 2.** Parameter estimates for the minimal adequate binomial GLM showing variables significantly associated with probability of giving birth to the first child with 8566 months records for 578 mothers across the years 1804–1874.

| fixed terms | estimate | s.e. | *z*-value | *p*-value |
|---|---|---|---|---|
| intercept | −1.498 | 0.1999 | −7.494 | <0.001 |
| parish (Ikaalinen) | 0.0000 | | | |
| parish (Tyrvää) | −0.3883 | 0.0996 | −3.900 | <0.001 |
| time | −0.0413 | 0.0095 | −4.361 | <0.001 |
| time$^2$ | 0.0002 | $4.555 \times 10^{-5}$ | 3.561 | <0.001 |
| social class (wealthy) | 0.000 | | | |
| social class (middle) | −0.1476 | 0.2741 | −0.539 | 0.590 |
| social class (poor) | 0.6535 | 0.5286 | 1.236 | 0.216 |
| rye (low) | 0.0000 | | | |
| rye (high) | −0.3016 | 0.3071 | −0.982 | 0.326 |
| time : rye (low) | 0.0000 | | | |
| time : rye (high) | 0.0051 | 0.0150 | 0.337 | 0.736 |
| time$^2$ : rye (low) | 0.0000 | | | |
| time$^2$ : rye (high) | $-3.654 \times 10^{-5}$ | $7.886 \times 10^{-5}$ | −0.463 | 0.643 |
| social class (wealthy) : rye (low) | 0.0000 | | | |
| social class (middle) : rye (high) | 0.3098 | 0.4018 | 0.771 | 0.441 |
| social class (poor) : rye (high) | −1.4820 | 0.8222 | −1.803 | 0.071 |
| social class (wealthy) : time | 0.0000 | | | |
| social class (middle) : time | 0.0035 | 0.0145 | −0.241 | 0.810 |
| social class (poor) : time | −0.0768 | 0.0354 | −2.173 | 0.030 |
| social class (wealthy) : time$^2$ | 0.0000 | | | |
| social class (middle) : time$^2$ | $5.094 \times 10^{-6}$ | $8.860 \times 10^{-5}$ | 0.575 | 0.565 |
| social class (poor) : time$^2$ | 0.0011 | 0.0004 | 2.889 | 0.004 |
| social class (wealthy) : time : rye (low) | 0.0000 | | | |
| social class (middle) : time : rye (high) | −0.0067 | 0.0207 | 0.323 | 0.747 |
| social class (poor) : time : rye (high) | 0.1408 | 0.0565 | 2.493 | 0.013 |
| social class (wealthy) : time$^2$ : rye (low) | 0.0000 | | | |
| social class (middle) : time$^2$ : rye (high) | $-3.870 \times 10^{-5}$ | 0.0001 | −0.310 | 0.756 |
| social class (poor) : time$^2$ : rye (high) | −0.0017 | 0.0007 | −2.373 | 0.018 |

such that it was initially high before declining. However, the three-way interaction suggested that the change in the monthly probability of giving birth to the first offspring following marriage varied considerably with time and the prevailing food (rye yield) availability exclusively among the poor women (table 2). For example, 40 months after marriage, 96% of poor women experiencing high rye yields after marriage had given birth to their first child, whereas only 87% of poor women experiencing low rye yields after their marriage had given birth (figure 2). There were no differences in the chance of conceiving following marriage in months when rye yields were high versus low among women belonging to the middle or wealthy socio-economic status groups. Thus, our prediction that the poor women would benefit most from high crop yields was partially true, since the three-way interaction suggested that this was only the case early in marriage. Also, the prediction that high rye yield would increase the probability of birth early in marriage was true, but only in the poorest women. Finally, the poor had a lower

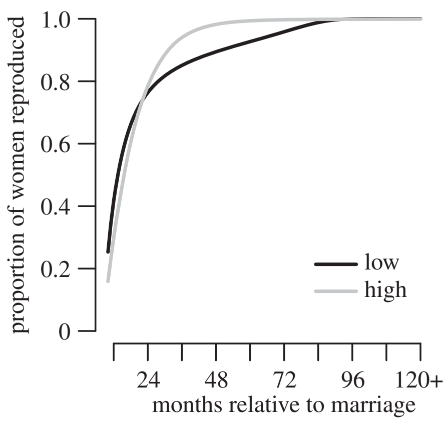


**Figure 2.** The monthly probability of giving birth to the first offspring following marriage varied considerably among the poor women depending on the prevailing food (rye yield) availability. The figure was generated by taking the predictions from the binomial model from table 2. We back-transformed the predictions, then calculated the cumulative probability of giving birth to a child by each month following marriage.

chance of reproducing soon after marriage, but only when crop yields were low; when they were high, they were equally likely to reproduce in any month after marriage as the rich and middle classes. These results were not confounded by variation in month of marriage, husband's age at marriage (neither linear nor quadratic terms), or women's age after marriage.

### (c) First birth interval and measures of reproductive performance

Shorter FBI was associated with a higher lifetime breeding success (figure 3*a*; electronic supplementary material, table S1a). Additionally, women with shorter FBI had a longer reproductive lifespan (see the electronic supplementary material, table S1c; figure 3*c*) and shorter mean inter-birth interval (electronic supplementary material, table S1d; figure 3*d*). FBI was not significantly associated with the proportion of children who survived to adulthood (see the electronic supplementary material, table S1b; figure 3*b*).

## 4. Discussion

In this study, we set out to test whether FBI can be used as a surrogate measure of nutritional status by testing whether women of poor socio-economic status had a longer FBI than women from the wealthier classes and whether annual food availability was positively associated with the probability of giving birth to the first child, in particular in the poorest group with the most limited access to food. We have shown that FBI can be used as an indicator of nutritional status. Women from the poorest socio-economic group with lowest access to food had a significantly longer latent period between marriage and first birth compared with women from wealthier groups. In addition, women from the poorest socio-economic group had a higher probability of conceiving in earlier months where food availability was high compared with where it was low. Finally, women with shorter FBI achieved higher overall breeding success and faster rate of reproduction. Taken together, these findings highlight the value of FBI as a tool to be used by researchers who study human life-history patterns, especially when using data on historical populations which lack information on social class or direct measures of food availability.

Our results show that food availability is related to the probability of giving birth to the first child in a natural fertility population. Poor women had a higher probability of conceiving their first child soon after marriage when food availability was high, revealing that those women benefited more when environmental conditions were favourable early in marriage. The probability of giving birth to the first child was not associated with our measure of food availability in women from the middle and wealthy classes at any stage following marriage. Although FBI was not a response variable in this analysis, calculation of cumulative probability of producing the first child revealed differences in length of FBI at different crop yields. These results are consistent with previous findings from the study population showing that landless women who were born in a good quality harvest year had a higher probability of marrying and reproducing than those women in low harvest years, but that birth year harvest quality did not affect women from the landowning classes [33].

Reproductive function is very sensitive to energy supply [38,39]. It has been shown that even mild changes in energy balance can lead to lower steroid hormone levels without leading to variation in menstrual cycles, which has direct implications for probability of conception [39,40]. For example, Lese horticulturalists in the Ituri Forest of the Democratic Republic of the Congo had lower steroid hormone levels because of weight loss during the pre-harvest season than during post-harvest season when women had a positive energy balance [41,42], a result which had consequences for the observed seasonal patterns of conceptions. Reduction in hormone levels during periods of low nutrition can be seen as adaptive: since reproduction is costly, it is not beneficial to invest in reproduction when resources are limited but rather wait until conditions improve, e.g. during the post-harvest season [39]. However, the majority of studies look at extremes of food deprivation such as famine (but see [13]). For example, severe food deprivation, such as that experienced during famines in China and Bangladesh [43], Russia [44], Finland [19], and in The Netherlands [45], causes a significant decline in population-level birth rate. Both during the Finnish famine of 1866–1868 and the Dutch famine of 1944–1945, women from all social classes experienced a drop in fertility, but the decline was most acute in the lowest social group [19,45]. Furthermore, the post-famine rise in conception in The Netherlands was also most clearly marked in the group of women with the lowest social status [45]. Nevertheless, times of severe restriction in caloric intake are relatively infrequent in human history, with most of the variation in food availability corresponding to small-scale seasonal or annual fluctuations [43]. Consequently, there has been a need to test how annual variation in resource availability and nutritional status shape fecundity, since little data is available, especially for historical populations which are best suited to testing hypotheses of effects on lifetime breeding success. In our study, the issue was addressed by combining data on crop yields and reproductive traits allowing us to show that even subtle changes in environmental conditions lead to changes in probability of giving birth.

Several confounding factors must be considered when evaluating our conclusions. First, our results could have been strengthened if individual resources had been used as a measure of food availability, but such information does not exist for historical populations. Grain yield, although not directly reflecting individual access, is a relative measure of food availability revealing year-to-year variation in harvest quality. In the Finnish population, it affects survival [19,20] and later-life reproduction [19,33] suggesting that it directly influences the fitness of individuals of all ages. Therefore, taking into account the above findings, we would argue that grain-yield data reflect nutritional conditions experienced by our study individuals, with direct relevance to their fitness.

Second, we surprisingly found no significant association between women's age and their probability of giving birth for the first time. It is well known that the probability of giving birth changes in a woman's lifetime. The most fecund women are between 20–24 years of age, from which point steroid hormone levels decline, with a sharp fall after age 35 [46]. It should be noted, however, that we included 'time' (months after marriage until first birth) in the model beside women's age. Therefore, in this type of model, time and women's age increase at the same rate and are therefore somewhat confounded.

Third, the results could be specific to the sample included in this study, or the sample might not be representative of

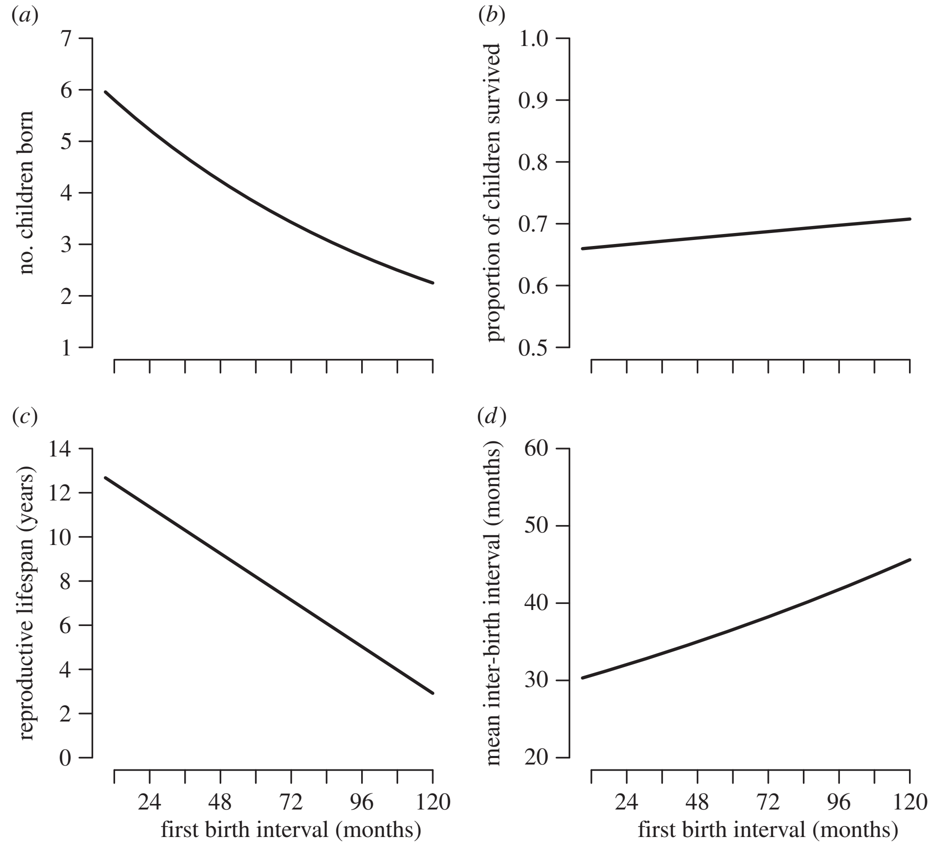


**Figure 3.** The association between FBI and measures of reproductive performance: (*a*) the total number of children born across the woman's lifespan (lifetime breeding success), (*b*) the proportion of children who survived to adulthood at 15 years (lifetime reproductive success), (*c*) the time between first and last reproduction (reproductive lifespan) and (*d*) the rate at which women produced their children (mean inter-birth interval). The figure shows back-transformed model predictions from the electronic supplementary material, table S1.

the entire population. In the study sample, among women who reproduced once in their lifetime, 38% of women gave birth to the first child within 12 months of marriage and for 2% it took longer than 10 years. It is probable that women with long FBI had some health problems or likewise their husbands had some congenital problems. In cases of fertility dysfunction, food availability could be a minor problem. However, excluding women with an FBI of longer than 10 years from the analysis did not qualitatively change the results. Moreover, in our population, 21.1% of women aged 25–29, and 27% of women aged 30–34 failed to have their first baby within 36 months of marriage. This is consistent with estimates of 20.2% and 25.9% for the same age groups observed in an English population monitored between 1550 and 1849 [47]. In addition, the ratio of births occurring in the first year of marriage in our study population is 0.38, which is within the range of estimates (0.34–0.49) calculated for five historical populations [48]. Since the pre-industrial Finnish population therefore appears to be similar to others populations with published data on them, these data suggest that FBI could be used as a marker of nutritional status in other populations, too.

Finally, it can be suggested that the frequency of intercourse may influence the chance of conception and thus potentially confound a relationship between food availability and conception. Variation in the frequency of intercourse among couples is observed later in the course of marriage, but probably much less at the beginning when children are desired. Additionally, it is suggested to vary with the duration of marriage after some children have already been born, but not before [49]. In any case, variation in the frequency of intercourse is not very strongly related to variation in a chance of conception. The recent guideline—by the Practice Committee of The American Society for Reproductive Medicine—for optimizing likelihood for achieving pregnancy for couples without fertility problems states: 'Frequent intercourse (every 1 to 2 days) yields the highest pregnancy rates, but results achieved with less frequent intercourse (two to three times per week) are nearly equivalent' [50, p. S5]. Therefore, it is unlikely that our results are confounded by the frequency of intercourse, although in the lack of direct data it remains a possible mediating factor for an association between food access and fertility.

In conclusion, we have shown that women from the poorest social group have significantly longer FBI than women from wealthier social classes. We also found that the probability of producing their first child is affected by a measure of food availability in the poorest women, but not in the wealthier classes. Moreover, FBI was associated with overall lifetime breeding success and rate of reproduction. The observed results suggest that, unlike social status, FBI reflects annually changing environmental conditions. Furthermore, since FBI is shaped by food availability, our results suggest that FBI could be used as a surrogate measure of nutritional status. FBI could therefore represent a useful tool for researchers who use parish records in the field of demography and evolutionary biology and have implications for research into life-history theory.

Acknowledgements. We thank Lasse Iso-Iivari, Kimmo Pokkinen, Aino Siitonen, Sinikka Toijonen, Jarmo Piippo and the Karelian database for data collection, Jari Holopainen for collating crop yield data, Alexandre Courtiol for advice on statistics, and Iain Kennedy Patten for comments on the manuscript.

Data accessibility. Access to the data analysed in this study may be requested by contacting Dr V.L. (v.lummaa@sheffield.ac.uk).

Funding statement. We are grateful to the European Research Council (A.D.H., V.L), Polish Ministry of Science and Higher Education (I.N.), and Foundation for Polish Science (I.N.) for funding.

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