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Food availability at birth limited reproductive success in historical humans

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Abstract. Environmental conditions in early life can profoundly affect individual development and have consequences for reproductive success. Limited food availability may be one of the reasons for this, but direct evidence linking variation in early-life nutrition to reproductive performance in adulthood in natural populations is sparse. We combined historical agricultural data with detailed demographic church records to investigate the effect of food availability around the time of birth on the reproductive success of 927 men and women born in 18th-century Finland. Our study population exhibits natural mortality and fertility rates typical of many preindustrial societies, and individuals experienced differing access to resources due to social stratification. We found that among both men and women born into landless families (i.e., with low access to resources), marital prospects, probability of reproduction, and offspring viability were all positively related to local crop yield during the birth year. Such effects were generally absent among those born into landowning families. Among landless individuals born when yields of the two main crops, rye and barley, were both below median, only 50% of adult males and 55% of adult females gained any reproductive success in their lifetime, whereas 97% and 95% of those born when both yields were above the median did so. Our results suggest that maternal investment in offspring in prenatal or early postnatal life may have profound implications for the evolutionary fitness of human offspring, particularly among those for which resources are more limiting. Our study adds support to the idea that early nutrition can limit reproductive success in natural animal populations, and provides the most direct evidence to date that this process applies to humans.

Key words: birth weight; cohort effect; delayed life-history effects; fetal growth; fetal programming; life-history evolution; maternal effect; parental investment; reproductive development; silver spoon.

INTRODUCTION

The environmental conditions that animals experience during development affect their reproductive performance and, ultimately, their fitness (Lindström 1999, Metcalfe and Monaghan 2001, Lummaa and Clutton-Brock 2002). Knowledge of these individual-level effects is essential for an understanding of the population-level consequences of environmental change in wild animals (Beckerman et al. 2002), as well as the selective forces that shape species' plastic responses to the environment (West-Eberhard 2003). One of the specific factors likely to be important in influencing individual fitness in early life is nutrition. A small number of laboratory (Meikle and Westberg 2001, Zambrano et al. 2005, Guzmán et al. 2006) and field (Descamps et al. 2008) studies of mammals have provided direct evidence that the supply of resources to individuals during development eventually constrains adult reproductive performance. In general, however, the role of nutrition in these processes in natural populations must be inferred through proxies such as population density and climate recorded in the early life of cohorts (Forchhammer et al. 2001, Reid et al. 2003).

Human populations represent potentially valuable sources of data for investigating the effects of early nutrition, because food supply and reproductive output can potentially be determined at an individual level. Two approaches have typically been used to examine reproductive performance in relation to early-life environment. The first has been to examine the predictive power of indirect measures of the intrauterine environment, such as birth weight or gestational age (estimated time from conception to birth) (Ekholm et al. 2005, Main et al. 2006, Nohr et al. 2009). However, interpretation of these associations in the context of nutritional supply to the fetus is far from simple (Wells 2006). Nohr et al. (2009) found that women with

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intermediate birth weight conceived most easily. Ekholm et al. (2005) found that women with very low birth weight had lower fertility, but this pattern was less clear once gestational age was taken into account. Second, several studies have correlated birth season and later-life reproductive traits in historical populations (Smits et al. 1997, Lummaa and Tremblay 2003). These studies probably indicate effects of the exogenous environment on the long-term reproductive outcomes under study, which include lifetime reproductive success. However, in any population many biotic and abiotic factors vary on a seasonal basis; thus such investigations have not been able to go beyond establishing patterns to pinpoint the specific environmental factors involved.

Research relating reproductive performance directly to known external environmental factors is rare, and we know of only one human population in which this has been investigated. Women exposed to the Dutch "hunger winter" of 1944–1945 while in utero (their mothers being famished during pregnancy) were more likely to reproduce in their lifetimes than women from control groups not exposed to famine (Lumey and Stein 1997, Painter et al. 2008). This result is particularly interesting because it appears contrary to the prediction from life-history theory that early nutrition should, if anything, constrain traits positively associated with fitness. However, interpretation of any biological mechanisms is limited by the unknown role of behavioral factors in the decline of family size in industrialized societies. Because we do not yet fully understand individual decisions governing the demographic transition toward low fertility in such societies (Mace 2008), more information on the effects of early nutrition on later fertility might be gleaned by examining data from populations prior to a fertility decline. Furthermore, to our knowledge no studies have investigated direct relationships between the early environment and reproductive outcomes in human males.

Here we investigate the effect of food availability (harvest yields) at birth on survival and reproductive parameters of men and women using data from a preindustrial, pre-fertility decline population. Specifically, we investigate the effects of fluctuating food availability on: (1) the probability of an individual surviving to adulthood; (2) the probability of and age at marriage; (3) the lifetime probability of reproducing; and (4) the probability of raising offspring to adulthood. Our data set has several benefits for addressing these aims. First, we measure the full life history (survival and reproductive success) of Finns (n = 470 men, 457 women) born between 1761 and 1799 and, hence, living in conditions of natural mortality and fertility (Lummaa et al. 1998). Second, by including social class in our analysis, we are able to consider the role of family-level variation in resources in modifying the role of the early environment on our outcomes (Pettay et al. 2007). Third, our food data are taken from crop yields extracted from annual records maintained by the estates farmed by our study population (Holopainen and Helama 2009), and because our measure of food availability varies on an inter-annual basis, we are able to compare multiple cohorts experiencing a range of early conditions. We predict a positive association between food availability at birth and later life success, although we expect such associations to be stronger among the landless, who will be more reliant on access to local food.

MATERIALS AND METHODS

The populations

All individuals were born between 1761 and 1799 in southwest Finland in five "parishes," three of which (Hiittinen, Kustavi, Rymättylä) were located in coastal areas and two of which (Ikaalinen and Tyrvää) were farther inland. During the study period, the population was sustained by local food production from cultivated arable land, supplemented by fishing in some areas. Local crop yields were the principal source of carbohydrates for all parishes (Holopainen and Helama 2009). Poor communication and transportation networks exacerbated the effects of food shortages, such that famines were relatively common (Jutikkala et al. 1980, Holopainen and Helama 2009). Approximately 40% of individuals in our sample died before the age of 15 years. The median number of children born per woman was five. However, up to one-quarter of adults did not produce a single offspring in their lifetime, despite the fact that reliable contraception was unavailable and 98% of individuals were married. Among married individuals in our sample, 12% produced no children before death. Divorce was not permitted by the church, remarriage was only possible in the event of death of a spouse, and adultery was punishable (Sundin 1992). Most individuals did not marry until their mid-twenties and 97% of children were born within wedlock. Extra-pair paternity is likely to have been lower than that recorded for contemporary, more sexually permissive European populations (median 3.7%) (Anderson 2006). In keeping with social mores, the average age of first reproduction as recorded by the church registers is very closely tied to the age at marriage for both men and women.

Demographic data

Pedigree data were extracted from church records maintained by ministers of the Lutheran church for tax purposes. Because these records contain all births, deaths, and marriages, family history can be reconstructed for several generations (Lummaa et al. 1998, Lahdenperä et al. 2004). We analyzed the life histories of individuals born during the years for which crop data are available (1761–1799). Our primary sample, used for the analysis of survival to adulthood, consists of 1934 individuals of known sex born to 512 mothers. We recorded parental social class (father's occupation) and survival to adulthood (age 15, the youngest age at marriage and reproduction in the population) for all individuals. The secondary sample (470 men and 457 women), used for the rest of the analyses, consisted of a subset including only individuals that survived to age 15, and were followed until age 45 (women) or age 50 (men) to ensure records on complete reproductive histories. Virtually all individuals (99.9% of women and 99.0% of men) who would ever reproduce in their lifetime had done so by these ages, and most children were born to women and men before these ages (99.1% and 96.7%, respectively). Reproductive success was defined as having produced at least one recorded child. The fate (survival to adulthood) of these children was known for the vast majority, with 91% of the focal adults having the fate of all of their children known.

Social class

In order to group together individuals who had similar access to wealth and resources, social class was determined at birth based on the father's occupation (Pettay et al. 2007); families were categorized as "landowning" or "landless" (Gillespie et al. 2008). The landowners included a few noblemen, priests, and free farmers ($n = 1299$); the landless class ($n = 635$) included tenant farmers, craftsmen, servants, and lodgers. Social class was inherited (Pettay et al. 2007), with three-quarters of individuals retaining the social class of their parents. Because of this, it is not possible for us to identify whether any interactions between social class and crop yield are due to resource access in childhood or in adult life.

Crop data

Winter rye and spring barley were the most important bread grains in these northern climates (Mukula and Rantanen 1989*a*, *b*). Oats were not grown or consumed in any significant amounts in Finland at this time by humans, but were used for animal food (Soininen 1974). Both crops were cultivated from arable land, with productivity being both variable and unpredictable (Holopainen and Helama 2009). Crop yield data (seeds yielded per seeds sown; also sometimes called "grain-figure") are available for our study period for eight estates in southwest Finland, based on estimates by contemporary officials, compiled by Tornberg (1989). Crop yields could have profound effects on some sections of the population: even in medium harvest years, some 5–10% of the population consumed emergency foodstuffs, such as tree bark (Soininen 1974). There is a qualitative correspondence between years of crop failure and documented famine (Jutikkala 2003*a*, *b*), although their relationships may have been rather complex and potentially mixed with direct and indirect (e.g., epidemics) effects to a hitherto unknown proportion. No information is available concerning whether the two crops are likely to have been consumed differently between the sexes or social classes. Annual yields were converted to three-year running averages, centred in the focal year (e.g., for the 1780 cohort, yields of rye and barley were calculated using yields from 1779, 1780, and 1781). This meant that food availability during gestation and lactation were encompassed and also acted to "smooth over" some of the artificial grouping together of individuals by calendar years. Values ranged from 4.1 to 6.5 for rye (median 5.5; time series for 1761–1799), and from 3.9 to 5.6 for barley (median 4.6; time series for 1770–1796) (Fig. 1a, b). It is important to note that annual rye and barley yields were not significantly correlated and so could have independent effects (Fig. 1c). Rye and barley yields in an individual's birth year were analyzed as continuous predictors, but for presentation in graphs, years are divided into "low" and "high" crop yield years (below or above median crop yields for the two crops).

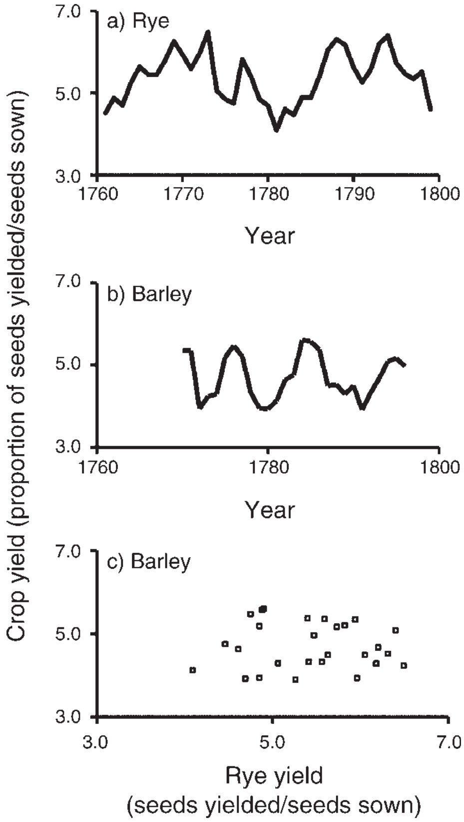

FIG. 1. Time series showing three-year running averages of the relative yields of (a) winter rye and (b) spring barley for eight estates in southwest Finland and (c) the non-correspondence between the two measures for a given year. Data were first compiled from historical documents by Tornberg (1989). Yield in any given year is measured as the three-year running average of seeds yielded as a proportion of the seeds sown.

Statistical analysis

We investigated the effects of fluctuating food availability on: (1) the probability of an individual surviving to adulthood; (2) the probability of and age at marriage; (3) the probability of reproducing over a lifetime; and (4) the probability of raising offspring successfully to adulthood. We used the statistical software program SAS 9.1 (SAS Institute 2002–2003). Analyses were conducted in the GENMOD procedure (SAS Institute 1990), which allow analysis of response terms with normally and nonnormally distributed error structures and inclusion of clustering terms to account for nonindependence of data (generalized estimating equations). In all analyses, a binomial error structure was used except for age at marriage, which was normalized by log-transformation, and then analyzed with a normal error structure. For the proportion of offspring surviving to adulthood, the response was the number of surviving offspring with a variable denominator equal to the total number of children born to the individual. For analysis of the proportion of offspring surviving to adulthood, and the probability of producing at least one child, the response was weighted by the proportion of offspring successfully followed to adulthood. Males and females were examined separately for each reproductive outcome.

Several factors were accounted for in order to control for potential confounders and nonindependence of data points. Cohort size and follow-up rate were included to account for selective fertility, survival, and attrition effects, which are candidate alternative explanations for relationships between the early environment and reproductive performance later in life (Painter et al. 2008). Cohort size was calculated as the number of individuals born in the same year as the focal individual, and was included to account for possible reproductive characteristics inherited by individuals whose parents were able to conceive during adverse conditions (Painter et al. 2008). Cohort follow-up rate was calculated as the proportion of individuals born in a given year surviving to adulthood and successfully tracked across their reproductive lives; it was included to allow for the possibility that the likelihood of an individual being lost to follow-up (either through death or migration) is related to the quality of their birth environment. Parish (five levels), social class (two levels), birth year (covariate), birth order (two levels), cohort size (covariate), and cohort follow-up rate (covariate) were entered into the models as potential confounders. Birth year was converted to an arbitrary cohort number (ascending from 1). Birth order was a two-level factor defined in a sex-specific manner; it indicated whether or not an individual was the first among his or her same-sex siblings to survive to adulthood, in order to allow for effects of familial inheritance or marriage conventions on life history. The exception to this was in the analysis of survival to adulthood, in which case birth order was a non-sex-specific covariate, and took account of deceased elder siblings. Maternal identity (ID) was included as a clustering factor to account for nonindependence of individuals born within the same families.

One parameter that may influence the traits under study is life span. For example, individuals who survive long into adulthood are more likely to marry and reproduce than those who die young. Nevertheless, we did not control for life span in the first instance in either analysis because doing so might obscure an effect of early nutrition on our outcome measures, were such an effect to be mediated through an effect of life span. We then further investigated whether any detected effect might be mediated through an effect of birth harvest yield on life span by fitting life span into the model secondarily. If effects of harvest yield at birth on the reproductive outcomes under study are mediated through an effect of harvest yield on life span, we would expect the inclusion of life span to remove or reduce the effect of harvest yield. However, inclusion of life span did not significantly change the parameter estimates of the effects of interest; hence all parameter estimates come from models excluding this term (see *Results*).

Confounding terms (excluding life span) that significantly influenced the explanatory power of the model were retained. Rye and barley yield were subsequently added to the model and their effects on the explanatory power of the model were determined. Rye and barley yields were never entered simultaneously into the model, despite being uncorrelated, because of the differing lengths of the time series for each crop (Fig. 1a, b; but see below). Two-way interactions with social class were assessed. All P values are two-tailed and significance levels are set at 0.05. Results given in the text and Appendices are χ^2 scores from Type III analyses. Model estimates for the primary effects of interest are included in Tables 1 and 2. χ^2 scores for the confounding factors in each model are either listed in the text (survival models) or included in Appendices A and B.

Additionally, using a shorter series of data where yields of both barley and rye were available for the same years, we tested the prediction that periods of low yields of both rye and barley would have the very worst effects, and periods of high yields of both rye and barley would have the greatest benefits, using the outcome most closely associated with variance in evolutionary fitness, the probability of reproducing over a lifetime. We split the years by the median yields of both crops (5.5 for rye, 4.5 for barley) to produce three categories of years (1, low rye/low barley; 2, low rye/high barley or high rye/low barley; 3, high rye/high barley), and we repeated the analysis of the probability of reproducing over a lifetime.

RESULTS

Survival to adulthood

We found no evidence for an effect of crop yield at birth on the probability that an individual would survive to adulthood. Of all 1934 individuals, 63.5% survived to age 15. Neither rye yield ($\chi^2_1 = 1.55$, $P = 0.21$) nor barley yield ($\chi^2_1 = 0.31$, $P = 0.56$) was associated with the probability of survival, irrespective of social class (interaction with rye, $\chi^2_1 = 0.02$, $P = 0.88$; interaction with barley, $\chi^2_1 = 0.23$, $P = 0.63$) or sex (interaction with

Table 1. Parameter estimates and χ^2 test scores for effects of rye and barley crop yield at birth and interactions between crop yield and social class on probability of marrying, age at marriage, and offspring survival rate for historical humans, by gender.

Relationship and parameter	Probability of marrying				Age at marriage				Offspring survival rate			
	Estimate (SE)	P	χ^2	P for χ^2	Estimate (SE)	P	χ^2	P for χ^2	Estimate (SE)	P	χ^2	P for χ^2
Rye yield effect on males	$N = 470$				$N = 391$				$N = 356$			
Intercept	−2.99 (2.37)	0.21			3.42 (0.077)	<0.0001			0.099 (0.96)	0.30		
Rye	0.98 (0.46)	0.031	0.66	0.41	**−0.032 (0.014)**	**0.026**	**4.79**	**0.029**	0.31 (0.17)	0.070	2.46	0.12
Social (landowners)	6.22 (0.81)	0.023							2.82 (1.23)	0.022		
Rye × social (landowners)	**−1.12 (0.54)**	**0.036**	**4.67**	**0.031**			0.11	0.74	**−0.52 (0.22)**	**0.019**	**6.11**	**0.014**
Barley yield effect on males	$N = 346$				$N = 291$				$N = 264$			
Intercept	−4.21 (3.25)	0.20			3.25 (0.11)	<0.0001			−0.11 (1.24)	0.93		
Barley	1.49 (0.73)	0.042	0.34	0.13	0.0007 (0.020)	0.97	0.00	0.97	0.13 (0.26)	0.60	0.38	0.54
Social (landowners)	7.61 (3.68)	0.039							1.20 (1.42)	0.40		
Barley × social (landowners)	**−1.67 (0.82)**	**0.041**	**4.82**	**0.029**			1.59	0.21	−0.26 (0.30)	0.38	0.41	0.52
Rye yield effect on females	$N = 457$				$N = 392$				$N = 354$			
Intercept	2.09 (2.23)	0.35			3.49 (0.081)	<0.0001			−0.75 (0.93)	0.42		
Rye	0.019 (0.41)	0.96	0.15	0.70	**−0.029 (0.014)**	**0.040**	**5.15**	**0.023**	0.31 (0.17)	0.070	0.09	0.76
Social (landowners)	−0.89 (2.63)	0.74			−0.042 (0.021)	0.043			2.75 (1.23)	0.025		
Rye × social (landowners)	0.099 (0.49)	0.84	**0.04**	**0.84**			0.20	0.66	**−0.51 (0.22)**	**0.021**	5.72	0.017
Barley yield effect on females	$N = 342$				$N = 291$				$N = 261$			
Intercept	−0.59 (3.29)	0.86			3.33 (0.10)	<0.0001			0.28 (1.22)	0.82		
Barley	0.62 (0.73)	0.39	1.78	0.18	−0.0034 (0.021)	0.87	0.76	0.38	0.13 (0.26)	0.63	0.27	0.60
Social (landowners)	0.89 (3.54)	0.80			−0.020 (0.024)	0.40			1.20 (1.43)	0.40		
Barley × social (landowners)	−0.31 (0.78)	0.69	**0.17**	**0.68**			2.05	0.15	−0.27 (0.30)	0.38	0.79	0.37

Notes: Estimates for confounding variables are not given (see Appendix A). With the exception of those parameters given for age at marriage, all estimates are those obtained when the interaction between social class and rye or barley yield was included in the model. Because there were no interactions between social class and crop yield on age at marriage, these estimates for this outcome are from models containing the first-order effect of crop yields only. Significant effects ($P \leq 0.05$) are indicated in bold. The χ^2 test scores for first-order effect of crop yield were also obtained without interaction terms being entered into the model.

rye, $\chi^2_1 = 0.81$, $P = 0.37$; interaction with barley, $\chi^2_1 = 0.13$, $P = 0.71$). These models control for effects of parish ($\chi^2_4 = 46.58$, $P < 0.0001$), higher survival in later cohorts ($\chi^2_1 = 7.39$, $P = 0.0066$) and firstborns ($\chi^2_1 = 4.65$, $P = 0.031$), and lower survival in twins ($\chi^2_1 = 33.24$, $P < 0.0001$). Offspring survival to age 15 did not differ between males and females ($\chi^2_1 = 0.06$, $P = 0.80$) or between the landowners and landless ($\chi^2_1 = 0.03$, $P = 0.85$).

Probability of and age at marriage

Overall, we found some support to suggest that the probability of marriage and the age at which marriage occurred were influenced by an individual's access to food at birth. Of the 470 males and 457 females surviving to age 15, 85% and 88% married, respectively. Among men, marriage probability was uninfluenced by either rye ($\chi^2_1 = 0.66$, $P = 0.41$) or barley ($\chi^2_1 = 0.37$, $P = 0.13$), on average, but was modified significantly by interactions between crop yield and social class (for rye, $\chi^2_1 = 4.67$, $P = 0.031$; for barley, $\chi^2_1 = 4.82$, $P = 0.029$). Crop yield was not significantly related to marital success among landowners (for rye, $\chi^2_1 = 0.29$, $P = 0.59$; for barley, $\chi^2_1 = 0.25$, $P = 0.62$), but among the landless, those born in high harvest years had a higher chance of marrying (for rye, $\chi^2_1 = 4.75$, $P = 0.029$; for barley, $\chi^2_1 = 5.62$, $P = 0.018$). The magnitude of this effect in landless individuals represented an increase in marriage probability from 82% to 88% in those born in low and high rye yield years, respectively (see *Methods*), and an increase from 76% to 95% in those born in low and high barley yield years. By contrast, the probability that women married was independent of the crop yield around the time of birth (for rye, $\chi^2_1 = 0.15$, $P = 0.70$; for barley, $\chi^2_1 = 1.78$, $P = 0.18$), irrespective of their social class (for the interaction of rye × social class, $\chi^2_1 = 0.04$, $P = 0.84$; for the interaction of barley × social class, $\chi^2_1 = 0.17$, $P = 0.68$); see Table 1.

TABLE 2. Parameter estimates and χ^2 test scores for effects of rye and barley crop yield at birth and interactions between crop yield and social class on probability of reproducing (all individuals), probability of reproducing (married individuals only), and the probability of raising at least one child to age 15.

Relationship and parameter	Probability of marrying				Age at marriage				Offspring survival rate			
	Estimate (SE)	P	χ^2	P for χ^2	Estimate (SE)	P	χ^2	P for χ^2	Estimate (SE)	P	χ^2	P for χ^2
Rye yield effect on males	$N = 470$				$N = 400$				$N = 470$			
Intercept	−2.31 (2.07)	0.27			2.47 (3.14)	0.43			−1.86 (2.20)	0.40		
Rye	0.54 (0.38)	0.16	0.54	0.46	−0.098 (0.57)	0.86	0.35	0.55	0.50 (0.40)	0.21	1.37	0.24
Social (landowners)	3.32 (2.30)	0.15			−1.74 (3.39)	0.61			2.67 (2.42)	0.27		
Rye × social (landowners)	−0.57 (0.42)	0.18	1.79	0.18	0.37 (0.62)	0.55	0.35	0.55	−0.50 (0.45)	0.27	1.91	0.17
Barley yield effect on males	$N = 346$				$N = 294$				$N = 346$			
Intercept	−8.99 (2.88)	0.0018			−9.99 (2.57)	0.0001			−5.61 (2.61)	0.032		
Barley	2.12 (0.65)	0.0012	1.37	0.24	2.60 (0.56)	<0.0001	0.65	0.65	1.40 (0.57)	0.015	0.70	0.40
Social (landowners)	11.78 (3.28)	0.0003			16.14 (3.85)	<0.0001			7.99 (3.02)	0.0081		
Barley × social (landowners)	**−2.52 (0.73)**	**0.0005**	**14.37**	**0.0002**	**−3.39 (0.81)**	**<0.0001**	**11.19**	**0.0008**	**−1.73 (0.66)**	**0.0087**	**8.42**	**0.0037**
Rye yield effect on females	$N = 457$				$N = 400$				$N = 457$			
Intercept	−2.58 (1.65)	0.17			−3.36 (2.18)	0.12			−4.18 (1.70)	0.014		
Rye	0.76 (0.31)	0.016	0.92	0.34	0.98 (0.43)	0.022	0.59	0.44	1.07 (0.33)	0.0011	2.18	0.14
Social (landowners)	3.97 (2.04)	0.051			6.15 (2.70)	0.023			5.10 (2.04)	0.013		
Rye × social (landowners)	**−0.80 (0.83)**	**0.038**	**4.13**	**0.042**	**−1.16 (0.52)**	**0.025**	**4.79**	**0.029**	**−1.06 (0.39)**	**0.0064**	5.48	0.019
Barley yield effect on females	$N = 342$				$N = 296$				$N = 342$			
Intercept	−5.37 (2.31)	0.02			−4.91 (2.53)	0.052			−4.86 (2.44)	0.046		
Barley	1.48 (0.52)	0.0042	3.76	0.052	1.43 (0.56)	0.011	1.08	0.30	1.35 (0.55)	0.013	0.38	0.54
Social (landowners)	5.79 (2.60)	0.026			7.57 (3.02)	0.012			6.59 (2.73)	0.016		
Barley × social (landowners)	**−1.32 (0.58)**	**0.021**	**5.56**	**0.018**	**−1.60 (0.66)**	**0.016**	**5.54**	**0.019**	**−1.53 (0.60)**	**0.012**	**8.10**	**0.044**

Notes: For estimates for confounding variables not given, see Appendix B. All estimates are those obtained when the interaction between social class and rye/barley yield was included in the model. Significant effects are indicated in bold. The χ^2 test scores for first-order effect of crop yield were obtained without interaction terms being entered into the model.

Furthermore, for those that married, we found that high crop yields around birth were associated with younger marriage ages in general. The median age at first marriage was 26 years for men (range 17–50) and 25 years for women (range 16–47 years). Men and women born in years of high rye yields married 10 and 11 months earlier, respectively, than those born in years of low rye yield (for men, $\chi^2_1 = 4.79$, $P = 0.029$; for women, $\chi^2_1 = 5.15$, $P = 0.023$), irrespective of social class (for men, interaction of rye × social class, $\chi^2_1 = 0.11$, $P = 0.74$; for women, $\chi^2_1 = 0.20$, $P = 0.66$) (Fig. 2). Interestingly, there was no similar effect of barley on either sex (for men, $\chi^2_1 = 0.00$, $P = 0.97$; for women, $\chi^2_1 = 0.76$, $P = 0.38$). These results were not modified by social class (for men, $\chi^2_1 = 1.59$, $P = 0.21$; for women, $\chi^2_1 = 2.05$, $P = 0.15$); see Table 1.

Probability of reproducing over a lifetime

Crop yield at birth influenced the probability that individuals would produce offspring in their lifetime. Of the 470 men and 457 women, 76% and 78%, respectively, produced at least one child. In this case, we found a predominant effect of barley rather than rye. Rye had no overall effect on the probability that men would produce offspring ($\chi^2_1 = 0.54$, $P = 0.46$), irrespective of their social class ($\chi^2_1 = 1.79$, $P = 0.18$). Nor did rye have an overall effect in women ($\chi^2_1 = 0.92$, $P = 0.34$), although in this case there was a significant interaction between birth rye yield and social class ($\chi^2_1 = 4.13$, $P = 0.042$). Women from landless families had a 74% probability of reproducing when born in low rye years, but an 89% chance when born in high years (Table 2).

By contrast, although barley yield had no overall effect on the probability of producing offspring in men ($\chi^2_1 = 1.37$, $P = 0.24$), there was a significant interaction with social class ($\chi^2_1 = 14.37$, $P = 0.0002$). This again indicates the benefit to individuals from landless families of being born during times of high crop yields and an absence of a benefit to those from the high social classes.

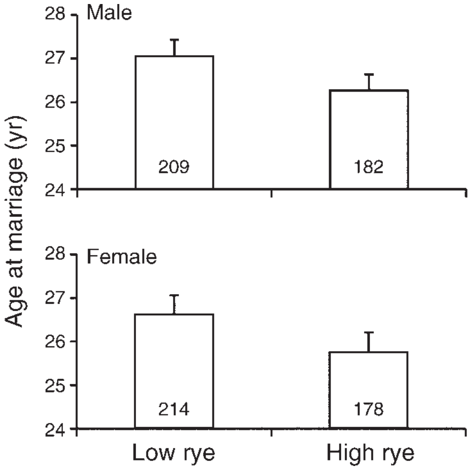

FIG. 2. Age at marriage according to birth rye yield in men and women. Birth rye yield is the average relative yield of rye/barley for the following years: the year before the individual's birth year, the actual year of the individual's birth, and the year following the individual's birth year. "Low" indicates <5.5 relative yield in an individual's birth year, and "High" indicates values above this. Histogram bars were calculated from raw data (mean + SE). Sample sizes are shown for each category.

Landless men born in low barley years had a 53% chance of reproducing, whereas those born in high barley yield years had a 92% chance of reproducing (Fig. 3). Similarly, among women, those born in high barley years benefited in terms of producing offspring ($\chi_1^2 = 3.76$, $P = 0.052$) and this was modified by social class ($\chi_1^2 = 5.56$, $P = 0.018$): Women from landless families had an increased probability of gaining reproductive success from 68% to 91% when born in a low vs. high barley yield year (Fig. 3). Finally, we found that the results were highly similar when we considered as the outcome the probability of an individual raising at least one offspring to age 15, and also when we only considered individuals who married (Table 2).

Proportion of offspring surviving to adulthood

Overall, we found some evidence to suggest that offspring survival to adulthood was influenced by food supply in the early life of parents. The 357 and 356 men who reproduced had a total of 3658 offspring (median 5, range 1–16 children). Of these, 2386 (65.2%) survived to 15 years of age. In neither men nor women were there any relationships between birth crop yield and offspring survival rate on this outcome overall (for men and rye, $\chi_1^2 = 2.46$, $P = 0.12$; for men and barley, $\chi_1^2 = 0.38$, $P = 0.54$; for women and rye, $\chi_1^2 = 0.09$, $P = 0.76$; for women and barley, $\chi_1^2 = 0.27$, $P = 0.60$). However, there was a positive effect of rye yield in landless men (interaction, $\chi_1^2 = 6.11$, $P = 0.014$) and women ($\chi_1^2 = 5.72$, $P = 0.017$). There were no such interactions for barley (for men, $\chi_1^2 = 0.41$, $P = 0.52$; for women, $\chi_1^2 = 0.79$, $P = 0.37$); see Table 1.

Probability of reproducing in a lifetime: cumulative effects of rye and barley

In support of our results concerning the independent effects of rye and barley on the probability of reproducing in a lifetime, there were also cumulative effects of the yields of both crops in an individual's year of birth on their probability of reproducing in their lifetime. We found that landless men and women born in years when both the rye and barley yields were low were the least likely to reproduce, whereas those born in years

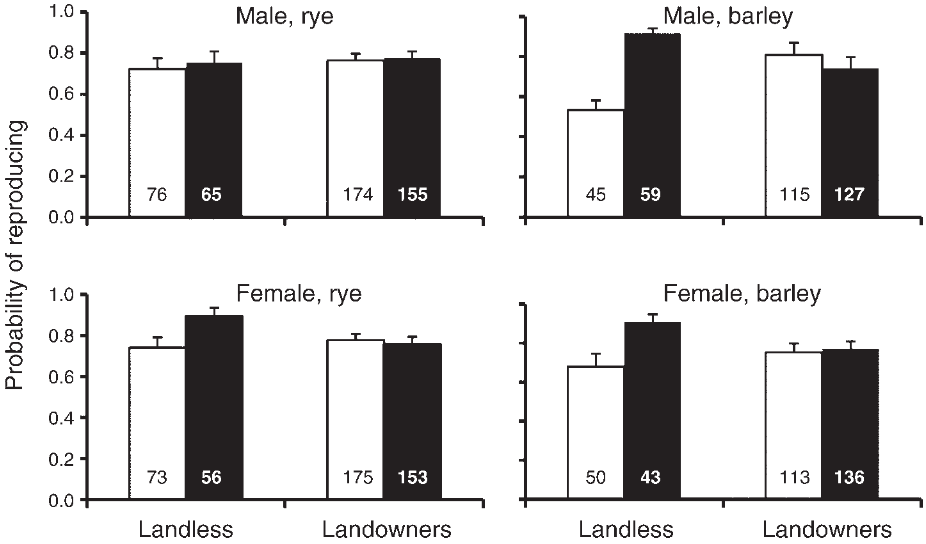

FIG. 3. Probability of reproducing in relation to birth rye or barley yield (low vs. high) and parental social class (landless vs. landowners) in men and women. Open bars represent those born during low crop yield years (<5.5 relative yield for rye; <4.5 relative yield for barley). Black bars represent those born during high crop yield years. Bars were calculated from raw data (mean + SE). Sample sizes are shown for each category.

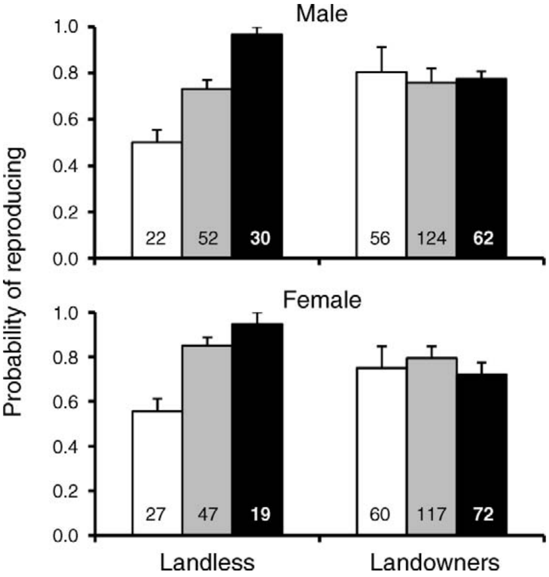

FIG. 4. Probability of reproducing in relation to a combination of birth rye yield and birth barley yield and parental social class in men and women. Open bars represent those born during years in which rye and barley were both low (<5.5 and <4.5 relative yields, respectively). Gray bars represent those born in years in which either rye or barley was high (>5.5 and >4.5, respectively), but one was low. Black bars represent those born in years in which both rye and barley yields were high. Bars were calculated from raw data (mean + SE). Sample sizes are shown for each category.

when both were high were most likely to reproduce (50% vs. 97% of men; for the interaction between three combined crop categories and social class, $\chi^2_2 = 12.70$, $P = 0.0017$; 55% vs. 95% of women, for the interaction, $\chi^2_2 = 9.18$, $P = 0.010$); see Fig. 4.

DISCUSSION

Environmental conditions experienced in very early life can have echoes in adult phenotype, causing variance in individual fitness, and thus interacting with other ecological and evolutionary processes (Lindström 1999, Metcalfe and Monaghan 2001). Inadequate nutrition during critical windows of early life may constrain development of organs and tissues and therefore be negatively associated with traits that increase reproductive success. To date, however, direct evidence in natural populations has been sparse, partly because of the difficulties in measuring individual access to food. Specifically in the case of humans, it has been entirely lacking, with one study showing a positive effect of early prenatal famine exposure on female reproductive success (Painter et al. 2008). In the present study we used demographic and agricultural data from preindustrial Finland to test the hypothesis that low food availability in very early life can constrain early development, with detrimental consequences for reproductive success. We found that although survival to adulthood was not dependent on early-life food availability, several measures of reproductive performance were.

Out of 16 analyses conducted on reproductive parameters (four parameters, two sexes, and two crops), two showed significant main effects of crop yields at birth and seven showed significant interactions between crop yield and social class. All reproductive parameters considered were significantly influenced by crop yield in at least one of the sexes. Finally, in all cases, a significant main effect was associated with a benefit of increasing crop yield at birth and a significant interaction was associated with disproportionate benefits to individuals from landless families. Our results represent what is, to our knowledge, the most direct evidence of nutrition in very early life constraining reproductive performance in humans.

Our study has been made possible because of the fortuitous documentation of agricultural productivity as well as family histories by officials of this historical population (Lummaa et al. 1998, Holopainen and Helama 2009). We have investigated both population-level and individual-level variation in access to resources, and were able to discount several competing explanations in favor of the likelihood that our results represent causal effects of individual food supply, most likely through maternal nutrition. We have found similar effects in components of reproductive success not necessarily directly related to the reproductive system (marital success and offspring survival). Furthermore, we have shown that these effects exist in both men and women. From a biomedical perspective, this research complements that relating birth weight and other measures of the intrauterine environment to reproductive health (Ibáñez et al. 2002, 2003, Ekholm et al. 2005, Nohr et al. 2009), by implicating an exogenous environmental factor. Integrating life-history data such as these with variation in the early environment thus can provide a source of direct evidence for early environmental factors shaping long-term reproductive outcomes. Most importantly from an evolutionary perspective, we found that the likelihood of an individual producing any surviving offspring was related to food availability in early life. As such, the way in which the developing individual responds to early nutrition is likely to be acted upon by natural selection.

For both men and women, the interactions between crop yield and social class on the probability of reproducing were evident even when the analysis was restricted to those who were married. Because marriage is a precondition for reproduction in this population, this strongly indicates that the effect on the probability of reproduction was not mediated by the likelihood of an individual marrying, and raises the likelihood that both landless males and females born in periods of low food availability (and/or their partners) suffered from some level of sub-fecundity. Given the lack of reliable contraception and the fact that the demographic transition had not begun in this population (Korpelainen 2003), we consider alternative behavioral explanations for this to be unlikely. Furthermore, given both the expectations of life-history theory and empirical evidence from laboratory studies of animals showing negative effects of early food availability on reproductive success (Zambrano et al. 2005, Guzmán et al. 2006), a physiological explanation is more parsimonious. Another mechanism through which reproductive success could be affected by early environment is through an effect on life span. However, as described above (see *Methods*), this was not a mediating factor in any of the effects under study.

In addition to the consequences for fertility, there were effects that may involve physiological processes or anatomical development other than those associated with the reproductive systems. There was no evidence that crop yield in early life influenced the probability that an individual would survive to adulthood. This may be partly because mortality is largely due to infectious disease (Turpeinen 1978). In support of this, there was also no difference between landowners and the landless in the probability of surviving to adulthood, as has also been found by previous studies of the same population (Pettay et al. 2007, Gillespie et al. 2008), suggesting that the risk of death from infectious diseases may have been to some extent independent of condition and nutrition. In contrast, in both men and women, there were associations between birth crop yields and either the probability of marriage or age at marriage. This occurred even while controlling for the possible effects of the presence of a (competing) same-sex elder sibling on marital prospects. One explanation is that individuals born in poor crop years may have been seen as providing less attractive marital prospects than individuals born in good crop years, reflecting their likely reproductive potential. In addition, there appear to have been intergenerational consequences of birth in a poor crop year, as has been reported elsewhere (Bygren et al. 2001): although an individual's chances of surviving to adulthood were not related to food availability in their year of birth, the proportion of their offspring who survived to adulthood was related (in the case of individuals from landless families). There are several potential mechanisms by which such an effect could occur. These could be direct (e.g., the ability to work to provision offspring or through a tendency of some women to produce small offspring with higher mortality risk). Alternatively, they could be indirect (e.g., through partner quality).

Although it is inevitable that even in strict societies such as this, there exist a small number of instances of mis-assigned paternity and infanticide, there are several reasons why these are unlikely to be important for the conclusions regarding reproductive success in the current study, in addition to the evidence that they are probably rare in this population as a general rule (see *Methods*). Crucially, such practices would generally have been most likely to increase the likelihood of type II errors being made (incorrectly accepting the null hypothesis), due to the specificity of the predictions we tested. For example, a competing hypothesis that invoked such covert practices as part of the explanation for the relationship between early-life crops and fertility would need to explain why landless women born in poor harvest years would be most likely to commit infanticide, and landless men born in poor harvest years would be most likely to gain paternity covertly. The former example does have some plausibility as a conditional strategy in which landless women with poor health as a consequence of poor early-life nutrition would be most likely to use infanticide to regulate their fertility. However, if this were the case, then we would predict a longer interval between marriage and first birth among women in this group who did reproduce, which is not the case. A final argument against this explanation being important is that in such a high-fertility population, it seems very unlikely that married women would use infanticide as a fertility regulator to such an extent as to actually prevent any successful reproduction during their entire lifetime.

It should be noted that our measures of food availability are proxies drawn from agricultural records and are not measures of individual food intake. However, the fact that despite this, there are strong associations between these measures and the life-history traits of individuals born in the corresponding year suggests that they capture important variation in the environment that each individual has experienced in his or her early life. A further argument in favor of this is the documented relationships between crop failures and famines (Jutikkala 2003*a*, *b*). Nevertheless, a competing explanation that must be considered is that our measures of crop yield also reflect aspects of the environment other than food availability (e.g., infectious disease, climate) that could have affected individual development. This is unlikely. As can be seen from Fig. 1c, there is no correspondence between the birth rye yield and birth barley yield in a given year, indicating that there should be no common environmental conditions responsible for simultaneously high rye and barley yields. Not only is rye a winter crop and barley a spring crop, but also they exhibit different climatic responses, yields in the former being related to temperature and yields in the latter being more related to precipitation (Holopainen and Helama 2009). Furthermore, as might be expected from a measure of food supply, the effects were generally restricted to the landless social class (i.e., those with less access to food). Individuals from landowning families may have experienced long-term effects of early nutrition on adult reproductive performance, e.g., through long-term consequences (Horta et al. 2007) of the reported lower rates of breastfeeding in landowning social classes (Moring 1998), but any such effects were evidently not related to crop yields. Finally, the likelihood of rye and barley yields being of nutritional importance can be further evaluated by considering the potential role of the cumulative effects of the two crop yields in an individual's year of birth. The chances of reproducing in a lifetime were 50% and 55%, respectively, for males and females from poor families born when both rye and barley yields were low, whereas they were 97% and 95% among those born when both yields were high (Fig. 4). The large difference in the proportions of reproductive landless between cohorts born during the very high food years vs. the very low food years, as determined by two independent crop yields, strongly supports our argument that cohort differences in reproductive success are related to early-life food supply per se.

Not only is it likely that our results reflect direct associations between food availability in early life and life-history traits, but also it is most plausible that these associations reflect causal effects upon the outcomes measured. In order to reduce the likelihood of alternative explanations for such patterns, we tested the significances in each of our models of two potential confounders. Cohort size was included because it allowed for the possibility of selective fertility effects (Painter et al. 2008): if individuals inherit from their parents the fertility traits that facilitate reproduction in adverse conditions, then individuals from smaller cohorts may have greater reproductive success for this reason alone. However, in no instances was cohort size a negative predictor of any of the traits measured. Furthermore, as can be seen from sample sizes in Figs. 2–4, there is no general tendency for landless individuals to be overrepresented in the birth years with poor crop yields, so this is not a likely explanation for our results either. In addition, we also included a term describing the proportion of individuals from each cohort who survived to adulthood and were selected for inclusion in the secondary sample. This was important to consider because, although there was no effect of any birth crop yield on survival to adulthood, it was also plausible that birth crop yield could, through an effect on migration propensity, be associated with the likelihood that individuals were followed for their reproductive lives. The most likely explanation for our results is therefore that food availability in early life had direct effects on the life-history traits measured.

A growing body of evidence from epidemiological studies of humans as well as experiments with model organisms supports the hypothesis that the environment experienced during an individual's early development can have profound consequences for health in adulthood (Bertram and Hanson 2001, Bateson et al. 2004). From a biomedical perspective, understanding the processes by which this occurs is important because it can help with prediction and prevention of disease and adverse health outcomes. From an evolutionary ecological perspective, aspects of individual health can be related to evolutionary fitness, and therefore an appreciation of their scope, mechanism, and ultimate effects contributes to an overall picture of the evolutionary processes affecting population dynamics and persistence. In reality, each approach benefits from a consideration of the other: Clinical data can inform our knowledge of phenotypic variation (Lummaa and Clutton-Brock 2002, Bateson et al. 2004), and evolutionary theory predicts that natural selection has shaped the constraints and decisions faced by our developing bodies so as to maximize individual fitness (Rickard and Lummaa 2007).

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APPENDIX A

Table showing χ^2 scores of confounding factors from Type III analyses of the probability of marrying, age at marriage, and the proportion of offspring raised to adulthood (*Ecological Archives* E091-248-A1).

APPENDIX B

Table showing χ^2 scores of confounding factors from Type III analyses of the probability of reproducing (all individuals as well as married individuals only), and the probability of raising at least one offspring to age 15 (*Ecological Archives* E091-248-A2).