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Month of birth predicted reproductive success and fitness in pre-modern Canadian women

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Conditions experienced during early development affect human health and survival in adulthood, but whether such effects have consequences for fitness is not known. One surrogate for early conditions is month of birth, which is known to influence health and survival in many human populations. We show that in nineteenth century Canada, month of birth predicted a woman's fitness measured by the number of grandchildren produced, with the genetic contribution to the following generations by women born in different months differing by over seven grandchildren. This difference was mainly caused by differences in the reproductive rates of both mothers and their offspring, rather than differences in their survival. Women born in the best months of the year had longer reproductive lifespans, larger numbers of live births and raised more offspring to adulthood than those who were born in the worst months. Furthermore, the offspring of those women born in the best months also had greater reproductive rates, suggesting that month of birth also influenced a mother's ability to invest in her offspring. Our results suggest that early conditions may have important consequences for human lifetime reproductive performance within and between generations, and that timing of birth had large effects on fitness in this rural community.

Keywords: early development; human; reproductive success; survival; timing of birth

1. INTRODUCTION

Measures of reproductive success in wild mammals can be influenced by the climatic, hormonal and nutritional conditions experienced during early development (Lindström 1999; Metcalfe & Monaghan 2001), which may generate subsequent downstream effects on the survival and reproductive success of their offspring (e.g. Huck *et al.* 1987; Meikle & Westberg 2001). However, the underlying mechanisms for such correlations are often unclear, and whether early conditions also influence some measures of long-term fitness is generally unknown in mammals (Lummaa & Clutton-Brock 2002).

For medical reasons, a number of studies have investigated how conditions experienced early in life influence subsequent growth and survival in different human populations. Such studies offer important insights into potential mechanisms through which early conditions influence subsequent survival and reproductive success. For example, early environmental conditions, such as the quality and quantity of nutrition received *in utero* and infancy, may predict the onset of many chronic diseases in adulthood (Barker 1994). Similarly, month of birth, reflecting differing early developmental conditions experienced by individuals born during different months of the year, is related to mortality rates in early adulthood (Moore *et al.* 1997), final height (Weber *et al.* 1998) and overall longevity (Doblhammer & Vaupel 2001; Gavrilov & Gavrilova 2003). Furthermore, month of birth has been shown to be linked to a range of diverse outcomes in both modern Western and more traditional societies, including mental health problems (Kinney *et al.* 2000; Joiner *et al.* 2002), diabetes (e.g. Fichera *et al.* 2001), eating disorders (Eagles *et al.* 2001), breast cancer (e.g. Kristoffersen & Hartveit 2000), and allergies (Kusunoki *et al.* 1999). These associations between early conditions and later growth, health and survival have been proposed to result from foetal programming (Lucas 1991), where a stimulus (or lack of stimulus) during a critical period early in life may permanently affect body structure, physiology and metabolism (McCance & Widdowson 1974).

While the impact of early conditions on disease and survival patterns in humans has been recognized for public health, their role in affecting individual reproductive success and fitness has not been considered previously (Lummaa & Clutton-Brock 2002). However, there are at least three alternatives for how month of birth effects could cause differences in fitness: (i) through differential survival of individuals born in different months; (ii) through their differential reproductive rates in adulthood; and (iii) through differences in their offspring's reproductive potential. First, month of birth could give rise to differential lifetime reproductive output of individuals if the timing of birth affects an individual's susceptibility to diseases (Barker 1994) and subsequent survival probability in adulthood (Moore *et al.* 1997; Doblhammer & Vaupel 2001; Gavrilov & Gavrilova 2003), and as a consequence individuals born during some months have shorter reproductive lifespan than individuals born during other months. Second, month of birth could also generate differences in reproductive output between women if, for example, conditions experienced early in life affect development of the organs producing and regulating reproductive hormones in adulthood (Lumey & Stein 1997). There is evidence that retarded foetal or infant growth rates, or foetal exposure to famine, may affect some reproductive traits of humans, such as an individual's marriage

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probability (Phillips *et al.* 2001) and age at menopause (Cresswell *et al.* 1997), as well as offspring birth weight (Lumey 1992) and early survival (Lumey & Stein 1997). Finally, the differences in fitness between individuals born during different months of the year could result from differences in their parental investment and subsequent quality of offspring, which results in differences between their offspring's capacity to themselves reproduce successfully. Experiments on other mammals have shown that early conditions may affect reproductive success across generations. For example, daughters of food-restricted female golden hamsters (*Mesocricetus auratus*), themselves reared on *ad libitum* diets, may produce smaller litters and relatively fewer sons over their lifetime than daughters of females that were not food-restricted (Huck *et al.* 1987).

Here, we investigate whether early conditions influenced fitness (number of grandchildren) in a rural human population experiencing conditions of natural fertility. We analyse complete reproductive histories of a cohort of over 3000 Saguenay mothers from Canada born between 1850 and 1879, and the survival and complete reproductive history of their surviving offspring (born between 1866 and 1926) who married in the same population. Like those of previous studies, we use birth month as a surrogate for early conditions, because in reality, early conditions are likely to be a complex interaction of nutritional and environmental effects. In addition, month of birth is known to influence disease susceptibility and survival in humans (Lummaa 2003), and there is some previous evidence to suggest that it may also influence reproductive characteristics, such as menarche or menstrual disorders (Jongbloet *et al.* 1994) and fecundability (Nonaka *et al.* 1990; Smits *et al.* 1997).

First, for each woman, we study the effect of month of birth on the number of grandchildren delivered into the population. Second, to investigate the pathways through which any relationships between timing of birth and fitness may arise, we analyse the effects of month of birth on a number of underlying individual life-history traits, including: (i) adulthood survival and longevity; (ii) age at first marriage; (iii) age at last delivery; (iv) length of reproductive lifespan (time between first and last delivery); (v) total number of live-born children; and (vi) number of children raised to adulthood and marrying in the population. Third, we evaluate the importance of differential adulthood survival, reproductive effort and offspring quality in determining the long-term fitness in the population in relation to the timing of birth.

2. METHODS

(a) *Study population*

The Saguenay region is located on the north shore of the St Lawrence River in Quebec, Canada (*ca.* 48° north). Average monthly temperature in the area fluctuates by more than 40 °C from −20 °C in January to +20 °C in July. The vegetative season expands from mid-May to mid-September, but frost at the end of May and at the beginning of September is not unusual (Pouyez & Lavoie 1983). The population is almost entirely French speaking and Catholic, and until the beginning of the twentieth century was mainly agricultural. The inhabitants expressed a high homogeneity in terms of rituals relating to family life events throughout the period of this study (Bouchard 1996), because the birth, marriage and death patterns of everyone were all within the influence of the same religion. For instance, during the nineteenth century, marriage seasons strictly followed religious and agricultural calendars. Few marriages took place in the months of March (Lent season) and December (Advent), or in July to August (fieldwork and harvest), whereas November, January and February were the most popular months for marriage. During the study period, illegitimate births were very rare and all children were baptized (Bouchard 1996). Female birth rate in the study area peaked in February, there was a trough in August and another smaller increase in September (figure 1).

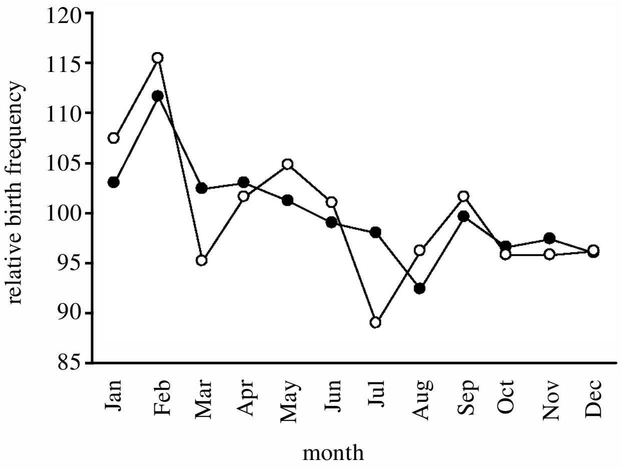

Figure 1. Relative monthly birth frequency of all females ($n = 9501$) born in Saguenay during 1850–1879 (filled circles) and women included in this study who survived to reproductive age and raised at least one offspring to adulthood ($n = 3290$, open circles).

(b) *Population data*

Data for the Saguenay population were obtained using the BALSAC population register at the University of Quebec at Chicoutimi (Canada) (Bouchard *et al.* 1995). This register contains demographical and genealogical information (collected from baptism, marriage and death certificates from the nineteenth and twentieth centuries) for several regions of the province of Quebec, Canada (Bouchard 1992), and its quality and accuracy are internationally recognized (Bouchard 1986, 1989; Scriver 2001). For the Saguenay region, the whole population has been recorded from the first settlements in the 1830s until 1971. This study includes all women ($n = 3290$) born in the Saguenay region from 1850 to 1879 (inclusive), who got married in the region and had at least one offspring who also married in the region. These women produced all of their children ($n = 29\,895$ of whom 16 618 survived, married and reproduced in the population) between 1866 and 1926, which is before the high fertility in the population (number of live births per mother 1–22, mean = 9.1) started to decrease rapidly in the 1930s and before any intentional birth control method other than prolonged lactation was widely used (Pouyez & Lavoie 1983). The information available for the Saguenay population in the BALSAC register enabled us to measure the fitness of these women, in terms of their numbers of grandchildren born to the population ($n = 100\,074$), according to their month of birth. The monthly birth frequencies of the whole birth cohort (1850–1879) and women included in this study who survived to reproductive age and raised at least one offspring to adulthood are

Table 1. Total sample size, range of monthly sample sizes (birth months with smallest and largest sample size).
(s.d., minimum and maximum for different fitness components of a cohort of pre-modern Canadian women (born 1850–1879). Note that the sample includes all born women surviving to reproductive age and raising at least one offspring to adulthood.)

reproductive trait	n	monthly n range	mean	s.d.	min	max
age at first marriage (years)	3290	249 (Jul)–300 (Jan)	21.6	4.2	14.0	41.0
age at last reproduction (years)	3268	248 (Jul)–297 (Jan)	38.7	6.1	16.0	49.9
reproductive lifespan (years)	3265	248 (Jul)–297 (Jan)	15.9	6.9	0.0	31.5
number of lifetime live births	3290	249 (Jul)–300 (Jan)	9.1	3.9	1.0	22.0
number of married offspring	3290	249 (Jul)–300 (Jan)	5.1	2.9	1.0	16.0
number of grandchildren	3290	249 (Jul)–300 (Jan)	38.2	28.0	0.0	157.0

shown in figure 1. Total and monthly sample sizes, means, standard deviations (s.d.) and ranges for the key fitness traits of the mothers are presented in table 1.

No information on the social class of these pre-modern mothers is available. This could pose a problem for this study if there were strong socio-economic differentiation within the whole population, so that differently endowed sectors of the population attended different seasonal events (rituals, holidays, customs), and as a consequence monthly conception rate or marriage consummation patterns differed for women from different social classes. In contrast to this, however, the population was very homogeneous in terms of rituals relating to family life events (births, marriages, deaths) throughout the period of this study (see above).

Previous studies have shown effects of early conditions, including month of birth, on infant survival (e.g. Lummaa *et al.* 1998). Because our aim was to investigate whether birth month affects lifetime reproductive success and fitness, we only included women who survived to adulthood, married and produced at least one viable offspring in their lifetime. Thus, any effects of month of birth on fitness of the Saguenay women detected in this study were mediated through long-term consequences of early conditions acting in adulthood, rather than through differential early mortality of babies born in different months (Lummaa *et al.* 1998). It should also be noted that because the reproduction and marital data concern only those individuals who were born and married in the Saguenay region, the total numbers of adult children and grandchildren per woman are probably underestimates. We have no data on possible differential migration probabilities of individuals born at different times of the year, but, to our knowledge, there is no such evidence for any human population. In any case, our measure of fitness (numbers of grandchildren born into the population) gives an accurate estimate of the reproductive success of a woman born during a given month relative to the reproductive success of an average woman in the same population.

(c) *Statistical analyses*

The effect of a woman's month of birth on her subsequent fitness (number of grandchildren) and reproductive traits was analysed using a multivariate analysis of variance (MANOVA), which allows correction for the significance levels of multiple tests when two or more interdependent response variables are tested from the same set of individuals (Scheiner 1994). In the MANOVA model, birth month was included as a factor and number of grandchildren born to the population, age at marriage, age at last reproduction, length of reproductive lifespan, numbers of live-born children and number of children raised to adulthood and marrying in the population were all fitted as response variables. To control for time trends in reproductive behaviour (decrease in family size and reproductive lifespan and increase in age at marriage and post-reproductive survival over the whole study period), the year of marriage of each individual was fitted in the model as a covariate ($F_{6,2927} = 130.30$, $p < 0.0001$). Because the birth month–marriage year interaction term was not significant ($F_{66,15609} = 0.83$, $p = 0.84$), it was removed from the final model. Because MANOVA revealed significant overall effects of month of birth on reproductive success, we also used the underlying univariate ANOVAs to investigate all of the response variables separately (figure 2). General linear models (GLMs) were preferred here to seasonality analysis (assumption of some birth-date based annual rhythm in reproductive performance), because our hypothesis was that month of birth would affect reproductive success, but we made no prior hypothesis about the success of mothers born in any particular month given that significant differences between any months of the year would be relevant for life-history optimization by natural selection. Running averages were not used because the birth-date data were highly accurate (Bouchard *et al.* 1995). In all analyses, the number of married children and age at marriage were logarithm (natural) transformed to ensure normal distributions of residuals. Residuals of all final models were normally distributed and variances were homogenous (Levene's test: $p > 0.05$). The analyses were performed with the GLM procedure of SAS, release 8.0 (SAS Institute Inc. 1990).

The analyses on month of birth effects on mortality were performed using GLMs for age at death and post-reproductive lifespan (defined as longevity after age 50) and GLMs with binomial error structure and logit link function for the probability that an individual died before reaching age 50 (GENMOD procedure of SAS, release 8.2).

The relationship between maternal month of birth and daughters' fertility ($n = 8537$ for married daughters) was analysed using a residual maximum-likelihood (REML) model in GENSTAT v. 5.4.2 (Genstat, Rothamstead Experimental Station, Harpenden, UK). A REML analysis is similar to that of a GLM with normal error structures except that it allows both fixed and random terms to be fitted to the model (Schall 1991). Number of offspring live born to daughters was fitted to the REML model as the response term, while their own month of birth, year of marriage, age at marriage, as well as their mother's birth month were fitted as potential explanatory effects. Mother identity was fitted as a random term to control for repeated measures ($n = 1$–11) of daughters from the same mothers. Because of the need to control for repeated measures within mothers the dataset was restricted to include only those mothers ($n = 1329$) who gave birth to more than two daughters who themselves subsequently married in the population (although, not all of the

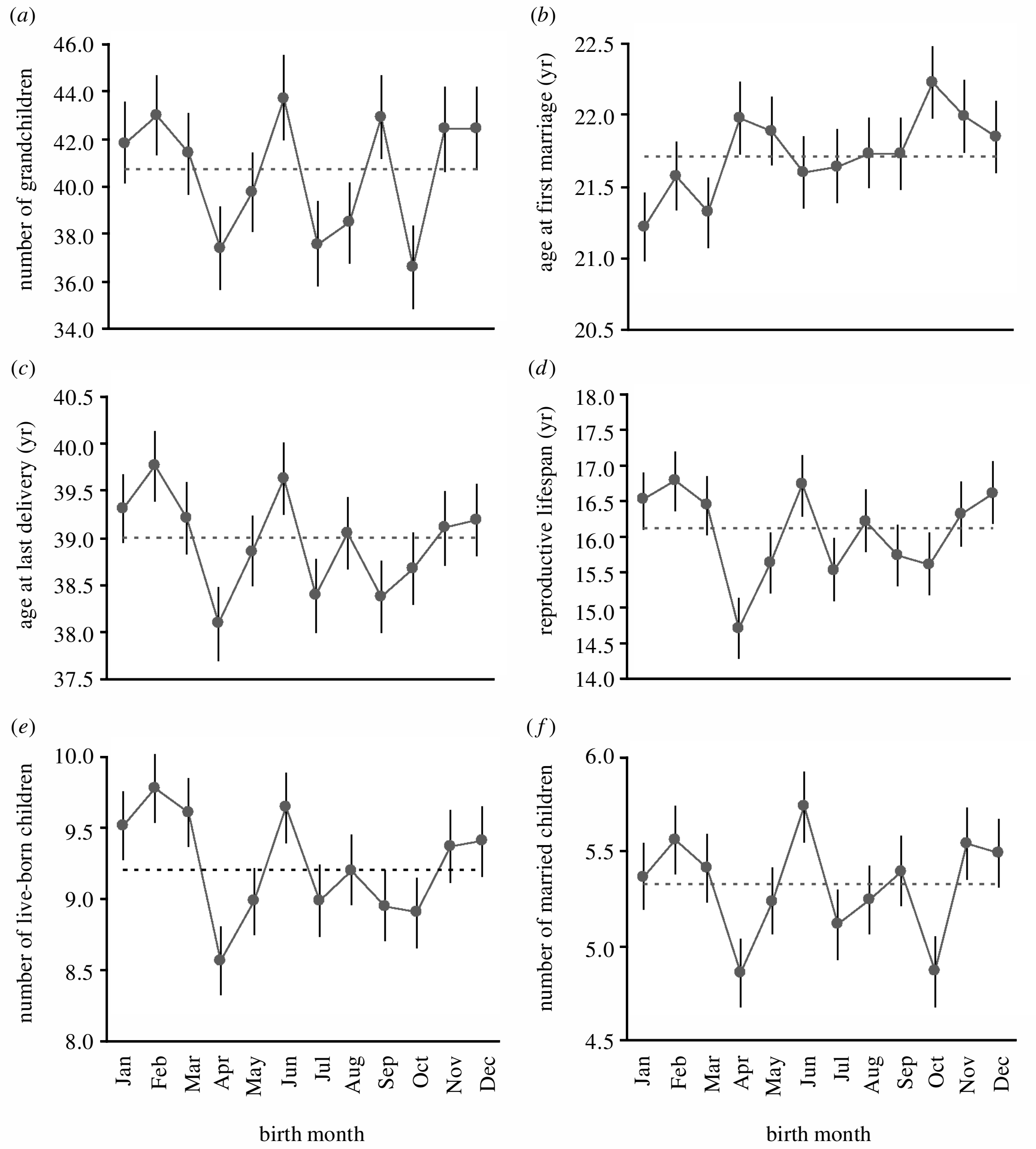

Figure 2. Effects of month of birth on subsequent reproductive parameters of pre-modern (born 1850–1879) Saguenay women. The graphs show mean effects (±1 s.e.) of month of birth on: (*a*) number of grandchildren born to the population (fitness) ($F_{11,2932} = 2.13$, $p = 0.016$); (*b*) age at first marriage ($F_{11,2932} = 1.51$, $p = 0.12$); (*c*) age at last delivery ($F_{11,2932} = 1.83$, $p = 0.045$); (*d*) length of reproductive lifespan ($F_{11,2932} = 2.14$, $p = 0.015$); (*e*) total number of live-born children ($F_{11,2932} = 2.35$, $p = 0.0071$); and (*f*) number of children raised to adulthood and marrying in the population ($F_{11,2932} = 2.19$, $p = 0.013$). All born women who married in the Saguenay region and raised at least one offspring who also married in the region are included. The horizontal dashed lines indicate the mean value of each trait for all months combined over the study period. When women marrying unusually late for the population (older than age 30, $n = 127$, 3.9% of all women) were excluded, age at first marriage also reached statistical significance ($F_{11,2805} = 2.01$, $p = 0.024$).

daughters had children). The output from a REML model is given as Wald statistic which is distributed approximately as χ^2 with each term fitted in the model last.

3. RESULTS

(a) *Month of birth and fitness*

The month of year in which females were born in the Saguenay population had a significant effect on their number of grandchildren produced ($F_{11,2932} = 2.13$, $p < 0.016$). Of all the reproductive women born in the population during the study cohort 1850–1879, those women born in winter (November–March), early summer (June) or early autumn (September) had the largest numbers of grandchildren in the following generation, whereas those born in early spring (April), mid to late-summer (July–August) and late autumn (October) had the fewest grandchildren (figure 2*a*). Saguenay women born in 'high-success' months averaged five more grandchildren than those born during other months, with the difference between the best (June) and worst month (October) being over seven grandchildren. These between-month differences remained unchanged throughout the whole study period (results not shown).

(b) *Why did grandchildren numbers differ between individuals born in different months?*

Differences in fitness (numbers of grandchildren) between women born during different months of the year could arise through three different mechanisms: (i) differential survival; (ii) differential reproductive rates; and (iii) differential reproductive rates of their offspring.

There is little evidence that the variation in fitness detected in this study can be explained by an effect of month of birth on adulthood survival. Month of birth did not significantly explain variation in the age at death of the Saguenay women ($F_{11,2932} = 0.82$, $p = 0.62$) or the length of their post-reproductive lifespan (after age 50) ($F_{11,2932} = 0.74$, $p = 0.70$). Furthermore, month of birth was not significantly associated with the probability that an individual survived until the end of reproductive age ($\chi^2 = 9.54$, d.f. = 11, $p = 0.57$). Only individuals born in April, one of the worst months in terms of fitness (see above) and reproductive output (see below) suffered from a significantly increased probability of dying before the age of 50 as compared with individuals born in other months of the year ($\chi^2 = 4.62$, d.f. = 1, $p = 0.032$).

By contrast, month of birth had a significant effect on a wide range of reproductive parameters, including age at marriage (under 30), age at last reproduction, length of reproductive lifespan, numbers of offspring live born and numbers of offspring surviving to marry in the population (figure 2*b–f*). Women born during the 'high-success' months married younger, continued reproducing to older ages and had longer reproductive lifespans (figure 2*b–d*). In addition, women born during 'high-success' months also produced more live-born children and raised more to reproduce (figure 2*e*,*f*). Moreover, the MANOVA analysis shows that all the different reproductive measures (including fitness) varied in a significantly consistent pattern from month to month ($F_{66,15667} = 3.37$, $p < 0.0001$). In other words, the month in which individuals were born significantly influenced the wide range of reproductive parameters and fitness in a similar way, suggesting that the effect of month of birth on fitness may, in part, be explained by the effect of month of birth on reproductive parameters. This conjecture was confirmed in a path analysis in which variation in these underlying reproductive traits explained over 77% of the differences in numbers of grandchildren born to individuals in this population.

To test the third possibility that differences in fitness between women born during different months of the year could be affected by differences in the quality and reproductive output of their offspring, we investigated the effect of a woman's birth month on her daughters' fertility. The REML model showed that women born during different months of the years between 1850 to 1879 gave birth to daughters whose reproductive success varied according to their mothers' birth month ($\chi^2 = 21.78$, d.f. = 11, $p = 0.023$), controlling for their marriage year, age at marriage and own month of birth.

4. DISCUSSION

Previous studies have shown that early environmental conditions experienced by individuals may be related to their health throughout their lives (Barker 1994), and that individuals born in different months of the year may vary in height (Weber *et al.* 1998) and survival probability in adulthood (Moore *et al.* 1997; Doblhammer & Vaupel 2001; Gavrilov & Gavrilova 2003). Here, we show that those born in different months of the year may also vary significantly in their fitness in a nineteenth century population of humans living in a rural community of Canada. These differences in fitness were caused primarily by variation in a number of personal reproductive traits, including age at first marriage (under 30), age at last reproduction, length of reproductive tenure, number of offspring delivered and the number raised to reproduce. However, fitness was also influenced by effects of a mother's birth month on the reproductive rates of their daughters, showing that birth-month effects spanned generations.

In a wide number of animal species, the conditions that individuals experience during development have significant effects on later survival and/or reproductive success (reviewed in Lindström 1999). However, whether such conditions affect the number of grandchildren produced, and hence some long-term measure of fitness, is generally unknown. Here, we show that month of birth significantly influenced the numbers of grandchildren produced in a pre-modern population of Canadians. Our analyses of a detailed dataset on life histories of whole cohorts of mothers showed that such differences in fitness may be pronounced, with mothers born during the most favourable month of the year having, on average, at least seven more grandchildren than those born during the least favourable month of the year. These results strongly suggest that the timing of birth had large effects on subsequent fitness in this rural community.

Using month of birth as a surrogate for early conditions could be suggested to be problematic, and certainly does not help to elucidate the underlying mechanisms behind any association between early conditions and fitness. For example, the high success in the winter is likely to be due to high food stocks after the autumn harvests and the low risks of disease. Mothers who gave birth in winter would have had access to plentiful food throughout most of their pregnancy; those who gave birth in spring and early summer would have experienced longer periods of inadequate nutrition, particularly in late gestation where foetal growth may be severely limited by nutrient supply (Harding 2001). Low success in April may be explained by the fact that this is the month when the winter stocks have run out and summer stocks are not yet available (Lummaa *et al.* 1998), and the conception of those born in April also coincided with the time of hardest physical work (the August harvest). Furthermore, those individuals born in the second worst month (October) were conceived at the beginning of the year: a time of austerity after the Christmas feasting, when temperatures could drop to −35 °C. However, the proximate reasons for some of the other peaks and troughs are less easily explained.

Indeed, it has proved incredibly difficult to identify a single cause for effects of early conditions on subsequent growth, health and survival in humans (Barker 1994; Moore *et al.* 1997; Weber *et al.* 1998; Doblhammer & Vaupel 2001), and studies on wild populations of mammals have demonstrated that the different measures of early environmental, ecological and demographic conditions all interact to influence subsequent survival and breeding performance in adulthood (Kruuk *et al.* 1999; Forchhammer *et al.* 2001; Lummaa & Clutton-Brock 2002). Thus, the differences in early conditions experienced by women born during different months of the year in this study are likely to be a consequence of several agents acting simultaneously, including photoperiodicity and the subsequent variation in maternal melatonin and hormonal levels (Kauppila *et al.* 1987), monthly variation in disease risk and weather, food quality and quantity, and maternal work load (Lummaa *et al.* 1998). For example, some studies on humans have found that correlates of health and survival in adulthood, such as birth weight of babies, can be influenced by the thermal conditions (temperature) experienced during gestation (Wells 2002), and in line with this, the birth weight of babies born in different months of the year in historical Canada differed significantly (Ward 1993). All of these seasonal factors could affect early 'foetal programming' (Lucas 1991). Therefore, because there are a vast number of different factors that could influence early conditions and such factors may interact in a complex way, the desirable aspect about month of birth is that it captures most such factors at the same time.

The differences in fitness associated with month of birth detected in this study may be a consequence of: (i) differential mortality in adulthood; (ii) differential reproductive rates as parents; and (iii) differential reproductive rates of subsequent offspring. We found little evidence to suggest that differences in fitness were likely to be caused by differences in survival during adulthood, with birth month having no significant effect on age at death, the probability that an individual survived until the end of their reproductive age (50 years), or the length of their post-reproductive lifespan. Some previous studies in humans have found significant relationships between month of birth and survival when using very large sample sizes (Doblhammer & Vaupel 2001), but our results suggest that any differences in adult survival are likely to be of minor importance compared with reproductive traits in determining eventual fitness in pre-industrial human populations. For example, compared with offspring born in poor success months, those born in high success months got married earlier (if under 30), gave birth to their last child later, had longer reproductive lifespans, gave birth to more children and raised more to reproduce. Month of birth had a significantly similar influence on each of these reproductive traits and fitness, and a path analysis revealed that these reproductive traits together explained 77% of the variance in fitness. Previous studies in populations of wild mammals have shown similar results. For example, in female red deer (*Cervus elephus*), weather conditions during an individual's early development before birth affect their subsequent survival, fecundity, offspring size and, finally, their lifetime reproductive success (Kruuk *et al.* 1999). Similarly, birth weight is a significant determinant of mating success and total lifetime reproductive success in red deer males, with heavier-born males being more successful in gaining breeding success than lighter ones (Kruuk *et al.* 1999). By contrast, previous studies in humans have seldom considered the effects of early development on subsequent reproductive capabilities. However, poor early conditions have been shown to impair menarche and be associated with early menopause (Jongbloet *et al.* 1994), and to influence fecundability (Nonaka *et al.* 1990; Smits *et al.* 1997). In addition, Weber *et al.* (1998) showed that birth month is associated with a short final height in adulthood, which itself has been shown to be linked to reproductive success (Pawlowski *et al.* 2000).

Finally, fitness was also influenced by differential reproductive rates of the daughters depending on the month in which their mothers were born. This raises the intriguing possibility that early conditions experienced by individuals are strong enough to span generations. This could arise if early conditions are linked to a mother's capability of investing in her offspring, giving rise to daughters that vary in their reproductive capabilities. Such inter-generational effects are not often investigated owing to the extreme difficulty of obtaining multi-generational data on reproductive success, but there is some suggestion for such effects from experimental studies on rodents (Huck *et al.* 1987; Meikle & Westberg 2001).

Our results add to other human studies that have shown early conditions and/or month of birth to influence health, susceptibility to disease and survival in other human populations (Lummaa & Clutton-Brock 2002). However, the implications of our results also have broader ramifications. First, although the effects of early conditions on subsequent survival and reproductive success are commonly investigated in wild animals (Lindström 1999), few studies have measured the influence of such effects on the numbers of grand-offspring (fitness). Furthermore, we provide one of the few pieces of evidence to suggest that effects of early condition can be strong enough to span generations. Such evidence will always be of importance because of the consequence of inter-generational effects on fitness calculations and the difficulty of obtaining such information from species with long lifespans. In conclusion, our results from pre-modern, rural Canadians show that the numbers of grandchildren born into the population, and hence an individual's genetic contribution to the next generation, appear to have differed considerably between individuals, depending on the developmental conditions they experienced early in life.

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