Original Research Article

First Birth Interval, An Indicator of Energetic Status, Is a Predictor of Lifetime Reproductive Strategy

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Objectives: Women should differ in their reproductive strategies according to their nutritional status. We tested a hypothesis that women who have a good nutritional status early in life, as indicated by a shorter waiting time to the first birth (first birth interval, FBI), are able to afford higher costs of reproduction than women who have worse nutritional condition.

Methods: We collected data on 377 women who got married between the years 1782 and 1882 in a natural fertility population in rural Poland. The study group was divided into tertiles based on the length of FBI.

Results: Women with the shortest FBI had a higher number of children ($P = 0.005$), higher number of sons ($P = 0.01$), and shorter mean interbirth intervals ($P = 0.06$). Women who had ever given birth to twins had shorter FBI than women of singletons (20.1 and 26.1 months, respectively; $P = 0.049$). Furthermore, women with a shorter FBI, despite having higher costs of reproduction, did not have a different lifespan than women with a longer FBI.

Conclusions: Our results suggest that women who were in better energetic condition (shorter length of FBI), achieved higher reproductive success without reduction in lifespan. FBI reflects interindividual variation, which may result from variation in nutritional status early in life and thus may be a good predictor of subsequent reproductive strategy. We propose to use FBI as an indicator of women's nutritional status in studies of historical populations, especially when information about social status is not available. Am. J. Hum. Biol. 25:78–82, 2013.

In women, nutritional status is one of the most important factors determining the functioning of reproductive physiology and, in particular, ovarian hormone levels (Ellison, 2003). Women, who have good nutritional status mature earlier (Chowdhury et al., 2000; Ellison, 1990), begin to ovulate earlier, and have higher estradiol levels in menstrual cycles for at least several years after menarche (Vihko and Apter, 1984) and perhaps during their entire reproductive life. Nutritional condition during fetal development is also important as it influences adult ovarian function and women who were larger at birth have higher levels of estradiol in later life (Jasienska et al., 2005, 2006b). Moreover, women with good nutritional status have a higher ability to conceive and establish a pregnancy (Jasienska et al., 2006b; Lipson and Ellison, 1996). Thus, it may be expected that in natural fertility populations, women with good nutritional status should be able to sooner conceive their first child. After marriage, people in natural fertility populations do not use any methods of family planning, children are desirable, and the waiting time to conception is constrained almost only by reproductive physiology. For women, reproductive physiology is constrained by nutritional status (Ellison, 1994; Jasienska, 2013).

Other features of reproductive strategies may also depend on maternal nutritional condition. As suggested by Trivers and Willard's (1973) hypothesis, a woman in good energetic condition should invest in sons, who are expected to be more competitive and, consequently, achieve higher reproductive success than daughters. Sons are more energetically expensive for mothers, as shown by higher rate of intrauterine growth, higher birth weight, and longer interbirth intervals observed after the birth of a son than a birth of a daughter (Loos et al., 2001; Mace and Sear, 1997; Maršál et al., 1996).

Mothers in good nutritional status, as indicated by their higher body height and body mass, are also more likely to have twins than mothers in poor status (Campbell et al., 1974; Sear et al., 2001). Mothers of twins have shorter interbirth intervals, longer reproductive spans, later age at last birth, and a higher overall fecundity (Gabler and Voland, 1994; Robson and Smith, 2011; Sear et al., 2001). Twins are more energetically costly than singletons (Sear, 2007).

Reproduction is costly, thus trade-offs between reproductive effort and lifespan are expected when resources are limited (Jasienska, 2013; Stearns, 1992). However, in many species, including humans, the results of studies investigating the relationship between reproduction and survival are inconsistent (Clutton-Brock, 1991). Some studies documented that women with higher reproductive investment had shorter lives (Alter et al., 2007; Doblhammer and Oeppen, 2003; Gagnon et al., 2009; Jasienska et al., 2006a), but others showed either a lack of statistically significant relationships between parity and lifespan (Hurt et al., 2004; Le Bourg et al., 1993), or even a longer lifespan for mothers with high parity (McArdle et al., 2006; Muller et al., 2002). While reasons for such discrepancies are clearly complex (Jasienska, 2009), it is likely that a woman's long-term nutritional status plays a crucial role.

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The relationship between reproduction and lifespan has been studied mostly in historical populations (Hurt et al., 2006), and data has often originated from parish records, which did not collect information about the nutritional status of individuals. Some studies used information about belonging to a particular social class as an indicator of well-being, including a nutritional status (Dribe, 2004; Lycett et al., 2000). While this approach provides some information about the average nutritional status of a group of people belonging to a social class, it cannot be used to determine the nutritional status of individuals, since within a social class considerable interindividual variability in lifestyle conditions was likely to occur (Dribe, 2004).

This study tests a hypothesis that FBI, an indicator of a woman's nutritional status, predicts her subsequent reproductive strategy. Women with shorter FBI are expected to be able to invest more in reproduction and thus have shorter mean interbirth intervals, a higher number of children, and a higher number of sons (the more energetically expensive sex). A historical Polish agricultural population characterized by a natural and high fertility provides a perfect setting for testing this hypothesis.

MATERIALS AND METHODS

We used demographic data for the period from 1782 to 1950, collected from parish records in the village of Slopnice in southern Poland, belonging to the area of Mogielica Human Ecology Study Site (Jasienska and Ellison, 2004). In 1563, the Council of Trent obliged vicars in Catholic parishes to record all births, marriages, and deaths (Kufel, 2005). Slopnice was governed by the Austrian administration during the years 1772–1918 when Poland was divided between Prussia, Austria, and Russia (Wojcieszak, 1999). Parish records from the Austrian partition have the most detailed information, which allows to reconstruct familial histories (Prinke, 2006). The population of Slopnice was characterized by natural fertility, due to strongly entrenched religious beliefs, as well as a lack of contraceptive methods, and mostly by a natural mortality, due to the lack of modern medical care. We analyzed data from all people who were married between January 1, 1782 and December 31, 1882. We reconstructed 677 couples, in which both women and men were married just once during their lifetime. Married couples were included in the analysis only when the dates of marriage and death of both spouses were documented in the records (deaths occurred between the years 1794 and 1950). Out of 677 women, 119 died before they were 50 years of age, 11 were childless, 15 had a non-natural cause of death or a cause of death that was unknown, 196 women had husbands who died before they had reached 50th birthday, and 65 had a first birth interval (FBI) shorter than 8 months (indicating a premarital conception or premature birth). All these factors may confound a relationship between reproduction and lifespan, and therefore, these women were excluded from analyses. Age 50 was taken as the end of reproductive span. Moreover, including the mean interbirth interval necessitated restricting statistical analyses to those women who had at least two children. Consequently, we used a group of 377 women in our analyses.

The interval from marriage to the first birth (FBI) was calculated for each woman. Women were divided into tertiles based on the length of FBI (first tertile – $<$18 months – short FBI, second tertile – $\geq$ 18 and $<$ 34 months – moderate FBI, third tertile – $\geq$ 34 months – long FBI). Differences in factors of reproductive history (the age at first and last reproduction, number of children, number of daughters, number of sons, and length of mean interbirth interval) among groups with short (n = 117), moderate (n = 132), and long FBI (n = 128) were analyzed in a model of two-way Multivariate Analysis of Variance (MANOVA). To account for additional variables that are potentially important when evaluating the costs of reproduction we also added to the model: the age of a woman at marriage, the percentage of children who survived until 15 years of age, maternal lifespan, husbands' age at marriage, age difference among spouses, and husbands' lifespans. Birth cohort (10 years' periods) was included in the model to account for temporal changes. FBI (when used as a dependent variable) and mean interbirth interval were log transformed prior to analyses to normalize the distribution. Wilks' Lambdas were used to assess statistical significance. Moreover, a post-hoc Bonferroni test was used to test for significant differences among groups. The second model was run with the number of sons and number of daughters who survived to adulthood (age 15), instead of the number of children born.

Moreover, we predicted that women who had ever had twins would have a shorter FBI when compared with women who never had twins. We also predicted that women would differ in the length of interbirth interval following sons versus daughters within FBI categories. Furthermore, the length of FBI was compared between groups of women who got married in October and February, to check whether the season of marriage influenced FBI, and consequently, the length of FBI was compared among seasons of conception in order to check whether environmental condition explained variation in FBI. Analyses were conducted with use of Statistica version 10.0.

RESULTS

Baseline statistics of studied women are presented in Table 1. A MANOVA model indicated overall differences among tertiles of women with short, moderate, and long FBI (Wilks' Lambdas = 0.46; $F_{22,\ 668} = 14.59$, $P < 0.001$). Interaction between birth cohort and FBI tertile was not significant ($P = 0.7$). Groups of women with short, moderate, and long FBI differed in mean number of children ($F_{2,\ 344} = 5.47$, $P = 0.005$; i.e., women from the first tertile had significantly more children than women from the third tertile, $P = 0.02$), number of sons ($F_{2,\ 344} = 4.70$, $P = 0.01$; i.e., women from the first tertile had significantly more sons than women from the third tertile, $P = 0.03$), age at marriage ($F_{2,\ 344} = 12.54$, $P < 0.001$; i.e., all groups of women differed significantly), and age at first birth ($F_{2,\ 344} = 4.46$, $P = 0.01$; i.e., women from the second tertile gave birth at a younger age than women from the third tertile, $P = 0.045$). Difference in mean interbirth interval among groups with different FBI was marginally significant ($F_{2,\ 344} = 2.79$, $P = 0.06$), and women from the first tertile had significantly shorter mean interbirth interval than women from the third tertile ($P = 0.04$). Groups of women with short, moderate, and long FBI did not differ significantly in the number of daughters ($F_{2,\ 344} = 1.66$, $P = 0.2$), percentage of children who survived to 15 years of age ($F_{2,\ 344} = 0.37$, $P = 0.7$), and age at last birth ($F_{2,\ 344} =$

TABLE 1. Mean (±SD) characteristics for the whole group of studied women and for women divided into tertiles based on length of FBI

	All women (n = 377)	Short (n = 117)	Moderate (n = 132)	Long (n = 128)
Age at marriage (years)	20.9 (4.05)	22.5 (3.96)	21.1 (3.63)	19.3 (3.98)
Age at first birth (years)	23.4 (4.00)	23.4 (3.91)	22.8 (3.63)	24.0 (4.36)
No. of children born	7.2 (2.64)	7.6 (2.64)	7.1 (2.72)	6.7 (2.50)
No. of sons born	3.6 (2.00)	4.0 (2.16)	3.6 (1.99)	3.3 (1.79)
No. of daughters born	3.5 (1.92)	3.7 (1.86)	3.5 (1.96)	3.4 (1.94)
Children survived to 15 years of age (%)	77.3 (18.19)	79.7 (17.9)	76.6 (18.07)	75.7 (18.48)
No. of children survived to 15 years of age	5.0 (2.06)	5.5 (2.12)	4.9 (1.91)	4.7 (2.08)
No. of sons survived to 15 years of age	2.5 (1.58)	2.8 (1.63)	2.5 (1.51)	2.3 (1.51)
No. of daughters survived to 15 years of age	2.5 (1.56)	2.7 (1.59)	2.4 (1.50)	2.4 (1.67)
Mean interbirth interval (months)	35.8 (1.35)	34.0 (1.30)	35.7 (1.39)	37.5 (1.35)
Age at last birth (years)	40.8 (5.02)	41.3 (4.97)	40.1 (5.17)	41.0 (4.88)
Maternal lifespan (years)	65.8 (8.01)	65.5 (7.64)	65.0 (8.37)	67.0 (7.90)
Husband's age at marriage (years)	26.0 (4.41)	27.0 (4.45)	25.8 (4.47)	25.2 (4.16)
Age difference between spouses (years)	5.1 (5.06)	4.5 (5.31)	4.7 (5.01)	5.9 (4.80)
Husband's lifespan (years)	67.3 (8.64)	66.7 (8.64)	67.3 (9.17)	67.8 (8.08)

1.69, $P = 0.2$). Furthermore, groups of women with short, moderate, and long FBI did not differ in their lifespan ($F_{2, 344} = 2.19$, $P = 0.1$).

In addition, groups of women differed in mean husband's age at the time of marriage ($F_{2, 344} = 3.97$, $P = 0.02$; i.e., women from the first tertile had significantly older husbands than women from the third tertile $P = 0.02$), however, the age difference between husband and wife did not differ among groups of women ($F_{2, 344} = 1.08$, $P = 0.3$). Moreover, groups did not differ in mean husband's lifespan ($F_{2, 344} = 0.23$, $P = 0.8$). Interactions between birth cohort and FBI tertile were not significant with the exception of number of children ($P = 0.04$). Residuals had normal distribution in the MANOVA model and there was no difference in variance among groups.

When the number of children, number of sons, and number of daughters who survived to adulthood instead of the number of children, number of sons, and number of daughters born was used in the model the results stayed quantitatively unchanged (Wilks' Lambdas = 0.46; $F_{20, 670} = 15.68$, $P < 0.001$). Women with the shortest FBI had significantly more children and more sons who survived to adulthood (respectively: $F_{2, 344} = 4.1$, $P = 0.02$, and $F_{2, 344} = 4.39$, $P = 0.01$). Groups of women did not differ in number of daughters who survived to adulthood ($F_{2, 344} = 0.3$, $P = 0.7$).

Interestingly, women who had ever given birth to twins ($n = 26$) had shorter FBI than mothers of singletons (20.1 and 26.1 months, respectively; $F_{1,375} = 3.88$, $P = 0.049$). In addition, women with the shortest FBI had the shortest interbirth intervals following sons ($F_{2,329} = 5.89$, $P = 0.03$) while there was no difference among groups in length of interbirth intervals following daughters ($F_{2,325} = 1.5$, $P = 0.2$). In our study group, we did not observe statistically significant differences in mean length of FBI according to the season of conception ($F_{3,373} = 1.05$, $P = 0.4$). Moreover, there was no difference in FBI length between women who were married in October and those who were married in February (27.1 and 23.2, respectively, $F_{1,187} = 0.81$, $P = 0.4$).

DISCUSSION

Our results show that women who had a shorter length of FBI could afford a more costly lifetime reproductive strategy and consequently were able to achieve a higher lifetime reproductive success. These women had a higher number of children, a higher number of sons, and reproduced at a faster pace than women with longer FBI, as documented by shorter mean interbirth intervals. Further, these higher costs of reproduction, indicated by higher fertility, having a higher number of sons, and taking less time to recuperate after a previous reproduction were paid by women with shorter FBI without suffering detrimental effects in terms of a shorter lifespan. We suggest that the FBI can be used as a good indicator of a woman's energetic condition at the beginning of reproduction. Birth weight, rate of childhood growth, adult body height, body weight, and for women, age at menarche, are relatively reliable indicators of nutritional status (Blell et al., 2008; Bogin and Rios, 2003; Koziel and Jankowska, 2002; Silventoinen, 2003), but these characteristics are usually not available for historical populations.

Energy availability is crucial for reproduction. It has previously been shown that energy expenditure of a woman predicts the length of the interval from marriage to first birth (Gibson and Mace, 2002a), and mean interbirth intervals (Gibson and Mace, 2002b). The FBI seems to be an important predictor of lifetime reproductive outcome, since it affects subsequent birth-spacing (Bumpass et al., 1978). A shorter waiting time to first birth suggests that these women had a higher chance of conception, and while many factors can influence this, the relationship between good nutritional status and high levels of reproductive hormones (Jasienska, 2003) that, in turn, leads to a higher chance of pregnancy, is very well established (Lipson and Ellison, 1996; Venners et al., 2006). This relationship can be especially expected in natural fertility populations, in the period soon after marriage, when the frequency of intercourse is high and children are desired.

In our study, the difference in the number of children among groups of women with shorter and longer FBIs occurred when a woman had an additional son (the groups of women did not differ in the number of daughters). In addition, women with shorter FBI had shorter interbirth intervals following sons. This indicates that women with shorter FBI were indeed in better energetic condition. In the community from southern Ethiopia, for example, women in good energetic condition were more likely to give birth to a son, than to a daughter (Gibson and Mace, 2003). We have also shown that women who had twins had shorter FBI than women who had singletons. This further suggests that FBI can be used as an indicator of nutritional status in historical, natural fertility populations, where it is impossible to obtain information about direct measures of nutritional status.

Life history theory predicts that in environments of poor quality (e.g., characterized by high early mortality) a better strategy would be to have more children rather than to invest in the quality of individual children. In our study, women with good nutritional status (short FBI) had more children, due to shorter interbirth intervals, but offspring quality was not much different from that of women with long FBI as indicated by a lack of differences in children's survival until the age of 15. This suggests that better quality women, who can afford to invest more in their offspring, follow a strategy of having a higher number of offspring, rather than offspring of better quality. Given the fact that in this population during the study period about 23% of children did not survive until the age 15, this maternal strategy may lead to a higher reproductive success. Indeed, in our study women with a higher number of children born had a higher number of children that survived to adulthood.

The length of FBI may be influenced by a woman's nutritional status early in life or by short-term changes in energy availability. Short-term energetic changes are important as indicated by the fact that levels of ovarian steroid hormones show seasonal variation due to changes in physical work or energy intake (Jasienska and Ellison, 2004; Panterbrick et al., 1993). For contemporary women from the village of Slopnice, the same population as studied here, progesterone levels were lower during summer time, when physical activity was most intense, indicating ovarian suppression (Jasienska and Ellison, 2004). To control for the effect that short-term changes in energy balance may have on FBI, we compared lengths of FBI among women who married at different times of the year. We did not observe statistically significant differences in mean length of FBI according to the season of conception. However, in the studied population most marriages occurred during late fall and winter (92% of marriages took place between October and February), when physical work was not very intense, and thus it is likely that inter-individual variation in short-term energetic condition of women during the time of marriage was low. Moreover, there was no difference in FBI length between women who were married in October and those who were married in February. October was a time of year with still abundant, postharvest food reserves, while in February food reserves were becoming depleted. It is likely, therefore, that variation in the length of FBI did not result from differences in short-term energetic condition, but rather from variation in a woman's long-term energetic condition. Good energy status during fetal development, indicated by a level of fatness at birth (Jasienska et al., 2006b), and energy status during childhood (Núñez-de la Mora et al., 2008) are related to high levels of reproductive hormones in cycles of adult women. Previous studies suggested a positive relationship between availability of resources and the number of children (Dribe, 2004; Low and Clarke, 1992; Lycett et al., 2000; Skjærvø et al., 2011); however, they always used social status as an indicator of access to resources. There are several problems with using social status as such an indicator. First, the social status of a husband is usually used as a predictor of a woman's social status (Smith et al., 2002). This is problematic because, especially at the beginning of reproduction, there may be a discrepancy between the social status of the husband and wife, since it was possible for women to marry men whose socio-economic status was different, usually higher, than their own. Second, some studies used information about social status at age 50, which means that availability of resources could impact an individual's post-reproductive lifespan, but it is unclear if it had any impact on the number of children born, because socioeconomic status may change during life. Furthermore, the use of social status as an indicator of nutritional condition requires an assumption that people had stable access to resources (Skjærvø et al., 2011).

In many populations, older and richer men often married younger women and had more children (for example Low, 1990). In our study, among women with short, moderate, and long FBI 6.8, 13.6, and 35.9% respectively married at a younger age than 18 years. For several years after maturation, women can have anovulatory cycles and cycles with low levels of hormones, and therefore among those that married at a younger age some have reduced chances of conception (Apter and Vihko, 1983). In the studied population, the average age at marriage was 20.9 years. As such, the majority of women married several years after menarche. Unfortunately, as in most historical populations, data about age at menarche is not available. Women with short FBI were, on average, older at marriage than women with moderate or long FBI. Perhaps, although this is only a speculation, women with shorter FBI came from better-off families, who could afford to keep their daughters longer in the household before marriage. Husbands of these women were also relatively older and age difference between spouses did not vary significantly among our study groups.

Studies of reproductive costs in non-human species imply that it is important to take into consideration heterogeneity in individual quality (Hamel et al., 2009; Weladji et al., 2008). In contemporary populations, indicators such as birth weight or age at menarche can be used to control for women's quality and as a consequence for "phenotypic correlations" (Sear et al., 2003). A similar approach should be used by studies investigating relationships between reproduction and maternal lifespan in historical populations. Our results indicate that the FBI can be used as an indicator of an individual's access to resources during early life, when an individual organism makes life history decisions, including the decision about lifetime reproductive strategy.

To summarize, among groups of women with variation in length of FBI different lifetime reproductive strategies were observed and, in consequence, these women differed in their reproductive success (indicated by the number of children born, those children surviving to adulthood, and the number of sons born). Women with short FBI, presumably in better nutritional condition, had higher fertility without suffering the detrimental effects of reproduction in terms of a shorter lifespan.

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