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Heritability of Human Lifespan is Affected by Parental Age at Childbirth

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Abstract

Familial resemblance in lifespan between children and parents was studied by many researchers for a century, but no attention has so far been paid to the possible effects of parental age at childbirth on familial transmission of longevity. In this study we have tested the hypothesis that familial resemblance between offspring and parental lifespan is higher for children born to younger parents, as expected both for genetic reasons (higher genetic diversity of younger parents) and for cultural reasons (higher overlapping between parental and offspring life cycles). For this purpose, high quality data (more than 15,000 records) on European aristocratic families (more than 900 families) were collected, computerized, and analyzed.

We have found that familial transmission of human lifespan is a function of parental age at childbirth. In particular, both daughters and sons born to older mothers (above age 35) do not demonstrate any inheritance of maternal lifespan. The regression slope (b) of sons' lifespan on maternal lifespan is substantial ($b = 0.124 \pm 0.063$; $n = 3,782$ cases, $p = 0.05$) when the mother is young (15-34 years), but it is negligible ($b = 0.014 \pm 0.105$, $n = 796$, $p = 0.90$, insignificant) for older mothers (35 years and above). The regression slope (b) of daughters' lifespan on maternal lifespan is also highly significant ($b = 0.21 \pm 0.08$, $n = 1,801$ cases, $p < 0.01$) when the mother is young (15-34 years), but it is statistically insignificant ($b = 0.01 \pm 0.15$, $n = 355$, $p = 0.96$) for older mothers (35+ years). These estimates were calculated for the range for maternal lifespan of 75-95 years. The scientific importance and practical implications of this observation are discussed. This study was supported by NIA grants AG12857, AG13698-01 and AG16138-01A1.

Introduction

Familial resemblance in lifespan between children and parents was studied by many researchers for a century (Beeton and Pearson, 1899; 1901; Bell, 1918; Pearl and Pearl, 1934; Jalavisto, 1951; Hawkins et al., 1965; Abbott et al., 1974; 1978; Murphy, 1978; Desjardins and Charbonneau, 1990; Bocquet-Appel and Jakobi, 1990; 1991; Mayer, 1991), but no attention has so far been paid to the possible effects of parental age at childbirth on familial transmission of longevity. In this study we have tested the hypothesis that familial resemblance between offspring and parental lifespan is higher for children born to younger parents, as expected both for genetic reasons (higher genetic diversity of younger parents) and for cultural reasons (higher overlapping between parental and offspring life cycles). Our preliminary results presented in this study demonstrate that the familial resemblance in lifespan between mothers and their children is lost when children are born to older mothers.

Data and Methods

Main Data Source. In this study we collected, computerized and analyzed the detailed genealogical records on lifespan of more than 15,000 adult individuals (30+ years) and their parents, using particularly reliable and complete data on European royal and noble families for extinct birth cohorts (born 1800-1880). The main advantage of these data is their high accuracy, reliability and completeness (to be discussed later). Another advantage of this kind of data is the relative homogeneity of this Caucasian population regarding social class and educational background. Since this privileged social group lived in favorable conditions for many centuries, one could expect less influence of adverse social factors (poverty, for example) on life span and hence lower bias caused by these factors. This kind of data allows us to minimize the social heterogeneity of the population under study. Thus, although the sample analyzed in this study does not represent the whole human population (as laboratory animals do not represent species in the wild), it is one of the best possible samples to test biodemographic hypotheses since the effects of population heterogeneity are minimized with regard to social status.

The database on European royal and noble families (a family-linked database) was developed and already used in our previous studies (Gavrilov, Gavrilova, 1997a; 1997b; Gavrilov et al., 1995; 1997; Gavrilova et al., 1995; 1997; 1998). To develop this database we have used one of the best professional sources of genealogical data available - the famous German edition of the "Genealogisches Handbuch des Adels" (Genealogical Yearbook of Nobility). This edition is known world wide as the "Gotha Almanac" - "Old Gotha" published in Gotha in 1763-1944, and "New Gotha" published in Marburg since 1951 (see Gavrilova, Gavrilov, 1999, for more details). Data from the Gotha Almanach were often used in early biodemographic studies of fertility (see Hollingsworth, 1969, pp. 199-224, for references) and are used now in the studies of human longevity (Gavrilova et al., 1998; Gavrilov, Gavrilova, 1997a).

Each volume of the New Gotha Almanach contains about 2,000 genealogical records dating back to the 14-16th centuries (to the founder of a particular noble genus). More than 100 volumes of this edition are already published, so more than 200,000 genealogical records with well-documented genealogical data are available from this data source. The high quality of

information published in this edition is ensured by the fact that the primary information is drawn from the German Noble Archive (Deutsches Adelsarchiv). The Director of the German Noble Archive (Archivdirektor) is also the Editor of the New Gotha Almanach. Our own experience based on cross-checking the data, has demonstrated that the number of mistakes (mostly misprints) is very low in the "New Gotha Almanac" (less than 1 per 1000 records), so this source of data is very accurate compared to other published genealogies.

The information on noble families in the New Gotha Almanac is recorded in a regular manner. The description of each particular noble genus starts with information on 2-3 generations of founders of male sex only. Then three to four the most recent generations are described in more detail, including information on individuals (e.g., first and last names; event data: birth, death, marriage dates and places; descriptive data: noble degrees, occupation if available, information on death circumstances if available), information on parents (e.g., first and last names; event data: birth and death dates and places), information on spouse(s) (e.g., first and last names; birth and death dates and places; first and last names of parents) and information on children (detailed as for each individual).

The process of data computerization was started from the most recent volumes of the New Gotha Almanac (published in 1990-1994) and reached now the volumes published ten years earlier. The database on European aristocratic families comprises more than 20,000 personal records and is growing further.

Supplementary Data Sources. Some other supplementary sources of data were used in the development of database. These data sources included two computerized data files on European royalty and British peerage (computerized database "Royal92" distributed on the Internet by Brian C. Tompsett at University of Hull, UK, and database on British Peerage distributed on CD by S&N Genealogy Supplies), as well as over 100 genealogical publications on Russian nobility listed elsewhere (Gavrilov et al., 1996). These data were used as a supplement to the main data source since their quality was not as high compared to the Gotha Almanac. Although data on European royalty were recorded in computerized data sources ("Royal92", British Peerage CD, see above) with sufficient completeness, data on lower rank nobility (landed gentry) were less complete and accurate. The same was true for the data on Russian nobility. All supplementary data were matched with the Gotha Almanac data, in order to cross-check the overlapping pieces of information. This cross-checking procedure allowed us to increase the completeness of the database by complementation of information taken from different sources.

The Structure of the Database on European Aristocracy. The database approach used in this study is similar to the approach used for existing family-linked databases, such as the Utah Population Database (Skolnick et al., 1979), Laredo Epidemiological Project (Buchanan et al., 1984) or other historical databases (Gutmann et al., 1989). Initially the information computerized from each volume of the New Gotha Almanac is stored in two files: the Individual File and the Marriage File. Then these two files are merged into one rectangular file with information on up to 4 spouses. Since marriages with 5th and higher orders comprise less than 0.1% of all marriages, the potential loss of information on spouses after data merge is negligible. Then these merged files are linked to the Master File (main database).

In the Master File each record is related to the duration of an individual's life. Each record represents an individual's event data (birth and death dates and places) and individual's descriptive information (identification number, sex, first and last names, nobility rank,

occupation, birth order, cause of death (violent/nonviolent), ethnicity, marital status, data source code number, data source year of publication). Individual information is supplemented by data for parents (identification numbers, first and last names, birth, death and marriage dates, cause of death) and spouses. Thus, the database that is used in this project is organized in the form of triplets (referred to as the "ego" and two parents). This structure of records is widely used in human genetics and is adequate for studies of parent-child relationships. Similar database structure was used in the recent study of kinship networks (Post et al., 1997).

Data Quality Control. Data quality control was an important part of our study designed to develop high quality family-linked databases for longevity studies.

The genealogical data sets were checked for: (1) *completeness* in reporting birth and death dates, which is crucial for calculating individual life span - the variable of particular interest in our study. (2) *accuracy* - whether the percentage of mistakes and inconsistencies between reported dates (such as, for example, birth by the dead mother) is low enough to be acceptable. (3) *representativeness* - whether the characteristics of investigated data sets (distribution by age, sex, marital status, age at death, etc.) is close enough to demographic characteristics of populations in similar geographic areas, historical periods and social groups. In our study we referred to the well-known publication by Thomas Hollingsworth (1962) on British peerage as a standard for European aristocracy, to check for data representativeness.

The completeness in birth and death dates reporting in the New Gotha Almanac was very high: dates of all vital events were reported for nearly 95% of all persons. Such high completeness is not common for many other genealogical data sources. For example, for British Peerage data published in Burke almanac in most cases there are no birth dates for women, which makes the calculation of their life span impossible. In fact, this problem with British aristocratic women was first noticed by Karl Pearson a century ago (Beeton and Pearson, 1899, 1901). He used the British Peerage data to study the longevity inheritance and had to exclude women from his consideration for the following reason: "The limitation to the male line was enforced upon us partly by the practice of tracing pedigrees only through the male line, partly by the habitual reticence as to the age of women, even at death, observed by the compilers of peerages and family histories" (Beeton and Pearson, 1901, pp.50-51).

The accuracy of data published in the New Gotha Almanac is also very high: the frequency of inconsistent records is less than 1 per 1000 records while for many other genealogical data sources it falls within 1 per 300-400 records. Comparison of our data with Hollingsworth's analysis of British peerage (Hollingsworth, 1962) revealed good agreement between his findings and our data on mortality patterns, including male/female gap in life expectancy.

The genealogies for the members of European aristocratic families presented in the "Gotha Almanac" are of descending type, tracing almost all the descendants of relatively few founders. This is an important advantage of this data source over other genealogies that are often of ascending type (pedigrees). It is known in historical demography that the ascending genealogies are biased, over-representing more fertile and longer-lived persons who succeed to become ancestors, and for this reason such genealogies should be treated with particular caution (Jetté and Charbonneau, 1984; Fogel, 1993).

Thus, the genealogical data published in the Gotha Almanac are characterized by high quality and accuracy. We have, however, encountered some problems regarding the data completeness that are discussed below, along with proposed solutions.

Censored, truncated observations and missing death dates. Our study revealed that the percentage of cases with unreported death dates is rather small in our main data sources (Gotha Almanac), and is caused mainly by right censoring of long-lived persons who were still alive by the date of data collection and publication. The percentage of non-reported death dates varies from 0 to 7% in extinct birth cohorts (1800-1880), while it is higher in later birth cohorts (1880-1899) - 23% for women and 8% for men, since some individuals were still alive by the date of data collection and volume publication. Note that women, who live longer, have a higher proportion of right-censored observations. The high proportion of censored observations in genealogies is not desirable, since the exact dates of censoring are often unknown. This uncertainty creates problems for data analysis, so the researchers working with genealogies prefer to use non-censored, extinct birth cohorts in their studies (Mayer, 1991; Pope, 1992; Kasakoff and Adams, 1995). We also used extinct (non-censored) birth cohorts in our study. For this purpose only those birth cohorts were used in the study that were born at least 100 years before the year of data publication (to be sure that the birth cohort under study is almost extinct).

Underreporting of women and children. In many genealogical books and databases non-married women as well as children died in infancy are often missed or reported with less completeness. Since genealogical records are focused on family names which are transmitted by males only, women could be lost in genealogies when they marry and change their family names (Hollingsworth, 1976). Also, in many cases data for women do not contain information on their birth and death dates resulting in biased sex ratio in the sample with complete dates. We have also encountered this problem in our studies although for somewhat different reason. Our analysis revealed that the main cause of the sex bias in the New Gotha Almanac is related to the manner of data representation: more recent generations are presented completely, while the earlier generations are limited mainly to the male ancestors (in order to avoid repetitive publication of individuals already presented in previous volumes). That is why, the sex ratio among early birth cohorts (1800-1860) is biased in favor of males while for more recent birth cohorts (1880-1899) it is within normal range. Since in our study the most recent volumes of the New Gotha Almanac (published after 1980) were computerized and analyzed (in order to avoid censoring), the proportion of males in the database was substantially higher than expected. Thus, the ideal way to overcome the sex bias problem is to ensure complete coverage of all aristocratic genuses and families ever published in the Gotha Almanac. However, it may take a long time to computerize all 100 volumes of the New Gotha Almanac. The alternative way is to computerize complete data on early birth cohorts published in old volumes. In this case the data will be heavily censored since many persons would not have death date (be still alive) by the date of publication. We plan to continue computerization of these genealogies that will allow eventually eliminate the sex bias and potential problems associated with it. Sex bias is an important issue in fertility studies since the fertility levels are understated when daughters are underreported, but in the case of longevity studies this issue is less important when non-censored, extinct birth cohorts are analyzed (Wyshak, 1978). According to Wyshak (1978, p.318), "in the ... analysis of longevity, there is no reason to believe that women about whom information is not recorded differ from those whose records have been traced".

The underreporting of children died in infancy may be also a serious problem, especially for studies that include fertility analysis. Fortunately, in the Gotha Almanac the noble families are described with remarkable completeness, especially those families which belong to the higher nobility rank (kings, princes, earls). In particular, all ever born children are recorded, including

those who died the same day. Another indicator of data completeness is the normal sex ratio at birth (101 to 108) observed among these families (according to our sample analysis). In our database over 90 aristocratic genuses belonged to the upper nobility were recorded completely, although data for lower rank nobility were not yet completed. Underreporting of children is not a problem for this particular study which is focused on adult life span for those who survive by age 30 years.

Analytical Methods. Since the data used in this study are characterized by remarkable accuracy and completeness, it was possible to apply simple and straightforward methods of data analysis without making heavy assumptions. In particular, since the length of life is known for every person (there were no right censored observations) it was possible to analyze the duration of life directly as a dependent, outcome variable in linear regression model. There was no need to apply the Cox proportional hazard model and to make a strong assumption about multiplicative effects of covariates on hazard rate. Instead, individual lifespan was considered as a linear function of maternal lifespan, and this assumption of linear dependence between parental and offspring traits is well justified both in the theory and practice of quantitative genetics (Falconer, Mackay, 1996; Lynch, Walsh, 1998).

To control for secular changes in life expectancy, an additional internal control variable was included into analysis as an independent predictor of individual lifespan. Specifically, the mean sex-specific lifespan of birth cohorts was calculated for each calendar year of birth (81 cases for years 1800-1880 per each sex). This variable was then included into linear regression model as a predictor variable for lifespan of each individual matched for the same year of birth and gender. This method was already applied earlier in a similar study (Gavrilova et al., 1998) to regress out the secular changes in lifespan.

Data for graphs (Fig.1-3) were calculated in the following way. First, the data on individual lifespan were centered around the mean lifespan in the same birth cohorts in order to control for secular changes in lifespan. In other words, the residuals were calculated as the differences between individual lifespan and the cohort mean lifespan for the same calendar year of birth. These residuals (deviations from population mean) were then plotted against maternal lifespan (Figure 2) to see whether the mean of these residuals is close to zero (expected if maternal lifespan is of no importance), or whether it is increasing with maternal lifespan. The dependence of averaged residuals on maternal lifespan was generated, that was then smoothed by 5-year moving average in order to decrease the statistical noise and to reveal the pattern of this dependence.

Results and Discussion

Figure 1 depicts a three-dimensional image for the dependence of sons' lifespan on two variables - maternal lifespan (horizontal X-axis), and maternal age when a particular son was born (vertical Y-axis). The picture looks like a geographical map where more intensive color (more dark) corresponds to higher levels of sons' lifespan.

Figure 1 about here

Note that the bottom-left corner of this picture ("South-West") has a light grey color. This means that sons born to young (15-25 years) shorter-lived mothers (died before 75 years) also have relatively short lifespan. Moving to the right ("East") of this picture the areas of more intensive color are observed corresponding to higher lifespan of the sons born to longer-lived mothers. Finally, the intensive black-colored areas are observed in the bottom-right corner of the picture ("South-East") corresponding to highest lifespan observed for sons born to particularly long-lived mothers, who died at age of about 95 years (Fig.1).

There is of course no surprise that sons' lifespan is increasing with maternal lifespan. What is really surprising is that this dependence is observed for sons born to young mothers only (data displayed in the bottom, "Southern", area of the map, Fig.1). For sons born to older mothers (above 35 years, see the top, "Northern", area of the map) there is no corresponding increase in lifespan with increasing maternal longevity. In fact, the paradoxical reversed trend seems to be observed (see Fig.1).

Figure 2 illustrates this new paradoxical finding in the form of traditional plots (scatter diagrams).

Figure 2 about here

Note that sons' lifespan is increasing by 3 years (in average) when mothers live 90 instead of 70 years (data in black circles at Figure 2). This is true, however, for sons born to young mothers only (15-34 years), while sons born to older mothers do not demonstrate any increase in their lifespan in response to higher maternal lifespan (see data in open circles at Figure 2).

These graphical observations (Figure 1 and 2) are also confirmed by statistical analysis presented at Table 1.

Table 1 about here

The slope coefficient (b) in the linear regression of sons' lifespan on maternal lifespan is substantial ($b = 0.124 \pm 0.063$; $n = 3,782$ cases, $p = 0.05$) when sons were born to young mothers (15-34 years). However, this regression slope is negligible ($b = 0.014 \pm 0.105$, $n = 796$, $p = 0.90$, insignificant) when sons were born to older mothers (35 years and above).

The loss of inheritance of maternal lifespan is observed not only among the late-born sons (Fig.1-2, Table 1), but also among the late-born daughters (Fig.3).

Figure 3 about here

The contour plot for levels of daughters' lifespan (Fig.3) is very much similar to those for sons (Fig.1) and also demonstrates that daughters born to older mothers do not inherit maternal lifespan. A statistical proof for this observation is presented at Table 2.

Table 2 about here

Note that the slope coefficient (b) in the linear regression of daughters' lifespan on maternal lifespan is highly significant ($b = 0.21 \pm 0.08$, $n = 1,801$ cases, $p < 0.01$) when daughters are born to young mothers (15-34 years). On the other hand, this regression slope coefficient is negligible ($b = 0.01 \pm 0.15$, $n = 355$, $p = 0.96$, insignificant) when daughters are born by older mothers (35+ years). In other words, daughters born to older mothers do not inherit maternal lifespan (Table 2).

The obtained results are consistent with evolutionary ideas that the age at reproduction is under strong selection pressure and, therefore, those women who maintain late fertility represent a highly selected group of the population with decreased genetic diversity. This diminished genetic diversity among late-reproducing women may account for shrinking of the additive genetic variance for human lifespan in this selected group of the population. When the additive genetic variance of lifespan becomes close to zero, so does the narrow-sense heritability of lifespan and its familial transmission through generations. Further studies on larger samples with additional consideration of many other explanatory and confounding variables are planned and may shed light on the mechanisms of interaction between lifespan heritability and age at reproduction. In any case, one of the obvious practical implications of this study is that lifespan heritability could not be fully understood and studied correctly without taking into consideration its interaction with parental age.

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Table 1

**Sons Born to Older Mothers (35-55 years)
Do Not Inherit Maternal Lifespan**

	Sons of <i>younger</i> mothers (15-34 years)	Sons of <i>older</i> mothers (35-55 years)
Regression slope (sons' lifespan on maternal lifespan)	<i>0.124</i>	<i>0.014</i>
Standard error for regression slope	0.063	0.105
t-ratio	1.96	0.128
Significance (P-value)	0.05 Significant	0.90 Insignificant
Number of cases	3,782	796
Range for maternal lifespan, years	75-95	75-95

The data are for extinct birth cohorts, born 1800-1880. European royal and noble families.

Table 2

**Daughters Born to Older Mothers (35-55 years)
Do Not Inherit Maternal Lifespan**

	Daughters of <i>younger</i> mothers (15-34 years)	Daughters of <i>older</i> mothers (35-55 years)
Regression slope (daughters' lifespan on maternal lifespan)	<i>0.210</i>	<i>0.009</i>
Standard error for regression slope	0.075	0.152
t-ratio	2.82	0.06
Significance (P-value)	0.005 Significant	0.955 Insignificant
Number of cases	1,801	355
Range for maternal lifespan, years	75-95	75-95

The data are for extinct birth cohorts, born 1800-1880. European royal and noble families.