

Human longevity and early reproduction in pre-industrial Sami populations

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Abstract

Senescence is predicted to be associated with the intensity and timing of reproduction at an earlier age. Here, we examine the phenotypic association between reproduction and post-reproductive survival in three pre-industrial human populations that lived in Northern Scandinavia during 1640–1870. In both sexes longevity was independent of the total number of born or adult children, whereas early reproduction was negatively associated with the longevity of females and males. Our results thus do not support the view that reproductive investment as such has a negative impact on longevity, but suggest that survival costs are associated with the scheduling of reproduction. We discuss, however, an alternative point of view suggesting that less intense selection for early reproduction, extended parental care, and social structure allowing kin selection through the effects of close relatives are factors that have selected for the long post-reproductive life span in humans.

Introduction

Senescence, i.e. decrease in survival and fecundity rates with advancing age (Rose, 1991), is predicted to evolve as a side-effect of life-history optimization, when longevity is traded for high early fecundity (Williams, 1957; Kirkwood & Rose, 1991; Partridge & Barton, 1993a,b). According to the antagonistic pleiotropy hypothesis, senescence is caused by pleiotropic effects of genes that enhance reproduction at young age, but suppress survival later in life (Williams, 1957; Charlesworth, 1980). Senescence may thus evolve as an unavoidable by-product of selection for traits expressed and favoured by natural selection at young age. Alternatively, the disposable soma theory predicts that allocation of limited resources to reproduction directly reduces the resources available for somatic maintenance and repair, that in turn reduce longevity (Kirkwood, 1977; Kirkwood & Holliday, 1979; Kirkwood & Rose, 1991). Both theories are based on the expectation that, because of the declining force of natural selection with age, fitness

traits expressed early in life are under more intense selection than traits expressed at later ages, and particularly at post-reproductive age (Charlesworth, 1980). Thus, they predict a rapid decline in survival rate at the post-reproductive period. However, extended parental care in humans has a crucial role for the performance of offspring and, thus, selection might have favoured prolonged survival at post-reproductive period (Hill & Kaplan, 1999; Alvarez, 2000; Sear *et al.*, 2000).

Antagonistic pleiotropy would show up as a negative genetic correlation between early fecundity and late survival (Reznick, 1985), with selection favouring early reproduction. At the phenotypic level one could then also find a negative covariation of reproduction at an early age and life span. According to the disposable soma theory negative phenotypic correlation between fecundity and post-reproductive survival is expected. However, one must pay special attention to the potential problem of phenotypic correlations when assessing any kind of trade-off in natural populations (Reznick, 1985). The results may be confounded by the fact that individuals do vary in their phenotypic quality, which results in that superior individuals have both a high fecundity and a

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long life span (van Noordwijk & de Jong, 1986; Hill & Kaplan, 1999).

The mechanisms of senescence are well studied in for example *Drosophila melanogaster* and *Caenorhabditis elegans* (see, e.g. Partridge & Barton, 1993a,b; Partridge & Mangel, 1999; Kirkwood & Austad, 2000; Partridge & Gems, 2002). Detailed studies of natural selection with respect to senescence in long-living vertebrates, such as humans, are rare and the results contradictory (Le Bourg, 2001). In contrast to theoretical predictions, several studies among premodern humans have found longevity to be positively correlated (Borgerhoff Mulder, 1988; Voland & Engel, 1989; Mace, 1996), or independent (Knodel, 1988; Le Bourg *et al.*, 1993; Korpelainen, 2000) of reproductive investment, whereas only two studies have found evidence for the predicted phenotypic trade-off between fecundity and longevity (Westendorp & Kirkwood, 1998; Thomas *et al.*, 2000). In addition, there is some evidence that this trade-off might be manifested only among low-status individuals, or under poor environmental conditions (Lycett *et al.*, 2000).

To our knowledge, there are no direct tests of antagonistic pleiotropy in humans, perhaps because it is a genetic theory and thereby relatively hard to address. There is, however, some evidence at the phenotypic level that longevity is related to a high age at first reproduction (Westendorp & Kirkwood, 1998; Korpelainen, 2000), and to the mother's ability to continue childbearing in her forties (Perls *et al.*, 1997). However, these studies do not report the actual timing of all reproductive events for the whole fertile period, or take the total fecundity into account. These equivocal results thus call for more detailed research in populations experiencing different ecological and demographic profiles.

In this study, we used demographic data from three pre-industrial and natural-state human populations to examine the association between reproduction and post-reproductive survival. We were interested in how the reproductive investment, i.e. the number of children produced, the number of children raised to adulthood, and average age at reproduction affected longevity. Furthermore, we examined whether males and females differed in their fecundity-survival patterns. The disposable soma theory also predicts sex-specific fecundity-survival

patterns for organisms where males and females differ in the direct physiological costs of reproduction. Hence, females should show higher reproduction-associated post-reproductive mortality as they, like many female primates, often invest more in reproduction in terms of gestation, lactation and parental care than males (Allman *et al.*, 1998; Käär *et al.*, 1998; Key & Ross, 1999).

Materials and methods

Study populations

Our data were collected from the parish registers kept by the Lutheran church. It includes complete information on the total of 1974 Sami families that lived in three different populations (Utsjoki, Inari, and Enontekiö) in northern Scandinavia between 1640 and 1870. Each population occupied a large, partially overlapping geographical area, where people lived in small family groups or villages (Itkonen, 1948). The Sami of Utsjoki population were semi-nomadic reindeer herders and fishers, the Enontekiö Sami practised nomadic reindeer herding and lived in temporary dwellings or tents, whereas the Sami of Inari lived mainly by hunting and fishing (Itkonen, 1948). These among-population differences were also reflected into the demography of the populations, which differed, for example, by the average number of offspring, age at first reproduction and life span (Käär *et al.*, 1996, 1998).

Statistical analyses

We retrieved age at death, total number of children, average reproductive age, spouse's age at death, gender and resident population for each individual in our data set. Average reproductive age was calculated as the mean over all children born. Spouse's age at death was used as control for the effect of shared environmental and socio-economical factors acting simultaneously on the longevity of both sexes within the family (Gavrilova & Gavrilova, 2001). We restricted our analyses to those individuals who survived beyond the age when 99% of individuals of a certain population had ceased their reproduction. These numbers were 50, 48 and 48 for

Table 1 Mean \pm SD (in years) for age at death, average reproductive age, and total number of children by gender in three pre-industrial Sami populations.

	Population					
	Utsjoki		Inari		Enontekiö	
	Females	Males	Females	Males	Females	Males
Life span	75.0 \pm 9.5	74.2 \pm 7.2	71.0 \pm 10.0	74.1 \pm 6.2	72.2 \pm 11.4	75.2 \pm 6.7
Average reproductive age	35.0 \pm 4.0	39.2 \pm 6.6	33.8 \pm 3.9	37.6 \pm 6.1	33.3 \pm 4.3	38.0 \pm 5.7
Number of children	5.0 \pm 2.2	5.0 \pm 2.2	5.2 \pm 2.4	5.4 \pm 2.3	6.9 \pm 2.6	7.1 \pm 2.6
<i>n</i>	64	50	160	107	103	79

females and 63, 64 and 64 years for males in Utsjoki, Inari, and Enontekiö populations, respectively. Population means (\pm SD) for studied life-history traits by gender are given in Table 1.

We used multiple regression to analyse the effect of number of children, average reproductive age, spouse's age at death, gender, and population on the longevity of the Sami. Interactions between all the main effects with gender and population were included in the regression model, and if statistically significant, included in the final model. We also repeated our analyses by including only children surviving to the age of 18 years to account for infant mortality and extended parental care as part of the reproductive investment. Multicollinearity diagnostics among the independent variables using condition index, variance inflation factors and tolerance values showed no serious collinearity. Residuals of models were normally distributed and therefore no transformations were used. We used SAS statistical software (SAS Institute Inc., 1990) to carry out the regression analyses.

Results

Our results show that the number of born children had no significant effect on longevity and this association did not differ between the sexes or populations (Table 2; Fig. 1). Instead, average reproductive age was positively correlated with the longevity of females and males in all populations (Table 2; Fig. 2). In addition, spouse's age at death was positively associated with longevity, suggesting that a fraction of variation in longevity was caused by the shared environment (Table 2). However, this covariation of female and male life span differed between the sexes and populations, indicated as a significant interaction between spouse's age at death, gender and population (Table 2). A closer look revealed that in Inari, spouse's age at death was significantly correlated with

Table 2 Multiple regression of longevity as a function of the number of children, average reproductive age, spouse's age at death, gender, and population.

Independent variables	$\beta \pm SE$	F	P
Number of children	0.057 \pm 0.156	0.14	0.7131
Average reproductive age	0.232 \pm 0.075	9.69	0.0020
Spouse's age at death	0.102 \pm 0.065	17.21	<0.0001
Gender	-	0.01	0.9107
Population	-	2.47	0.0856
Spouse's age at death \times gender \times population	-	2.51	0.0291
Model	-	4.58	<0.0001
R ²		0.084	
n		563	

Interactions that did not reach the statistical significance at $\alpha < 0.05$ are omitted from the final model. Significant terms are given in bold case.

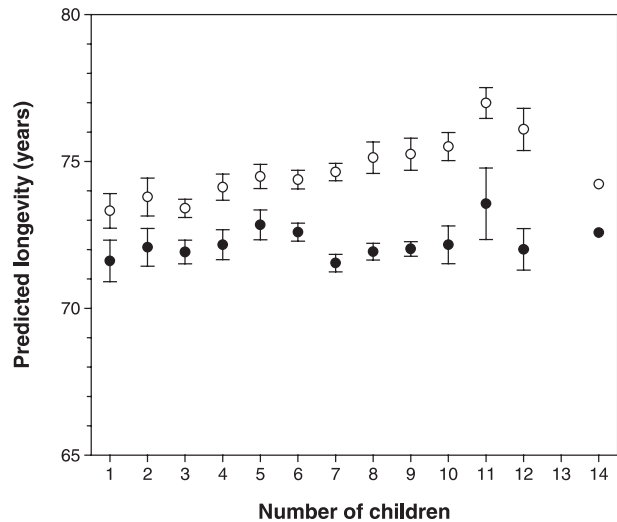


Fig. 1 Mean (\pm SE) predicted values of age at death as a function of the number of children born in pre-industrial Sami populations. Filled and empty circles represent females ($n = 327$) and males ($n = 236$), respectively. Note that males' higher life-span is because of the selection of different age criteria used in the analysis (see Methods).

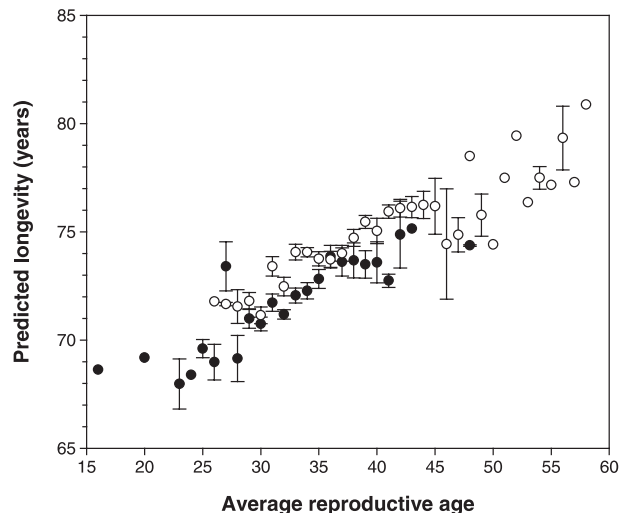


Fig. 2 Mean (\pm SE) predicted values of age at death as a function of average reproductive age in pre-industrial Sami populations. Filled and empty circles represent females ($n = 327$) and males ($n = 236$), respectively.

the life span of males only (females, $F_{1,158} = 0.81$, n.s.; males, $F_{1,105} = 3.88$, $P = 0.051$), and in Enontekiö population, spouse's age at death had no significant effect on the longevity of either males or females (females, $F_{1,101} = 0.77$, n.s.; males, $F_{1,77} = 2.79$, n.s). In Utsjoki, both male and female life spans significantly covaried positively with each other (females, $F_{1,62} = 11.91$,

$P = 0.001$; males, $F_{1,48} = 4.85$, $P = 0.032$). Finally, gender and population were not related to individuals' longevity (Table 2).

We also repeated the above analysis using the number of children who survived to the age of 18 as a measure of total fecundity to exclude the potentially confounding effect of infant mortality. The results remained unchanged indicating that raising the produced children to adulthood incurred no detectable extra cost for parents in terms of their survival (results not shown).

Discussion

The longevity of women and men was not related to the number of born or adult children in the studied pre-industrial Sami populations. Instead, longevity was positively correlated with the average reproductive age, and this effect was independent of family size and sex.

Absence of any longevity effect of increased reproductive success does not support the disposable soma theory of senescence. Instead, our results are in agreement with several studies that report no phenotypic trade-off between fecundity and longevity in humans (Borgerhoff Mulder, 1988; Volland & Engel, 1989; Le Bourg *et al.*, 1993; Mace, 1996; Knodel, 1988; Korpelainen, 2000; see also Lycett *et al.*, 2000). Also, the similarity of female and male fecundity-survival patterns strengthens the interpretation that disposable soma theory is not a valid explanation for human longevity in these Sami populations. However, trade-offs in natural populations can be masked by phenotypic correlations (van Noordwijk & de Jong, 1986; Hill & Kaplan, 1999), which may have prevented the detection of underlying trade-off between reproduction and survival.

Absence of a negative phenotypic correlation between fecundity and longevity calls for an alternative explanation for longevity in these premodern humans. Several components of human biology may directly select for increased longevity, downplaying the importance of high fecundity and early reproduction. For instance, humans reach maturity relatively late and, accordingly, have a long prereproductive period compared with other large primates (Schultz, 1969; Hill & Kaplan, 1999; Alvarez, 2000). As a result, the highest intensity of reproduction is achieved at the proximity of 25–30 years of age (Wood, 1990), and hence the intensity of natural selection on early fecundity may be relatively weak in humans (see Käär & Jokela, 1998). Likewise, long post-reproductive life span is a specific human character (Schultz, 1969; Hill & Hurtado, 1991; Pavelka & Fedigan, 1991). Hill & Kaplan (1999) suggested that human life history in a hunter-gatherer society included a long prereproductive period for training and accumulation of resources needed for successful reproduction. Hence, one explanation for the evolution of extended post-reproductive life span is the positive effect of parental care (e.g. through improved health and social skills) to success of children and

grandchildren during their long prereproductive period (e.g. Williams, 1957; Sear *et al.*, 2000; Carey & Judge, 2001; Peccei, 2001). This view implies that natural selection favours post-reproductive survival, and therefore suppresses senescence. These characteristics may also be responsible for the lack of evidence for a steep decrease in survival at the beginning of the post-reproductive age, as predicted by the theories on senescence. Weak natural selection for early fecundity, combined with direct positive selection for long post-reproductive life span, may have been factors that have reduced senescence in premodern humans.

Individuals who reproduced relatively late lived longer than individuals who reproduced at younger ages. This seems compatible with the phenotypic predictions of the pleiotropy theory (Williams, 1957), and, in part, with those observations that suggest positive correlation between high age at first reproduction and long life span (Westendorp & Kirkwood, 1998; Korpelainen, 2000). Alternative explanations for this result exist, however. While in line with the observation that giving birth in one's forties is associated with life span in some women (Perls *et al.*, 1997), social family structure may also be important in determining the longevity of the elderly members. In premodern Sami populations family resources were shared, and individuals who reproduce at an early age may overlap with their grandchildren for a longer period of time than individuals who reproduce late. This may put extra pressure on the survival of the elderly when resources are scarce. Further studies regarding the association between the age-structure of the family and the survival of the elderly are needed to test this hypothesis.

In summary, we suggest that the long prereproductive period that was needed for successful reproduction suppressed selection for early reproduction. This, together with the direct fitness benefits of long post-reproductive life span may have selected for extended post-reproductive life span in humans. We propose that evolution of these life-history traits should be studied in the context of social structure of human populations and families. When social processes become important for fitness, the predictions of classical senescence theories have to be revised accordingly. For example, if the post-reproductive life span is important for fitness, natural selection should effectively purge mutations that express their deleterious effects later in life. The evolutionarily interesting aspect of the human life-cycle may not be the universal process behind senescence (i.e. why we die?), but rather the reasons why we have a long post-reproductive life span (i.e. why we die so late?).

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