

Longevity and the costs of reproduction in a historical human population

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It has been argued that the priority that natural selection places on reproduction negatively affects other processes such as longevity and the problem posed by this trade-off underlies the disposable soma theory for the evolution of human ageing. Here we examine the relationship between reproduction and longevity in a historical human population (the Krummhörn, north-west Germany 1720–1870). In our initial analyses, we found no support for the hypothesized negative effects of reproduction on longevity: married women who remained childless lived no longer than women who reproduced and women who had few children lived no longer than women who had many children. However, more detailed analyses in relation to socio-economic class revealed that the extent to which reproduction has an effect on longevity is a function of the level of economic deprivation. We found that, when possible sources of confound were controlled for (e.g. duration of marriage and amount of time spent in fecund marriage), there is an increasingly strong relationship between longevity and reproduction with increasing poverty.

Keywords: reproduction; longevity; disposable soma theory; Krummhörn; humans

1. INTRODUCTION

Life-history theory is concerned with the trade-off that an organism makes between investment in somatic growth (i.e. the accumulation of reproductive potential) and investment in reproductive effort (i.e. the exploitation of reproductive potential) (Stearns 1992; Jönsson & Tuomi 1994). Among iteroparous species, individuals are confronted with the problem of maximizing their reproductive success within the context of a finite lifetime (Kirkwood & Rose 1991). Unlike organisms such as higher plants (Kirkwood 1977), most higher animals have a limited period in which to reproduce and, in particular for human females, this reproductive life span is itself abbreviated with the onset of menopause.

The problem posed in the trade-off between reproduction and longevity underlies what has been termed the disposable soma theory of the evolution of human ageing. Underpinning theories of the evolution of ageing is the assertion that the priority that natural selection places on reproduction impacts negatively on other processes such as somatic growth or longevity (Kirkwood & Rose 1991). Evidence for the antagonistic relationship between longevity and reproductive success has been sought in both inter- and intraspecific comparisons (Fowler & Partridge 1989; Gustafsson & Pärt 1990; Chapman *et al.* 1995, 1998; Volland 1998). It has been shown that, at least in fruit flies, it is not so much reproduction *per se* which affects longevity negatively, but rather the costs which are associated with mating (Fowler & Partridge 1989; Chapman *et al.* 1998). Fowler & Partridge (1989) suggested that mechanical injury experienced during mating, the transfer of parasites or an effect of sperm on accessory fluids might be possible explanations for the cost of mating on longevity. More recently, Chapman *et al.* (1995) demonstrated that the cost of mating for females

was due solely to the transfer of seminal fluid molecules from males and that an increased female death rate was associated with increased exposure to those products.

In humans, evidence for the relationship is rare, but where data are available the relationship is unexpected: for post-menopausal women, a positive relationship between fertility and longevity has been generally reported (Borgerhoff Mulder 1988; Volland & Engel 1989). It is only for women who have considerably more than average numbers of children that the predicted negative effects of reproduction on longevity become marked (Volland & Engel 1989) and this is in line with an early theoretical perspective which suggested that it is only when parents exceed a certain optimal threshold level of reproductive investment that negative effects on longevity are apparent (Lack 1954; see Jönsson & Tuomi 1994). Some further evidence that reproduction *per se* does not have a negative effect on longevity in humans comes from a study which showed that women who lived to especially old ages had continued to reproduce into their fifth decade of life. In contrast, women in the sample who died earlier had ceased reproduction earlier in life, leading the authors to suggest that the driving selective force of life span in humans is maximizing the time-period during which women can bear children (Perls *et al.* 1997).

This relationship between longevity and reproduction was the focus of a recent analysis of pre-modern British aristocracy (Westendorp & Kirkwood 1998). These authors reported a negative correlation between the number of progeny and female longevity which, they concluded, provided evidence that human life histories involve the expected trade-off between longevity and reproduction. This finding thus stands in marked contrast to previous studies which suggested that no such relationship existed in humans.

Here we examine the same relationships as Westendorp & Kirkwood (1998) using data from a historical population which inhabited the Krummhörn region of

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north-west Germany between 1720 and 1870. We test two specific predictions which follow from the disposable soma theory.

- (i) If reproduction negatively affects longevity, then we would expect that women who marry but remain childless should live longer than women who marry and have children.
- (ii) A more powerful test of the relationship might involve the amount of reproduction. Thus, we might expect that women who have many children will die earlier than women who have only a few children.

In addition, we explore three further factors which might influence the relationship between longevity and reproduction, namely duration of marriage, amount of time spent in a fecund marriage and socio-economic status.

2. METHODS

Our data were extracted from the Krummhörn database which contains demographic data on around 16500 families who lived in 13 north-west German parishes during the 18th and 19th centuries (see Voland & Engel (1989) and Voland *et al.* (1997) for details on the Krummhörn region and the database). From the database we selected first-marriages of males and females for which we had complete records, which provided exactly known birth dates for both spouses and all children and exactly known dates of death for both spouses, as well as the exactly known date of marriage. The duration of marriage is calculated from the marriage date through to the death of whichever spouse died first, while the amount of time spent in a fecund marriage is calculated from the date of marriage to 50 years of age, or age of death if either spouse died before that time.

Whereas Westendorp & Kirkwood (1998) reported on a single homogenous population which was relatively unaffected by the economic deprivation which might have interfered with longevity, we were able to assess the relationships for the population as a whole, as well as for clearly defined social groups within the population. The latter analysis (social group comparisons) will allow an examination of the possible effects of socio-economic status on reproduction and longevity. Within the Krummhörn, social status is defined by access to land (see Voland 1990, 1995) and three social groups are clearly identifiable: the relatively wealthy farmers, the intermediate smallholders and the poor landless.

We present results for the Krummhörn population as a whole, as well as for the three social groups within the population. The combined sample sizes for the three social groups did not equal those for the population in all cases due to missing socio-economic data for some families. In all analyses we included only those women who survived to at least 50 years of age. We did this in order to exclude women who died prematurely for reasons related to complications associated with childbirth or diseases whose effects are unrelated to reproductive effort. Thus, our sample includes only women whose reproduction was complete (or potentially complete in the case of women who remained childless) and so we were able to isolate the effects of reproduction *per se* on longevity.

3. RESULTS

We present the data reported by Westendorp & Kirkwood (1998) in table 1 as well as the same

associations for the Krummhörn. Note that the Krummhörn data yield the same basic patterns as the Westendorp & Kirkwood (1998) study, although in one respect the two data sets do differ. One of the more surprising finds of Westendorp & Kirkwood (1998) was that almost half of the women who survived to 80 years or more remained childless and this was used as partial support for the claim that reproduction and longevity are negatively related. In contrast, in the Krummhörn sample only 10% of women who reached 80 years or more remained childless. We found no differences in the mean number of children by female age at death (grouped by decades): women who lived to especially old ages (80 years or more) did not have significantly fewer children than women who died relatively early (ANOVA $F_{3,1072} = 0.426$ and $p = 0.734$) (table 1).

We now proceed to test the two predictions from the disposable soma theory. Although childless married women tended to live slightly longer, there was a significant difference in only one of the three social groups: at the population level and within the two remaining social classes, the mean age at death for married childless women was not significantly different from that of married women who reproduced (population $t_{1194} = 0.717$ and $p > 0.1$, farmer $t_{84} = 1.235$ and $p > 0.1$, smallholder $t_{138} = 2.191$ and $p < 0.05$, and landless $t_{301} = 0.603$ and $p > 0.1$) (table 2). (As a check on these results, we compared the survivorship curves implied by these ages at death, but the results were the same: Kolmogorov–Smirnov $Z = 0.385$ and $p = 0.998$.) Equally, there was no effect of wealth on the mean age at death for either women who reproduced or for childless married women (ANOVA, with children $F_{2,476} = 1.364$ and $p = 0.257$, and childless $F_{2,49} = 0.571$ and $p = 0.569$).

Similarly, we found no significant relationship between the number of live births and female age at death at either the population level or within social groups (population $r_p = 0.006$, $p = 0.847$ and $n = 1073$, farmer $r_p = 0.120$, $p = 0.302$ and $n = 76$, smallholder $r_p = 0.022$, $p = 0.810$ and $n = 122$, and landless $r_p = -0.041$, $p = 0.494$ and $n = 279$). While there was a tendency for women who had one or two children to live slightly longer than their counterparts who had nine or more children, there were no significant differences in the mean age at death for the two categories of married women (population $t_{327} = 0.929$ and $p > 0.1$, farmer $t_{19} = 0.684$ and $p > 0.1$, smallholder $t_{32} = 1.012$ and $p > 0.1$, and landless $t_{68} = 0.277$ and $p > 0.1$) (table 2). In fact, if we compare the two extremes, the mean age at death for women who had many children was no different from that for women who remained childless (mean \pm s.e. 68.5 ± 0.92 years and 69.5 ± 0.95 years, respectively). There was also no effect of wealth on the age at death for women who had either few or many children (ANOVA, few children $F_{2,67} = 1.072$ and $p = 0.348$, and many children $F_{2,53} = 0.021$ and $p = 0.980$).

Taken at face value, these data do not provide support for the hypothesized negative effects of reproduction on longevity. Therefore, we examined the relationships between longevity and a number of key life-history variables, including age at marriage, age at first birth, age at last birth, duration of marriage and amount of time spent in a fecund marriage. Of the five, only the

Table 1. Mean number of children (\pm s.e.) born to women in the Krummhörn population by the mother's age at death, together with the relevant comparative data for the British aristocracy reported by Westendorp & Kirkwood (1998)

(Also presented (by decade of death) is the proportion of women which remained childless. Note that for the Krummhörn, three women who died older than 90 years of age have been included in the women who died during their 80s.)

age at death (years)	mean number of children								proportion childless		
	<i>n</i>	Krummhörn farmers	<i>n</i>	Krummhörn smallholder	<i>n</i>	Krummhörn landless	<i>n</i>	Krummhörn population	British data	Krummhörn population	British data
20–29	13	1.54 (0.18)	15	2.33 (0.37)	21	1.81 (0.22)	117	1.74 (0.09)	1.35	0.15	0.39
30–39	20	4.45 (0.44)	25	4.00 (0.40)	49	3.08 (0.23)	219	3.55 (0.13)	2.05	0.08	0.26
40–49	17	6.76 (0.80)	18	5.83 (0.55)	52	5.04 (0.33)	203	4.94 (0.18)	2.01	0.08	0.31
50–59	17	5.06 (0.57)	25	5.60 (0.60)	56	4.98 (0.36)	208	4.87 (0.18)	2.40	0.11	0.28
60–69	26	5.35 (0.55)	35	4.89 (0.50)	77	5.60 (0.30)	318	4.98 (0.15)	2.36	0.09	0.33
70–79	23	6.17 (0.59)	47	5.85 (0.35)	99	5.12 (0.25)	370	5.06 (0.14)	2.64	0.09	0.31
80–89	10	5.10 (0.66)	15	5.47 (0.88)	47	4.89 (0.33)	177	4.82 (0.19)	2.08	0.10	0.45
90+	—	—	—	—	—	—	—	—	1.80	—	0.49

Table 2. Mean age at death (\pm s.e.) for Krummhörn women who married and had children and married women who remained childless, as well as the mean age at death for women who had few (two or less) and many (more than nine) children

(Also presented are the mean ages at marriage for women who married and had children and women who remained childless.)

	mean age at death						mean age at marriage			
	<i>n</i>	with children	<i>n</i>	childless	<i>n</i>	two or less children	<i>n</i>	nine or more children	with children	childless
population	1082	69.6 (0.31)	14	69.5 (0.95)	224	69.6 (0.68)	105	68.5 (0.92)	25.9 (0.13)	34.23 (0.97)
farmer	76	67.9 (1.07)	10	71.8 (3.67)	11	65.4 (2.48)	10	67.9 (2.69)	24.8 (0.50)	30.80 (3.20)
smallholder	122	69.0 (0.88)	18	74.2 (2.10)	17	71.2 (2.58)	17	67.5 (2.58)	25.4 (0.44)	31.00 (2.80)
landless	279	69.9 (0.59)	22	71.1 (1.90)	41	68.7 (1.71)	29	68.0 (1.76)	25.8 (0.25)	34.50 (1.92)

latter two were significantly associated with longevity. However, it is possible that longevity may be confounded with the duration of marriage: women who marry late may live longer and, because of reduced opportunity, have fewer children. In fact, for both the landless and smallholder groups, women who remained childless married at significantly later ages than did women who had children (smallholder $t_{17}=2.41$ and $p < 0.05$, and landless $t_{21}=4.96$ and $p < 0.01$), while among farmers there was a similar but non-significant trend ($t_9=2.16$ and $p < 0.1$) (table 2). Moreover, for females in each of the social groups, the age at death was positively associated with the amount of time spent in marriage (landless $r=0.280$, $p=0.0001$ and $n=225$, smallholders $r=0.288$, $p=0.003$ and $n=106$, and farmers $r=0.252$, $p=0.05$ and $n=61$). In addition, the duration of marriage was positively correlated with the number of children (landless $r=0.316$, $p=0.0001$ and $n=225$, smallholders $r=0.310$, $p=0.001$ and $n=120$, and farmers $r=0.384$, $p=0.002$ and $n=61$), suggesting that this may indeed be a source of confound.

When the duration of marriage is controlled for, longevity is negatively associated with the number of children for all three social groups, although only among the landless was this relationship significant (landless partial $r=-0.139$, $p=0.04$ and $n=223$, smallholders partial $r=-0.040$, $p=0.689$ and $n=103$, farmers partial $r=-0.008$, $p=0.954$ and $n=58$, and population partial $r=-0.072$, $p=0.041$ and $n=820$). However, note that the strength of the association

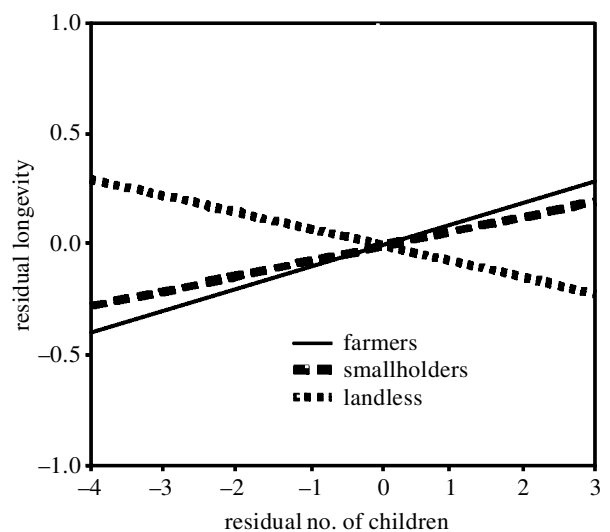


Figure 1. Regression lines for the relationship between longevity and number of children for each socio-economic class (when the duration of a fecund marriage is held constant).

increases with increasing economic deprivation such that the weakest association between longevity and the number of children is among the relatively wealthy farmers. This same trend is evident when we consider the relationships between longevity, number of children and amount of time spent in a fecund marriage.

As expected, the amount of time spent in a fecund marriage is significantly associated with the number of children at both the population level and within social groups (population $r=0.435$, $p=0.0001$ and $n=1073$, farmers $r=0.526$, $p=0.0001$ and $n=76$, smallholders $r=0.481$, $p=0.0001$ and $n=122$, and landless $r=0.468$, $p=0.0001$ and $n=279$). When the amount of time spent in a fecund marriage is controlled for, there is a non-significant positive relationship between longevity and the number of children at the population level. However, when the data are examined across social groups, figure 1 suggests a graded shift in the direction of the relationship between longevity and the number of children: for farmers the relationship is positive and significant (partial $r=0.099$, $p=0.043$ and $n=73$), for smallholders it is positive but not significant (partial $r=0.068$, $p=0.082$ and $n=119$) and for landless women the relationship is negative and significant (partial $r=-0.074$, $p=0.005$ and $n=276$).

4. DISCUSSION

The data we presented in the first part of this paper do not provide support for the negative relationship between longevity and reproduction in a human population as reported by Westendorp & Kirkwood (1998). This is made clear by our initial tests of the disposable soma theory: if reproduction *per se* negatively affects longevity, then we would have expected to find that women who married but remained childless lived longer than did their counterparts who had children. This was not the case. Similarly, it might have been anticipated that women who had a large number of children would have had shorter lives than did women who had only a few children. Again, there was no significant difference in the mean age at death, either at the population level or for individual socio-economic classes.

However, our further analyses suggested that data in the form used both here and in the Westendorp & Kirkwood (1998) study may be confounded by the duration of marriage (and, thus, probably the age at which women married). Westendorp & Kirkwood (1998) reported data from an aristocratic population which was relatively unaffected by economic deprivation which might be expected to interfere with longevity. Our social group analyses allowed us to determine whether or not this is the case. We have shown that, for all social groups, the duration of marriage is positively associated with both longevity and number of children. This might have been anticipated: a relationship between longevity and lifetime reproductive success has been widely reported in both the non-human and human literature (Borgerhoff Mulder 1988; Clutton-Brock 1988). However, when we control for the duration of marriage, we find the expected negative relationship between longevity and number of children and this relationship becomes stronger with increasing economic deprivation. Perhaps a more biologically valid test of the relationship is to be found in the analyses in which we control for the amount of time spent in a fecund marriage: by considering only the period during which women are capable of bearing children, the effect of children on longevity might be interpreted as the fitness costs of maternal depletion. In these analyses we again found a graded shift in the relationship across social groups, with pronounced

negative effects among the impoverished landless. This makes sense, given that the trade-off between longevity and reproduction is expected to be strongest under constrained conditions of existence.

Some support for this interpretation is provided by Westendorp & Kirkwood (1998) themselves. Inspection of their figure 2 suggests an interesting distinction between women in the pre- and post-1700 cohorts, with the pre-1700 cohort being mainly responsible for their relationship between longevity and reproduction. The mean age at death for women increased quite dramatically from around 1700 onwards (table 2) (Westendorp & Kirkwood 1998) and this suggests an improvement in living conditions. The association between extreme longevity and reduced fertility was most pronounced among the pre-1700 women, with a much-reduced effect for women in the post-1700 cohort. In effect, as living conditions improved with time, the differential effects of reproduction on longevity appeared to be reduced. This is not unlike the effect we observed in the demographic cross-section among the different social classes in the Krummhörn: as relative wealth increases, the strength of the association between reproduction and longevity weakens.

The positive relationship between longevity and number of children for women in the smallholder and farmer social groups (figure 1) is noteworthy. As we have suggested, it is possible that their enhanced socio-economic status buffered them against the normal costs of reproduction and, thus, the reduced longevity for women who had only a few children might be accounted for by other sources of mortality such as those reported by Lund (1992). Among Norwegian women, for example, Lund (1992) found a negative relationship between the number of children and susceptibility to ovarian cancer.

Thus, while our data do not at first appear to provide support for the disposable soma theory for the evolution of human ageing, our subsequent analyses of social groups within the Krummhörn suggest that, at least for the poorest social group, there is a trade-off between reproduction and longevity. The Krummhörn social group analyses, in combination with closer inspection of the British aristocracy data, suggest that the trade-off is context contingent.

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