Post-reproductive survival in a polygamous society in rural Africa

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Chapter 7

Selection for longevity in a polygamous society in rural Africa

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Abstract

Human longevity was long thought to be non-adaptive, resulting from better environmental conditions. Later, a selective advantage of grandmothers has been suggested. Recently, it was put forward that continued reproductive success of older men in polygamous societies provides an evolutionary explanation for the length of our lifespan. Here, we tested these hypotheses simultaneously by prospectively following 28,994 individuals of a polygamous culture in rural Africa, where the conditions likely mimic our evolutionary past. Presence of post-reproductive women increased the number of newborns by some 2.7%. However, 18.4% of offspring was sired by fathers aged 50 and above. These results suggest that length of our lifespan may have evolved predominantly through selection for longevity of men, rather than through selection favouring post-reproductive survival in women.

Longevity is often considered to be non-adaptive and the result of recent environmental improvements[1,2]. In historical times, however, human life expectancy of around 40 years was mainly determined by high child mortality but a significant number of people lived to old age; a notion that is confirmed by observations among present day hunter-gatherers[3]. A first adaptive explanation of our longevity was the 'mother' hypothesis, which suggests a selective advantage for older women as their presence would increase survival probabilities of their offspring[4]. The 'grandmother' hypothesis added the notion that help from older women may have had a selective advantage through increasing the reproductive success of their offspring[5,6]. Previous research has found that the presence of post-reproductive women allows their children to reproduce earlier, more frequently and more successfully, but the effects are context dependent and not undisputed[7-9]. It is noteworthy that currently available studies originate mostly from historical populations with nuclear families and largely from monogamous populations[7].

Recently, it has been suggested that, in polygamous populations, older men could also have played an important role in the evolution of longevity through continued reproduction up to high age[10,11]. Both Y-chromosomal and anthropological studies indicate that during our evolutionary past, in which our longevity evolved, the human species predominantly lived in polygamous populations[12,13].

Here we present the outcome of a prospective analysis in a large polygamous, patrilineal African population from the upper east region in Ghana. The people here are subsistence agriculturalists. Child mortality has recently started to decline but remains high and the corresponding population structure is dominated by children with relatively few older people[14-20]. From 2002 onwards, we have followed life history characteristics of 28,994 individuals, comprising 1,703 extended families in separate households. We were able, in a full kin analysis of two sexes, to compare the effect of older women and older men on offspring survival and reproduction and to adjust for socioeconomic status, anthropological, and environmental factors to a degree that has often been impossible in historical studies. The characteristics of the population under study are summarized in supplementary table 1.

Table 1. Hazard ratios for mortality up to reproductive age

	HR (95%CI)	p
Presence of kin members		
Mother (present vs absent)	0.67 (0.53-0.85)	**0.002**
Father (present vs absent)	0.81 (0.61-1.07)	0.13
Paternal grandmother (present vs absent)	0.99 (0.76-1.29)	0.93
Paternal grandfather (present vs absent)	0.92 (0.67-1.26)	0.58
Number of siblings (effect per sibling)	1.00 (0.98-1.02)	0.85
Number of adults (effect per adult)	1.00 (0.98-1.02)	0.74
Environmental determinants		
Socio-economic status (rich vs poor)	0.77 (0.61-0.96)	**0.02**
Drinking water (safe vs unsafe)	0.66 (0.52-0.84)	**0.001**

Results from multiple Cox regression analysis of 16,332 children, clustered on household, corrected for tribe, sex and all other variables in the model. Estimates express the hazard ratio for mortality up to age 18 years dependent on the presence of kin and environmental determinants during an eight year prospective follow-up during which 471 died. HR = hazard ratio; CI = confidence interval.

First, we studied the survival probabilities of offspring. To this end we have followed 16,632 children up to reproductive age (≤18 years) during an eight-year prospective follow-up, in which we observed 471 deaths. Figure 1 shows Kaplan-Meier survival plots dependent on kin members. The presence of the mother was associated with a 33% lower mortality risk (HR 0.67, p=0.002) pointing to increased survival probabilities. In contrast, the presence of the grandmother was not associated with a mortality difference (HR 0.99, p=0.93). Presence or absence of fathers and grandfathers did not affect offspring survival. Table 1 shows hazard ratios (HR) for mortality dependent on the presence of kin members and environmental determinants, as derived from multiple Cox regression. Children in rich households had significantly lower mortality when compared to poor households (HR 0.77, p=0.02) and children with access to safe drinking water also had a reduced mortality risk (HR 0.66, p=0.001).

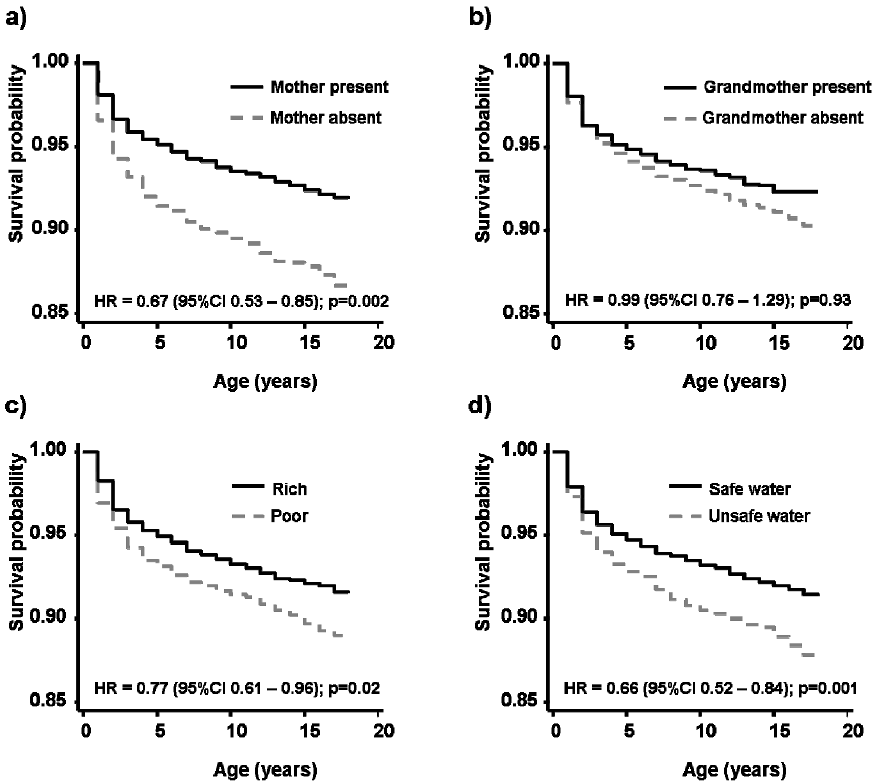

Figure 1. Survival probabilities dependent on the presence of kin and environmental determinants. a) mother, b) grandmother, c) socio-economic status, d) drinking water. Hazard rates (HR) with 95% confidence intervals (95%CI) from multivariate Cox proportional hazards model, adjusted for all other variables in the model (table 1).

Next, we studied the reproductive success of households. Table 2 shows the number of newborns dependent on the presence of kin members and environmental determinants as derived from multiple regression analysis. In line with their polygamous culture, for each additional woman aged 18 to 50 years, we observed an extra 0.42 number of newborns during the eight year observation period (p<0.001). Reproductive success was not higher when there were, next to the landlord, additional men in the household. Counter intuitively, there was a lower number of newborns when men over 50 were around (Table 2). In this patrilineal society older men, most often the landlord, monopolize resources and women, and it is them who delay the marriage and reproductive success of the younger men in their household. In line, we observed young men up to 50 years to have an average number of 5.1 newborns when an older men was absent, while they had only 3.7 newborns when an older man was present in the household. Oral history taking has identified a plausible mechanism that explains these observations; not before the 'old man' dies, the younger son inherits his livestock and is able to marry a (next) wife.

Table 2. Number of newborns in households

	Extra newborns (SE)	p	Explained variance
Effect for each additional kin member present			
Parental generation			
for each additional woman (18-49 years)	0.42 (0.02)	**<0.001**	11,7%
for each additional man (18-49 years)*	0.02 (0.03)	0.55	1,0%
Grandparental generation			
for each additional woman 50 years and above	0.13 (0.05)	**0.007**	2,7%
for each additional man 50 years and above	-0.22 (0.07)	**0.001**	6,7%
Environmental determinants			
Socio-economic status (rich vs poor)	0.72 (0.10)	**<0.001**	1,8%
Drinking water (safe vs unsafe)	0.14 (0.12)	0.24	0,0%

Results from multivariable linear regression analysis, corrected for tribe and all other variables in the model. Estimates indicate the extra number of newborns observed in an average household dependent on the presence of kin and environmental determinants during an eight year follow-up period in 1,703 households during which a total of 3,645 newborns were registered. * 92% of compounds have at least one man 18-49 years present. SE = standard error.

Since women are no longer able to reproduce after age 50 because of the onset of menopause, any selection for longevity in women must be by increasing the fertility or the survival probabilities of her kin in the household. We found the presence of post-reproductive women to give rise to an additional increase in the number of newborns in the household. For each extra woman aged 50 and above, the number of newborns additionally increased with 0.13 during the eight year observation period (table 2, p=0.007), indicating a selective advantage for post-reproductive survival in women. Analysis of variance showed the presence of post-reproductive women to increase the number of newborns by 2.7%. One could hypothesize on the nature of the effect of older women on household reproduction. One possible explanation is that elderly women allow fertile women to reproduce with shorter birth intervals because they assist with supplementary feeding or lighten the burden of child care, as has been suggested earlier[21]. Apart from accidental observations during our surveys we do not have quantitative data to test this hypothesis.

Finally, to assess the effect of continued reproduction on the selection for longevity, we calculated the fertility rates and the cumulative survival probabilities up to different ages, as shown in figure 2a and 2b. The polygamous culture of the population resulted in a higher fertility rate for men than women. Since it is customary that older men sequentially marry young fertile women, men are able to continue reproduction up to old age. By multiplication of sex-specific survival probabilities (l_x) and fertility rates (m_x), we have calculated the reproductive probability of men and women of different ages based on our prospective observations over eight years. These estimates are shown in figure 2c. At younger ages, reproductive probability is somewhat higher in women than in men. After age 35, however, reproductive probability is considerably higher in men. Since they continue to reproduce up to higher age, men have positive reproductive probabilities after age 50.

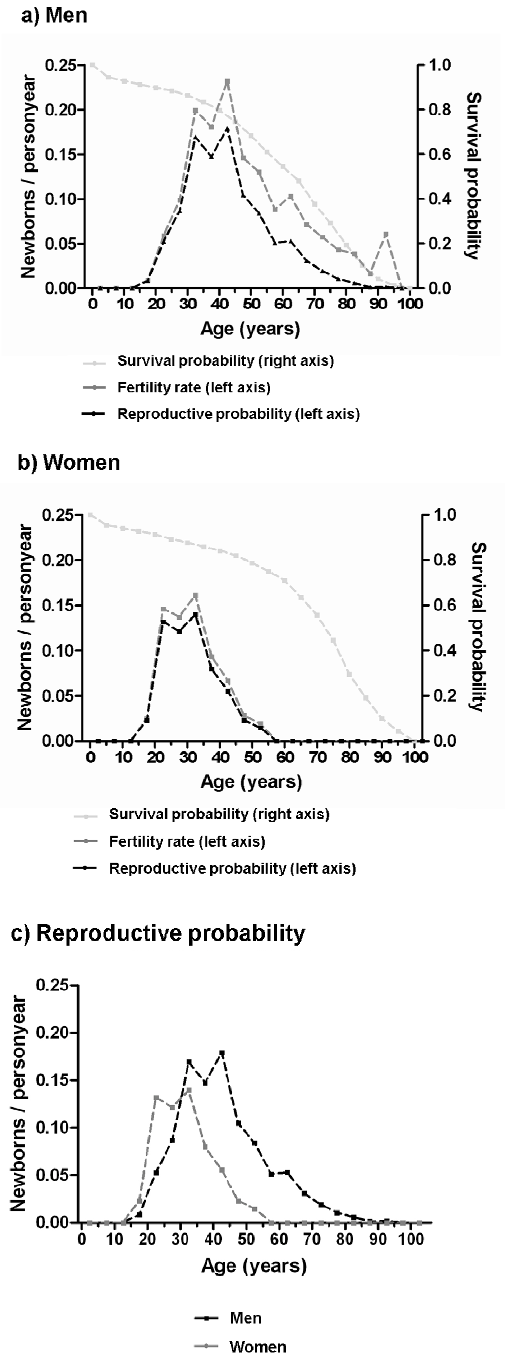

Figure 2. Selection for longevity, observed during an eight year prospective follow-up. Fertility rate, survival probability and reproductive probability for a) men and b) women of different ages and c) reproductive probability for men and women of different ages.

The net result of the continued reproduction of older men is shown in figure 3. Cumulated over an eight-year follow-up period, including a total of 3,645 newborns, 18.4% of this offspring were sired by fathers aged 50 and above, with whom they share 50% of their genome. In an additional analysis we found that children born to fathers aged 50 and above had similar survival probabilities up to reproductive age as did children born from younger fathers (HR 1.14 [95%CI 0.87 – 1.51], p=0.35). As older women increased the number of newborns with only 2.7% (see above) with whom they share 25% of their genome, these data suggest that the selective advantage of the continued reproduction of older men is far larger than the selective advantage of post-reproductive survival of women.

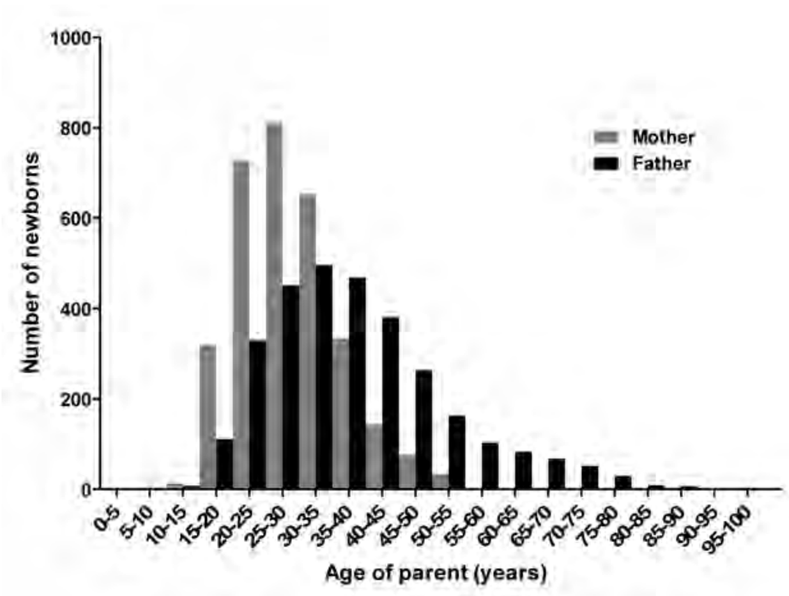

Figure 3. Number of newborns of parents from different ages. Of all 3,645 newborns observed during the eight year follow-up, 18.4% were sired by fathers aged 50 and above.

It needs to be considered that in this patrilineal society, virtually all grandparents in the household are paternal grandparents. Previous research has shown different effects of maternal and paternal grandparents on offspring survival[7,22]. It is possible that depending on the social structure, paternal or maternal grandparents may have larger effects on selection in different populations. In this light it would be interesting to also assess the selective advantages of longevity in matrilineal populations.

An important consideration is that in this polygamous, patrilineal society, some men never find a partner and consequently will not reproduce. There is both outmigration of men to the south of Ghana and inward migration of women from as far as neighboring Togo. We do not have follow-up of the males that have permanently left the research area. Outward migration is limited to an average 2% per year. For estimating reproductive probability and selective advantages, only reproducing males are important and those are all included in the present study.

Outcomes of recent collaborative studies into the genetic underpinning of human longevity have not identified particular loci with strong effects[23]. There are likely many genes involved and these are probably spread across many different chromosomes, and not just restricted to sex-chromosomes only. Long-lived fathers would therefore pass on their genetic disposition for longevity equally to their daughters and sons. Consequentially, women are long-lived because of the selection for longevity in men via continued successful reproduction into old age. The residual question is why most comparisons show that women live even longer than men. It needs to be emphasized however, that best estimates for male and female longevity come from present day societies that enjoy dramatically improved environmental conditions[24]. In our evolutionary past, the average lifespan of women, taking into account the risk of for instance childbirth, could have been markedly different. Furthermore, female longevity under present affluent conditions has a myriad of biological underpinnings, including the non-adaptive, cultural or epiphenomenal.

The contribution of kin members to reproductive success of men and women is highly dependent on the environmental conditions, the population structure and cultural aspects. Therefore, the data presented here are by no means applicable to all populations. However, since a polygamous society with extended families is most likely to resemble the population structure of our evolutionary past, the data presented here suggests that longevity has primarily evolved through the effect of continued reproduction of men after age 50, more than through effects of post-reproductive survival in women.

Supporting material

This study was conducted in the Garu-Tempane district in the Upper East region of Ghana and has been described in more detail elsewhere[14-20]. The people are patriarchal, patrilineal and patrilocal and live in extended families of which 48% are polygamous (Supplementary figure 1). Since the elderly live with their oldest son, 99% of the grandparents are paternal grandparents. During eight years of follow-up from 2002-2010 we followed 28,994 participants for reproduction and survival. The area is currently undergoing the epidemiological transition[15]. For each member of the household, the father and mother were identified if they were living in the same household. The socioeconomic status was assessed for all inhabited households in accordance with the Demographic and Health Survey (DHS) methods[17]. We defined poor and rich as divided by the median. Drinking water from bore-holes was considered safe drinking water, water drawn from wells or rivers was considered unsafe[14]. Informed consent was obtained after the nature and possible consequences of the studies were explained. Ethical approval was given by the Ghana Health Service, the Leiden University Medical Centre in Leiden, The Netherlands and by the local chiefs and elders of the research area.

Reproductive probabilities were calculated as the multiplication of the age specific fertility rates (m_x) and the cumulative survival probabilities (l_x)[2]. For the reproduction analysis we used a multiple linear regression analysis, adjusted for tribe and all other variables in the model. For the survival analysis we used a multiple left-censored Cox regression analysis adjusted for sex and tribe and all other variables in the model. The left-censored plots represent age-specific survival probabilities based on eight year follow-up. All analyses were performed with Stata 11.0 (StataCorp LP, Texas USA).

Supplementary table 1. Characteristics of the study population

Participants (n)	28,994
Male (n (%))	13,323 (46%)
Female (n (%))	15,645 (54%)
Tribe	
Bimoba (%)	66%
Kusasi (%)	26%
Mamprusi (%)	2%
Fulani (%)	2%
Busanga (%)	2%
Other (%)	2%
Households (n)	1,703
Polygamous households (%)	48%
Mean value of household possessions in US$ (mean (SD))	1,063 (1,021)
Safe drinking water (%)	80%
Numbers of newborns registered 2002-2010 (n)	3,645
Presence of kin members in household	
Men 19-49 years (median (IQR))	2 (1-3)
Women 19-49 years (median (IQR))	3 (2-5)
Men >49 years (median (IQR))	1 (0-1)
Women >49 years (median (IQR))	1 (0-2)
Survival analysis	
Offspring ≤ 18 years (n)	16,632
Follow up (calendar years)	2002-2010
Person years (years)	91,256
Mean follow up (years)	5.5
Deaths during follow up (n)	471
Presence of kin members with offspring	
Mother (%)	77%
Father (%)	71%
Paternal grandmother (%)	29%
Paternal grandfather (%)	13%
Maternal grandmother (%)	1%
Maternal grandfather (%)	1%
Number of siblings ≤18 years (median (IQR))	12 (8-17)
Number of adults > 18 years (median (IQR))	9 (6-13)

IQR = interquartile range; SD = standard deviation,

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