Post-reproductive survival in a polygamous society in rural Africa

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Chapter 1

General introduction

Introduction

Humans have a long post-reproductive life span. In this thesis we study this post-reproductive life span from an evolutionary perspective. Why did humans evolve such a long post-reproductive life span? What was the selective advantage of prolonged survival after the reproductive period?

It has long been thought that post-reproductive survival was beyond evolutionary control[1,2]. Because of the high external mortality from predators, infectious diseases and accidents in our evolutionary past, only few individuals would survive more than 50 years. Consequently, humans never evolved maintenance and repair mechanisms that would allow our bodies to reproduce after age 50 since most people would have passed away at that time. This reasoning was later amended with the principle of antagonistic pleiotrophy, which stated that the benefits of variants that lead to an advantage at young age greatly outweighed the benefits of variants that have their advantage at later ages because of the larger number on which they apply[3]. According to this line of thought, post-reproductive survival is largely a recent epiphenomenon resulting from our increased lifespan[4].

Others argue that our post-reproductive survival is not an epiphenomenon, but an adaptive trait with a selective advantage. In this reasoning, humans in past times also lived considerable years after reproductive age. Our historical life expectancy of around 40 years was mainly caused by high child mortality. Observations in present day hunter-gatherers also confirm that a significant number of people experience a post-reproductive life span[5]. Second, the orchestrated way in which menopause is regulated with distinct hormonal shifts, suggests that menopause, and therefore post-reproductive survival, could be an evolved mechanism rather than the consequence of accumulated damage.

A first adaptive explanation of our post reproductive survival was the 'mother' hypothesis, which suggests a selective advantage for older women as their presence would increase survival probabilities of their offspring[3]. 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[6-8]. Previous research has shown that the presence of post-reproductive women allows their children to reproduce earlier, more frequent and more successful, but the effects are not undisputed and context dependent[4,8]. It is

noteworthy that many currently available studies[7] originate from historical monogamous populations.
There are three arguments why historical populations are sometimes not optimal for the study of the evolution of our post-reproductive survival.

First, most historical studies, often based on church records, are from monogamous populations that live in nuclear three generational families. It is argued that this environment does not reflect our recent evolutionary past, during which we lived, as both y-chromosomal and anthropological studies indicate, in polygynous, extended families[9,10]. The selective advantages of post-reproductive survival could be very different in these populations compared to the historical populations.

Second, male longevity after age 50 has been recently suggested as an important selective advantage in our evolutionary past. In polygamous societies, men are able to reproduce up to high ages through the marriage of young fertile women[11]. This effect of older males in polygamous societies can also not be studied in the historical, monogamous populations, because monogamous men can no longer reproduce when their wife reaches the post-reproductive age. Although serial polygamy is sometimes practiced, this does not result in large numbers of offspring.

Third, in historical studies there is often no accurate measurement of socioeconomic status. This is essential, since richer households would have both better reproductive success and better survival of elderly persons, suggesting that the presence of long lived elders is responsible for the enhanced reproductive success. It is therefore possible that some of the previously found effects of post-reproductive women on subsequent generations are confounded by socioeconomic status.

To investigate whether our post-reproductive survival evolved as an adaptive mechanism it is essential to study the effect of post-reproductive kin members on reproduction and survival in an environment that resembles our evolutionary past. There is discussion during which time period in evolution our longevity evolved[12]. We studied the selective advantage of old age survival in both males and females in a large rural population of over 25,000 participants in northern Ghana who live in patrilocal, polygamous extended families and were prospectively followed for

reproduction and survival. We think this environment better resembles the evolutionary adaptive environment than most historical studies. We also collected extensive measures of other determinants of survival, most notably socioeconomic status and drinking source.

Aim of this thesis

In this thesis we study post-reproductive survival. We tested the hypothesis that males and females after age 50 are able to enhance their fitness either direct through continued reproduction or indirect through the improvement of the reproductive success of their offspring. We studied the effect of different kin members on offspring production and offspring survival in a prospective study in a polygamous African population. This environment could reflect our recent evolutionary past taking into account the anthropological and environmental determinants.

The Ghana study

All studies described in this thesis were conducted in the Garu-Tempane district in the Upper East Region of the Republic of Ghana[13]. The area has a semi-Saharan climate with an average maximum temperature of 32 ^{o}C throughout the year and only one rain season (June–August). The research area measures approximately 375 km^2 with approximately 25,000 participants living in around 40 villages. Figure 1 is a map of the research area that we created using GPS mapping of the compounds superimposed on existing hydrographic, altitude and road maps of the Centre for Remote Sensing and GIS (CERSGIS) of the Legon University in Accra, Ghana.

The participants in the research area live in extended families, with a median of fifteen persons per household. The head of the family, the landlord, is married to up to four wives. Approximately half of the landlords have more than one wife. The families live together in compounds; clay structures with thatched roofs, connected by clay walls. Figure 2 is an example of a compound. There are approximately 1,700 compounds in the research area. The people belong to several different tribes, the Bimoba (65%), Kusasi (25%) and several smaller tribes (Mamprusi, Busanga). A small group of more nomadic Fulani are living in the area as well. The vast majority of the people are farmers. The total agricultural process is done by hand. Migration is very low and amounts to less than 1% per year.

There is some additional seasonal migration of young men who move to the larger cities in Ghana to work in seasonal occupations. Illiteracy is very high, among adults it is almost complete and among children it is still very high (>50%). The average per capita income corrected for purchasing power parity of the Upper east region of Ghana in the year 2006 was US$ 304[14].

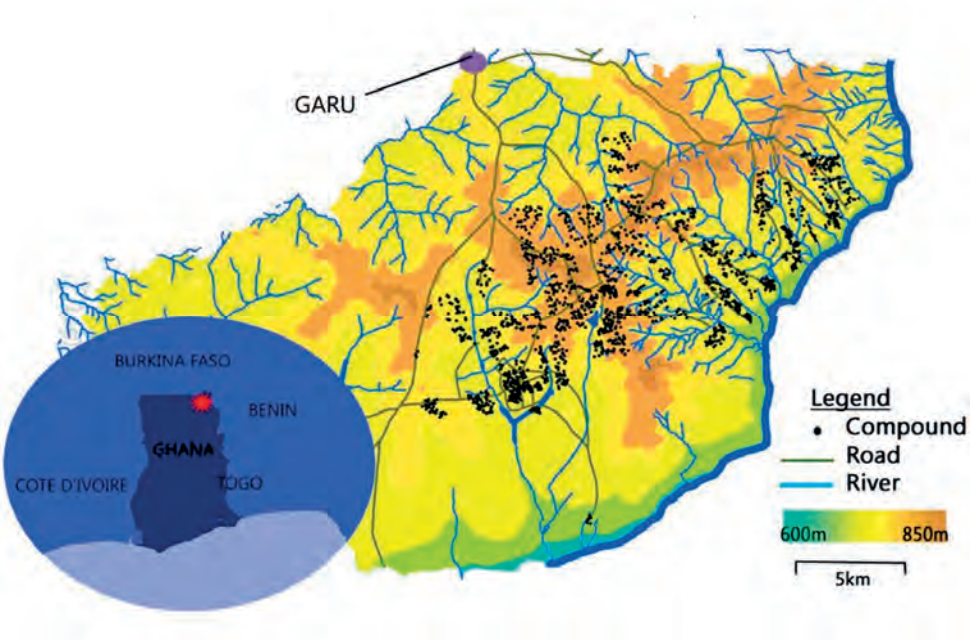

Figure 1. Map of the research area, the Garu-Tempane district in the Upper East Region of the Republic of Ghana. Map by Dr. L. May

Most people in the research area rely on traditional medical care, which is equally distributed throughout the area. There is no medical doctor working in the research area and the nearest hospital is at a 30 mile distance from the research area. Vaccination of children was introduced in the early nineties of the last century and at least 50% of the children under ten years have been vaccinated at least once. Birth control is virtually absent, although spacing of children by means of prolonged breastfeeding is sometimes practised by younger women. Most women want to have as many children as possible, since large families are highly regarded. In the past decades, clean drinking water from boreholes has been gradually introduced into the area.

Figure 2. Typical compound in the research area. Huts are made of mud with thatched roofs. In this patrilocal, polygamous population the landlord lives with his wives, sometimes accompanied by a (half-) brother or son and their wives. 48% of the households include a man who married more than one wife.

Table 1 summarizes the characteristics of the research area. In 2001, the research area was explored by the Department of Parasitology of the Leiden University Medical Centre that set up a database for parasitological research[13]. During eight years of follow-up from 2002-2010 we followed 28,994 participants for reproduction and survival. The area is 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. From this we identified the grandparents. The socioeconomic status was assessed for all inhabited households in accordance with the Demographic and Health Survey (DHS) methods[16]. We defined poor and rich as the poorest 50% and the richest 50% divided by the median. Drinking water was assessed at household level, water from bore-holes was found to contain less pathogens and considered safe drinking water, water drawn from either open wells or from rivers were found to contain more pathogens en were considered unsafe drinking water[17].

Ethical approval was given by the Ethical Review Committee of the Ghana Health Service, the Medical Ethical Committee of the Leiden University Medical Centre in Leiden, the Netherlands and by the local chiefs and elders of the research area.

Table 1. Study characteristics

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
Median number of inhabitants per compound (n)	15
Polygamous households (%)	48%
Mean value of household possessions in US$ (mean (SD))	1,063 (1,021)
Safe drinking water (%)	80%
Reproduction	
Numbers of newborns registered 2002-2010 (n)	3,645
Survival	
Follow up (calendar years)	2002-2010
Person years (n)	164,565
Mean follow up (years)	6.0
Deaths during followup (n)	1,344

Outline of this thesis

This chapter, **chapter one** provides a general introduction to the thesis.

Chapter two provides the theoretical background to the study, explaining the principles of life history theory. According to life history theory different physiological and behavioural characteristics of an organism's reproduction and survival are linked. Changes in one of the characteristics influences the other characteristics and only certain combinations lead to successful evolutionary strategies with high fitness. Post-reproductive lifespan is hypothesized to provide a selective advantage through investments in offspring that affect different life history characteristics; birth interval, total fertility, offspring growth and offspring survival among them. Life history theory is therefore important to understand the evolution of our longevity and the selective advantage of old age survival.

Chapter three provides a detailed description of the research area, the Garu Tempane district in the upper east region of Ghana. It provides the environmental, social and anthropological background of the area and the participants, most notably the Bimoba tribe to which most participants of this study belong. To come to an understanding and interpretation of the findings of the studies described in this thesis, this anthropological background is essential.

Chapter four describes the socioeconomic studies we undertook in the research area. Socio-economic status is a well known determinant of offspring survival and it was therefore important to measure it in the research area. Also, socioeconomic status could confound the relation of kin members and offspring survival. In richer households, children would have better survival but other kin members, e.g. post reproductive kin members, would also have better survival, creating the false impression that the presence of post-reproductive kin members improves offspring survival.

Life history theory predicts that maintenance trades off with fertility. In **chapter five** we test this prediction. We study the relation between offspring survival, reflecting the investments in maintenance, and the number of siblings, reflecting investments in fertility of the mother. We make use of the assumption of life history theory that these investment patterns are hereditary. By comparing co-wives in polygynous compounds we were able to maximally control for

differences in (micro) socioeconomic status. It is important to study the effect of the number of offspring on their survival in order to be able to study the effect that kin members have on offspring production and survival.

To elucidate the mechanism through which kin members and environmental factors influence offspring survival, we also studied the early growth patterns of the offspring in **chapter six**. The weights of offspring are not only determined by environmental determinants and in chapter six we also studied the genetic background of the weights of the children. We studied the CFTR gene, which causes cystic fibrosis in mutated form, the most common recessive genetic disease. It has been hypothesized that in our recent evolutionary past heterozygous carriers of CFTR mutations had a survival advantage. An understanding of the genetic component of the offspring weights is important to be able to asses the effect of kin members on offspring weight.

In **chapter seven** we describe our final analysis. Here, in a two sex model, we studied the selective advantage of old age survival for both males and females on survival and reproduction. We studied both the direct effect of continued reproduction and the indirect effect of the presence of elderly men and women on reproduction and child survival in the household.

In **chapter eight** we study the effects of the socioeconomic status on reproduction and survival in more detail. Socio-economic status can have large effects on these characteristics and these effects could be different in men and women. These differences are expected to be larger in a polygamous society. Since in this society it is custom that men pay a brideprice of four cows, rich men can afford to marry more wives and consequently it can be expected that they sire more offspring. For women, the effects of socioeconomic status on reproduction are expected to be less pronounced. We study these differences and the consequences for the reproductive prospects of sons and daughters in poor and rich households and investigate whether there are differences in the survival and nutritional status of sons and daughters in poor and rich compounds.

In **chapter nine** we discuss the grandmother hypothesis, which states that post-reproductive women improve the reproductive success of their children and the implications of this theory for the study of ageing. In this chapter we comment on

earlier studies and discuss the importance of environmental and anthropological determinants in the study of the grandmother effect. We also compare studies of the grandmother hypothesis in historical populations and studies in contemporary populations under adverse conditions.

In **chapter ten** we summarize the main conclusions and discuss the implications of the research described in this thesis. Also, we describe how evolution continues to shape our life histories, both for reproductive characteristics and (post reproductive) survival.

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