Post-reproductive survival in a polygamous society in rural Africa

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Chapter 10

General discussion

Discussion

In this thesis we studied post-reproductive survival from an evolutionary perspective. We tested the hypothesis that men and women after age 50 are able to contribute to their fitness either direct by continued reproduction or indirect through improving the reproductive success of subsequent generations. In a prospective full kin analysis in the Upper East Region in Ghana, we studied the effect of different kin members on offspring production, survival and early growth patterns in a polygamous population that lives in an environment that could reflect our recent evolutionary past.

Main conclusions

Chapter two describes a theoretical framework for the study. In this chapter we set out the principles of life history theory and apply this theory from the field of evolutionary biology to humans. Life history theory postulates that different physiological and behavioural characteristics of an organism's reproduction and survival are linked. There is growing evidence that a trade-off between maintenance and longevity is equally applicable to humans. We further hypothesized a mechanism that could underline this trade-off. Human survival has been strongly dependent on resistance to infectious diseases during our evolution. Resistance to infectious diseases is strongly dependent on an inflammatory host response. Pro-inflammatory signals, however, are negatively associated with fertility, since immunotolerance for the paternal antigens of the foetus is essential for normal pregnancy. In this way we hypothesize that the immune response could be the underlying mechanism for the trade-off between maintenance and fertility. We also note that humans are genetically still optimized for an environment with scarcity and infectious diseases and that our thriftiness and strong immune response evolved in an environment that has dramatically changed. In our new environment a predisposition for thriftiness could lead to obesitas and strong immune responses to many chronic diseases, most notably atherosclerosis. Life history theory and evolutionary theory can help us to better understand these epidemics of chronic diseases which are now starting to affect the rapidly changing developing countries to an even greater degree. These observations warrant a shift in focus of traditional healthcare in developing countries from mother- and childcare and acute medicine to the prevention and management of chronic diseases.

Chapter three provides a 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. This anthropological background is essential to interpret the findings of the studies described in this thesis.

In **chapter four** we studied the socioeconomic status of the participants, which was essential to study of the effect of different kin members on offspring survival, since socioeconomic status would confound the relation between kin members and offspring survival. In richer households, children would have better survival, but other kin members, e.g. grandmothers, would also have better survival, creating the impression that the presence of grandmothers improves offspring survival. Traditional socioeconomic assessments use a composite measure of education level, job status, income and savings. This could not be applied in this pre-transitional research area and we had to develop another method. We made use of an anthropological method of the 1970's: the rapid appraisal method, consisting of an interviewer- perceived wealth status and a self-perceived wealth status. We compared these methods to a more traditional measurement of socioeconomic status, the DHS wealth index, based on the possession of valuable items. We conclude that rapid appraisal can be used as a practical method to assess socioeconomic status in health studies in rural Africa. The rapid appraisals are correlated with the DHS wealth index but are more practical; it takes only a minute to rate the wealth status of a compound as average, below average or above average. The rapid appraisal methods also identify individuals at higher risk of mortality. Individuals that were ranked as below average wealth had a 30% higher mortality risk compared to average, while those that were ranked as above average wealth had a 20% reduction in mortality risk compared to average. One of the strengths of the rapid appraisal is that it could measure relative wealth, derived from the social status of the household members in the community. This position in family or clan structures is of utmost importance in the rural areas of developing countries and is not always reflected in their property. Therefore, the rapid appraisal method is not only more practical but could indeed be more accurate to identify individuals at risk. These findings could also be of benefit to health policy makers or non governmental organisations that need a quick and reliable method to identify individuals at risk of mortality.

In **chapter five** we studied the effect of the number of offspring on offspring survival. Before studying the effect of kin members on offspring survival, it is important to quantify this effect. A trade-off between the quantity and quality of offspring is a central paradigm in life history theory. In birds for example larger litter sizes are associated with lower survival. In chapter five we investigated this trade-off in humans. Several studies have investigated this trade-off in humans, but data are inconclusive, perhaps because prosperous sociocultural factors masked the trade-off. With our previous assessment of socioeconomic status, we were able to better study the trade-off. We found a 2.3% decrease in proportional survival of offspring with each increasing number of offspring. We also made use of the polygamous population structure and compared co-wives within one compound. In this way, we were able to maximally control for (micro) environmental differences. The tradeoff was still found even when the environment was the same, thereby providing additional arguments that genetic or biological mechanisms could be at the basis of the observed tradeoff. The effect remained significant after adjustment for socioeconomic status. The present data set from an adverse contemporary environment provided robust arguments for quantity to be traded off against quality in humans, a central paradigm in life history theory, an effect well known in different plant and animal species. Despite the ultimate explanation of the theory, the proximal explanation that accounts for this trade-off has yet to be fully unravelled.

Next to mortality, we also studied the nutritional status of the children by taking extensive biometrical measurements of the offspring, described in **chapter six**, through which we were able to detect smaller differences in nutritional status of the offspring as an intermediate phenotype. The weights of offspring however, are not only determined by environmental determinants and we investigated whether genetic variants also determined the weights of the children. We identified genetic variants in the CFTR gene, which causes cystic fibrosis in mutated form, that influence body composition in children and survival in the population at large. Using a sliding window technique we identified a haplotype which was depleted among people of old age (≥65 years) compared to young study participants (≤5 years). In addition, offspring carrying this haplotype had lower body weight and height compared to non-carriers. This shows that in an environment where the availability of food is critical, next to environmental factors, genetic variants influence body composition. This is in line with evolutionary theory, which

predicts that in environments that have strong selective pressures (e.g. with periodic food scarcity) genetic variants that provide small advantages can quickly spread in a population. A possible mechanism in which this genetic variation plays a role could be the ability to metabolise and store the scarce food supply, whose availability is highly dependent on the season, as additional analyses later showed.

In **chapter seven,** we describe our final analysis, combining all findings from previous chapters. Here we studied the selection advantage of survival past age 50 for men and women. In a full kin analysis, using a two-sex model, we assessed both the direct effect of continued reproduction in men and the indirect effect of the presence of older men and women on the reproduction and offspring survival in the household. We observed selection for longevity in men; of all 3,645 observed newborns, 18.4% were born of fathers aged 50 and above. We also observed selection for post-reproductive survival in women; the presence of women aged 50 and above increase the total number of offspring in the household with 2.7%. We also observed that the presence of older men suppressed the total number of newborns in households by 6.7%. Offspring survival up to reproductive age was not affected by the presence of either older women or older men. Our results suggest that human longevity evolved predominantly through a direct effect for longevity in older men, more than through the indirect effects of post-reproductive survival in older women, as earlier suggested.

In **chapter eight** we study the effects of socioeconomic status on survival and reproduction. 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 sire more children. For women, the effects of socioeconomic status on reproduction are less pronounced. We found that in rich households men had three times higher reproductive prospects compared to women. In poor households, the reproductive prospects of men was comparable to that of women. Evolutionary, rich households would therefore benefit more from male offspring. In line with this, we found that male to female survival probabilities were higher in rich compounds when compared to poor compounds. We also found that male offspring weights were higher in rich households while female offspring weights were higher in poor households. These observations could reflect a higher vulnerability of male offspring to adverse conditions. However, they are also in line with differences in parental investment as hypothesized by Trivers and Willard. Irrespective of the

underlying mechanism however, the differential survival of male and female offspring dependent on socioeconomic status maximizes reproductive success of the households in this polygamous society.

In **chapter nine** we comment on other studies on the effect of grandmothers on offspring survival. We conclude that the environment in which you study these effects is crucially important. Here we stress the difference between historical studies and contemporary studies in adverse environments. Many historical studies, often based on church records, are from monogamous Christian farming populations. It is possible that in these populations grandmothers have a larger influence, because there is only one mother to take care of all the children and household tasks, who would greatly benefit from an assisting grandmother. This environment does not reflect our recent evolutionary past since both y-chromosomal and anthropological studies indicate that we lived in polygynous, extended families. Also, in historical populations, 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. Also, we suggest that dependent on the environment, not only grandmothers but also other kin-members contribute to offspring survival.

Addition to previous research

We were able to study post-reproductive survival in an environment that resembles our evolutionary past more than studies in modern monogamous environments[1,2]. This is important when post-reproductive survival is an adaptive trait, the selective advantages can only be studied in an environment that resembles the environment where post-reproductive survival has evolved. We were also able to measure different environmental determinants, that would otherwise confound our results, most notably drinking source and socioeconomic status This was often not possible in previous studies which were mostly conducted in historical, Christian farming communities[3]. In this population we could therefore for the first time study both the direct selective advantage of old age survival in males through continued reproduction with younger females and the indirect effect of older women and men in the extended families of the research area.

In this study, we were able to confirm that post-reproductive survival in females indeed has a selective advantage. However, in this population, the advantage was not through increased survival of offspring as found by others, but through increased reproduction of their household. Also, we found that grandfathers, through continued reproduction up to high age created a large selective pressure for old age survival. This direct effect was much larger than the indirect effect of post-reproductive survival in women which points to a more important role of men in the evolution of longevity than previously thought. This also translates to a selection for post-reproductive survival in women since both sons and daughters of long-lived men inherited the genes that made possible their longevity.

Limitations

During our studies we noticed that the population was undergoing the demographic transition[4]. Observed mortality levels were lower than expected from the population distribution. This low mortality resulted in lower power to pick up determinants of child mortality. The demographic transition could also change the role different kin members have in offspring survival. Since the area was only at the start of the demographic transition we think the cultural patterns might not have changed dramatically, child mortality was over 5% and our analyses did show large effects on child mortality of both socioeconomic status, drinking source and the presence of the mother. Our large data set and long prospective follow-up allowed us to pick up these effects with considerable certainty and therefore the demographic transition did not inflate the outcomes of our study.

Our annual follow-up could have resulted in an underestimation of child mortality since we did not register children that were born and died between two field visits. Although this limited the power of the study, it did not create bias, since we have no reason to believe that the children that we did not register were a selected group.

Since there was no civil register in the research area, not all people were aware of their age. Also, since old age is highly regarded, participants could have been inclined to overestimate their age. If age was unknown, we estimated the age, as the average of several individual observations of both local and Dutch fieldworkers.

Although this study provided further insights in the evolution of our longevity, residual questions remain. The existence of menopause per se can not be explained from the effect of older men. It is possible that the age difference of co-wives within the polygamous household could play a role in this, but other socio-cultural factors could also play a role. If men preferably have children with their younger wives, there could never be a selective advantage to counteract wear and tear of the reproductive system, resulting in menopause. Although we have no formal anthropological observations, we have noticed that it is custom in the research area that men have less sexual intercourse with their older wives compared to their younger wives.

Another limitation to this study is that we have no data on the activities of elderly men and women which could give an indication of the mechanisms through which e.g. grandmothers increase the reproduction of the household. Previous research in the Hadza has shown that grandmothers make a large contribution to the household food supply[5]. Assistance in childcare however has been repeatedly observed in many different societies in anthropological studies[3]. Further studies of the investment patterns could give further insight in the possible role of different kin members in offspring production, survival and health in this population which would provide further arguments for the selective advantages of post-reproductive survival of both male and females.

This study was conducted in a polygamous society in rural Ghana. Therefore it is questionable to what extend these results could be extrapolated to other times, places and other cultures. In the last part of this discussion, we will discuss some key differences between our study population and others. These differences point out that there is no general pattern for the role that kin members have in child care and as such also invites to continued research of the role of kin members on reproduction and offspring survival in other societies.

Extrapolation of study results

How can the results of this study be extrapolated to other populations? The role of elderly people differs considerably in different societies. In this part, we discuss four major distinctions that could partly determine the role that elderly play in child care. First, we discuss patrilocal versus matrilocal societies, which determines whether maternal or paternal grandmothers live with the (grand)children.

Second, we consider the differences between polygamous and monogamous populations. Third, we discuss the differences between people living in nuclear families and in extended families and finally we consider the shift from pre-transitional societies to post-transitional societies. Here, we also discuss future implications of the results in this study.

Patriarchal versus matriarchal

The rural society in the research area is classic patriarchal, which means it is patrilocal, patrifocal and patrilinear. In patrilocal societies women move into the household of the men. In patrilinear societies inheritance is through the male line and in patrifocal societies the men is the head of the household and has authority over women and children. These differences could also determine which kinmembers are involved in child rearing. The most important consideration here is the patrilocality, since this determines to a large part which kin members assist in child rearing.

In patrilocal societies men continue to live in the house of their elders or in a house very close to this and women move into the household of the man after marriage. The result of this pattern is that in patrilocal societies the grandparents that live with the children are paternal grandparents. In matrilocal societies on the other hand, men move into the household of the women and almost all grandparents will be maternal grandmothers. Different studies have found that maternal grandparents and paternal grandparents have different effects on offspring survival[3]. A study of 19th century Krummhorn in Germany found that paternal grandmothers had a negative impact on child survival while maternal grandmothers had a positive effect on child survival[6].

Different mechanisms have been proposed to explain the different effects of maternal and paternal grandmothers. Since women in general have a larger role in child care than men, it has been proposed that grandmothers could be more inclined to assist their own daughters with child rearing in matrilocal societies than their daughters-in-law in patrilocal societies[7]. This could explain why maternal grandmothers in matrilocal societies would be more inclined to assist in child care than paternal grandmothers in patrilocal societies.

Because of the polygamous nature of the research population, reproduction is almost twice as high in men, as was shown in chapter seven. In this population, paternal grandmothers that live with their son, could therefore exert their influence on twice as many children compared to maternal grandmothers who live with their daughter. From an evolutionary perspective, it could therefore be more beneficial for a grandmother to live with their son, although the dilution of the resources that could be directed to the children should be taken into account. With twice the number of children, a quality quantity trade-off in the attention and resources that could be directed to the individual children could be expected.

Socio-biologists explain the higher tendency of maternal grandmothers to assist in child care with the principle of paternity uncertainty. Mothers are always more certain children are theirs while fathers can never be certain. A grandmother can therefore be certain that the children of her daughter and son-in-law carry her genes while the children of her son and daughter-in-law could be from her son, but she can not be completely certain.The extent and effect of paternity uncertainty has been highly debated. A review found that paternity uncertainty rates differed between 1% and 10% in populations worldwide[8].

It is important to note that in the research population, even when a large percentage of the offspring would be from other men, because of the much larger number of offspring of men, grandmothers could still exert their influence on a larger number of genocopies when they live with their son as paternal grandmothers compared to when they would live with their daughter. Second, in a separate analysis, we have cross-checked the DNA of the newborns with their fathers and found the number of false paternities in the research area to be below 5%.

Polygamous versus monogamous

In polygamous populations older men continue successful reproduction up to high age through the marriage of younger fertile women[9,10]. In monogamous societies, men are not able to continue reproduction when their wife is post-menopausal. Since in general men and women are of similar age, monogamy in practice also makes men post-reproductive around age 50.

Since, in polygamous societies, men that live to 80 have more offspring compared to men that live to 50 and this continued reproduction of elderly men results in a selection on longevity. Longevity has a known genetic component and since both sons and daughters inherit the genes that allowed the men to live long, this selection for longevity in men also results in long lived women. In monogamous populations this selective pressure is no longer present and as a result there is less selection on longevity in monogamous populations. Some older men continue reproduction in monogamous societies also, through the (re)marriage of younger women. However, the percentage of children born to men older than 50 years in the Netherlands in 2006 was only 1.0%, compared to 18.4% in the polygamous society in Ghana[11].

Nuclear versus extended family

In nuclear families, a man and woman live together with their children and, up to recent times, grandparents often co-resided or lived close to these families. In this situation, an extra pair of experienced hands from a grandmother or grandfather to assist in child care could be most welcome. The grandparents could be expected to plat a large role in child care in societies where people live in nuclear families. Previous research in Finland, Canada and other societies with nuclear families has shown that the presence of post-reproductive women here allows their children to reproduce earlier, more frequent and more successful[3,12].

In societies where people live in extended families, larger kin groups live together and in these households many different kin members, can assist in child care. It has been found that other kin members, older siblings, co-wives, aunts, also assist in child care in different populations[3]. In extended families the role of the grandparent is more easily substituted by other kin members when compared to nuclear families where they are the only other adults around are the grandparents. Whether people live in nuclear or extended families will therefore be of great importance to who will assist in child care.

Pre-transitional versus post-transitional

To understand how evolution shaped human life histories and our long post-reproductive life span in particular, it is essential to study this in the environment where this long reproductive life span evolved. Only in this environment, with these population structures, it is possible to measure the selective advantage that

shaped our life history. Our life histories evolved in societies that were pre-transitional; societies that had not experienced the demographic transition and where reproduction and mortality were both high and death was largely due to infectious diseases

There are two reasons why the findings in pre-transitional societies are of interest to contemporary societies. First, life history traits that have evolved in the past still exert a large influence on many aspects of life. Even though the contemporary post-transitional societies look remarkably different from pre-transitional societies, gestation still takes nine months, litter size is in general limited to a single child and the fertile period for women is still from around 18 to 49 years. These life history traits, that evolved long ago are therefore still of key importance today. There is however, a second reason to compare our findings in the light of contemporary societies. Contemporary societies are not the end product of evolution, selection still takes place and has seen a large shift as to which (genetic) traits are selected in today's post-transitional societies. The traits that are selected for today will influence subsequent generations. Considering how these selective pressures have changed and what traits are selected for today is important if we want to consider what the results of this study could learn us about the future of our life histories.

In the transition from pre-transitional to post-transitional societies, first mortality reduced dramatically, largely due to a control of infectious diseases by preventive measures. Second, reproduction declined. Increased child survival reduced the need to give birth to many offspring and many other cultural factors reduced the number of desired children which was also made increasingly controllable through contraceptive methods.

Contraceptive methods made possible the restriction of the number of offspring, while fertility assisting techniques made possible the reproduction of less fertile couples. The result is that in contemporary post-transitional societies there is less variation in the number of offspring. Most couples will have two children and there is only limited variation in the number of offspring. Low fertile couples can have children with the aid of fertility assisting techniques and high fertile couples can limit the number of offspring through contraception. This is remarkably different from the situation in pre-transitional societies where a small group of

highly fertile women produced a large proportion of the next generation. More fertile people had more offspring in the past and the result was a high selection on fertility in pre-transitional societies that is no longer present in post-transitional societies. This selection could partly explain the increasing number of couples experiencing fertility problems, which is often only attributed to the higher age at which couples start reproducing.

Contraception made possible, not only the restriction of the number of offspring, but also the timing of reproduction. As a consequence women have children much later in post-transitional societies compared to pre-transitional societies. In the Netherlands, the mean age a mother delivers her first child was 29.4 years in 2009[13]. Since reproduction becomes increasingly difficult with advancing age, some women that postpone their reproduction, will not have the desired number of offspring. The result is that the next generations will become enriched with individuals capable of reproducing at higher ages since there is selection of those individuals that have the (genetic) capability of reproduction at higher ages, while those that were unable do not contribute genes to the gene pool of the next generation. This is partly counteracted by fertility assisting techniques, but this is only partly able to counteract this effect as many couples are still left without children or without the desired number of children. The result of this is that there is selection for late fertility, through which future generations could easier have children at later ages.

In many post-transitional societies women are engaged in professional work and the raising of children is shared with either professional child care or other family members. Grandparents in particular are increasingly involved in child care now that more women have entered the labor market. In the Netherlands it was found that child care support from grandparents increases the probability that the parents have additional children[14]. This strikingly mimics the findings in the Ghanaian population described in this study. This finding that in a post-transitional society, grandparents could also increase the reproductive success is interesting from two perspectives.

First, it could indicate that ancient, evolved behavioral patterns are still influencing the way we raise children today. Many physiological but also behavioral traits can still be related to traits that have evolved in history of our evolution. In this light

many research has focused on differences in male and female behavior and physiology that can be understood by the different roles they had in our evolutionary past. Everybody is aware that grandmothers spoil their grand children the world over. Few might however realize that –next to the fact that their grandmother is probably the nicest grandmother on earth- grandmothers could actually display this behavior because it has been selected for in the past. Grandmothers that felt spoiling grandchildren was something desirable, had more surviving grandchildren than those who did not and this grand offspring carried the 'spoil-your-grandchildren-gene' with them. Economical reasons might also partly underlie the common observation that grandmothers enhance the reproductive success of their families. By taking care of the children, grandmothers alleviate the mothers and allow them to take up other (paid) labor. The enhanced family income could also make it possible for the family to have more children.

Second, the finding that also in contemporary post-transitional societies grandmothers can increase the reproductive success has important implications for the future of our life histories. If grandparents that assist in child care have more grandchildren than those that do not assist in child care or are not able to assist, there is selection for those individuals that both live long and are stay healthy enough to assist in child care. Both these factors are partly genetically determined and will be enriched in the gene pool of the next generation. In the future, more and more people will therefore live longer lives and longer healthy lives, and in this way a spiral could start. Longer healthy lives would again make possible prolonged assistance in child care. If this would lead to more offspring, the next generation would again have more individuals with healthy long lives that can assist in child care, and this reasoning can go on for generation after generation *ad infinitum*.

The conclusion is that as long as people are both healthy and active, there will be selection for long healthy lives. The prerequisite is that elderly people continue to invest in their (grand)children.

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