Post-reproductive survival in a polygamous society in rural Africa

Bodegom, D. van

Chapter 5

Quality-quantity tradeoff of human offspring under adverse environmental conditions

J.J. Meij*, D. van Bodegom*, J.B. Ziem, J. Amankwa,
A.M. Polderman, T.B.L. Kirkwood, A.J.M. de Craen, B. J. Zwaan,
R.G.J. Westendorp

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* These authors contributed equally to this study

Abstract

A central paradigm in life history theory is the tradeoff between offspring number and quality. Several studies have investigated this tradeoff in humans, but data are inconclusive, perhaps because prosperous sociocultural factors mask the tradeoff. Therefore, we studied 2,461 offspring groups in an area under adverse conditions in Northern Ghana with high fertility and mortality rates. In a linear mixed model controlling for differences in age and tribe of the mother and socioeconomic status, each additional child in the offspring group resulted in a 2.3% (95%CI 1.9%-2.6%, $p<0.001$) lower proportional survival of the offspring. Furthermore, we made use of the polygamous population structure and compared offspring of co-wives in 388 households, thus controlling for variation in resources between compounds. Here, offspring survival decreased 2.8% (95%CI 2.3%-4.0%, $p<0.001$) for each increase in offspring number. We interpret these data as an apparent quality-quantity tradeoff in human offspring.

Introduction

Life history theory predicts that during evolution resource acquisition is maximized and that adaptation to the prevailing environmental conditions is realized by differential resource allocation. For any plant or animal species, reproduction is a costly process, and many resources are allocated to reproduction, at the expenses of other processes such as growth and maintenance.
For reproduction a further division of resources can be predicted; reproductive investment in quality and quantity of offspring. For different species or different populations of the same species, the precise balance between quality and quantity of offspring will depend on the selective forces operating, such as the shape of the reproductive effort curve, the presence of parent offspring conflicts and the availability of resources in the environment[1,2].

The tradeoff between quality and quantity of offspring is well known in plants, for example in seed number and size[3,4]. Also, both between and within animal species, a strong negative association between number and survival of offspring is found[5-7]. Most evidence of animal studies comes from birds. Here, increasing clutch size was found to be related to lower offspring survival[8], a finding also reproduced in experimental studies in diverse species[9-13] including non-human primates[14]. As early as Becker there has been an interest in the tradeoff in humans[15]. To date, the evidence for the tradeoff in humans, however, is inconclusive. The study of these biological principles in humans, besides being of general interest, can also lead us to better understand different health care issues[16].

Several studies have investigated the tradeoff between quality and quantity of offspring in both historical and contemporary human populations. These studies largely differ in their assessment of quality. From a biological or evolutionary point of view the best measurement of quality would be the number of surviving offspring that are capable of successful reproduction. In contemporary societies this is difficult to study because socio-cultural factors such as birth planning and high survival chances may mask the predicted tradeoff[17]. Some studies have therefore investigated cultural or sociological features such as school results, job success or socioeconomic status as a measure of quality[18.19]. Several of these studies find evidence for a quality-quantity tradeoff as defined above. Because survival can be difficult to assess, some have also chosen to measure the health of the offspring as a proxy for survival (probabilities) and found some evidence for the tradeoff[20,21]. Different historical studies have also assessed the tradeoff in humans, using survival as a measure of quality, and found contrasting results[14,22-25]. Historical studies always rely on written records which are only generated in societies with a certain level of civilization. It is possible that in these civilizations, the tradeoff is difficult to find, because resources are not scarce enough. Three studies, however, have investigated the tradeoff in present day pre-transitional, natural fertility populations under resource-poor conditions using the survival of offspring as a measurement of offspring quality. A small study among 167 women of the Dogon of Mali showed evidence for the tradeoff with decreasing offspring survival with an increasing number of offspring[26]. Several larger studies however, among 491 women of the !Kung of Botswana[27], among 324 women of the Ache of Paraguay[28] and among the Kipsigis in Kenya[9], found no evidence for the quality-quantity tradeoff. Instead they found that with an increasing number of offspring, the number of offspring that survive also increased. The absence in these studies of a clear quality-quantity tradeoff, however, could be explained by confounding by socioeconomic status, whereby women with higher status have larger families that also experience higher offspring survival because of better environmental conditions.

In this study we investigate the relation between the number of offspring and proportional offspring survival in a large cohort of 2,461 women of a rural community in northern Ghana, an environment we think resembles our recent evolutionary past. This allowed us to circumvent some of the problems encountered in other studies. First, because of the scarcity of resources in the research area, it is expected that the tradeoff is maximally apparent. Second, we also assessed the socioeconomic status, and were therefore able to control for this common confounding factor in our analysis. Third, the polygamous structure of the research population allowed us to compare 388 pairs of co-wives within their compound in a pair wise analysis, further controlling for differences in (micro) socioeconomic status.

Materials and methods

Research area

The study was conducted in the remote Garu-Tempane district in the Upper East region of Ghana, a densely populated agricultural area. In 2001, the research area was explored by the Department of Parasitology of the Leiden University Medical

Centre which set up a database for parasitological research[30]. In this database name, sex, estimated age, tribe, and location of the compound were registered. We started our study by using this database and added detailed demographic information about fertility and child mortality.

The Garu-Tempane district is inhabited by several tribes; mostly Bimoba (66%) and Kusasi (24%). Compared to the south of Ghana, the whole of the Upper East region, and especially the Garu-Tempane district, is underdeveloped. The estimated gross domestic product per capita is less than US$ 100 in this region, while the gross domestic product per capita for the whole of Ghana is US$ 2,700[31]. The region has a semi-Saharan climate with an average maximum temperature of 32 °C throughout the year with one annual rain season from June to August. The research area around the village of Garu measures approximately 375 km^2 with an estimated density of 66 inhabitants per km^2. Most of the people are farmers and the agricultural process is entirely done by manual labour. There are some schools in the area, but illiteracy among adults above 30 is estimated to be around 90%. Recently, some small health clinics have been set up in the area, but these are not fully in service yet. Vaccination of children was introduced in the early 1990s. In 2003, about 50% of the children under ten years had been vaccinated at least once for either measles, polio, or diphtheria.
As estimated from our annual surveys from 2003 to 2007, 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. All individuals live in extended family compounds. Each compound consists of a number of separate huts linked by a surrounding wall. The oldest man in the compound is head of the family (land lord) and takes care of up to four wives. Within the compound the individual women have their own hut, but activities such as farming and child care are a shared responsibility. Although food preparation and cleaning are private activities, food at the compound is shared during communal meals. All children share the same hut, and the custom of formula-feeding infants is absent.

In the study area, most women begin sexual activity around the age of sixteen, and most give birth before the age of twenty. 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.

Subjects and methods

All villages and compounds were mapped with the Global Positioning System in 2001 and 2002. Since there are no civil registries, all villages and compounds within the study area were registered and assigned a unique identification number. The name, sex, age, and tribe of each individual were registered. In total 24,801 individuals were registered in the original database, living in 2,350 compounds, including 4,016 women aged 25 years and over.

In 2003 we revisited all compounds in the research area. During these fieldvisits the database was updated and all women of 25 years and older who were present at their compound (n=2,479) were invited to participate in the present survey of which 2,461 women agreed to participate. As most women are illiterate, witnessed oral informed consent was obtained by a local translator. Nineteen women refused co-operation. Both the Ethical Review Committee of the Ghana Health Service and the Medical Ethical Committee of the Leiden University Medical Centre in Leiden, the Netherlands, approved this study.

Demographic characteristics

If the age of a woman was unknown, it was calculated as the average from three independent estimations by local and Dutch researchers in 2003. Data on the number and survival status of all births were retrieved in line with the Ghana Demographic and Health Surveys (DHS), an internationally representative household survey for monitoring and impact evaluation of indicators in the areas of population, health, and nutrition[32,33]. To obtain the most accurate information, we set up compound interviews under supervision of local co-workers, assisted by translators, in which all women who were present in the compound participated. During these interviews the women discussed with each other the number of offspring they had had, including the number of offspring who had died and the number of offspring who were still alive at the time of the interview. These interviews increased the accuracy of the information considerably, and we did not encounter any hesitation to openly discuss these matters. Based on the number of offspring and the number of offspring still alive, we calculated the proportional survival of the offspring for each mother as the number of surviving offspring divided by the total number of offspring.

Village interviews
To obtain information on reproductive strategies of women we set up a series of village interviews. Five groups of twenty women, all coming from different villages, were interviewed by two female co-workers. During these interviews information was obtained about the desired number of offspring, reproduction, spacing strategies, and the use of contraceptives.

Socio-economic study
In 2007 we designed a questionnaire to asses the socioeconomic status of the study participants using a free listing technique whereby we asked people from different villages of the research area, both male and female, in focus group discussions to list the household items of most value[34]. These self-listed property questionnaires are reported to be highly correlated to longer property questionnaires[35] The resulting list of valuable items was comparable to the Core Welfare Indications Questionnaire (CWIQ) from the World Bank or the DHS, adapted to our region[36,37]. The valuable items included mainly domestic livestock and different valuable household items such as motorbikes, bicycles, and iron roofing. The value of the different items was also discussed in focus group discussions and consensus was found on the value of all different items. The total value of the compound property was calculated by taking the sum of the number of the items possessed by the compound, multiplied by the value of these items.

Statistical analysis
Proportional survival for the different offspring groups was calculated using a linear regression model. To correct for possible confounding factors, we also performed multivariate linear regression analyses, adjusted for age of the mother, tribe of the mother and socioeconomic status. In the same way we also calculated the number of offspring alive for different numbers of offspring. Especially the correction for age is important because older women have not only more offspring but as offspring is of higher age they had more accumulated risk of dying. We also performed a restricted analysis of people of the Bimoba tribe only to further minimize the influence of tribe on the proportional survival, and a restricted

analysis to women above 45 years, who were considered 'post-menopausal'. We estimated the menopausal age in this area to be around 40 years.

We modelled our data using three different regression models. First we used a linear model described by the function $y(x)=a+bx$, secondly a quadratic model $y(x)=a+bx+cx^2$ and lastly a plateau model $y(x)=a+b*\arctan(cx)$.

We made use of the unique polygamous structure of the research population and compared offspring groups of co-wives in 388 households who share the same environmental conditions. To do this, we selected pairs of co-wives with the smallest difference in age from compounds with at least two co-wives with a maximum of ten years difference. The mean offspring survival in the smallest offspring group was calculated. We then used regression to calculate the difference in offspring survival dependent on the difference in number of offspring within the pair of co-wives. A pair-wise analysis was also applied using a linear mixed model, clustered on compound, in which we included all 2,443 women with at least one delivery, adjusted for age of the mother, tribe of the mother and socioeconomic status. All calculations were performed with SPSS version 14.0.

Results

We interviewed 2,461 women on their past fertility histories. Table 1 shows the demographic characteristics of these women. We found 18 (0.7%) women who reported to have had no offspring, whereas seven women (0.3%) reported having had fifteen offspring. Proportional offspring survival decreased with an increasing number of offspring, reducing from around 90% among offspring groups of less than four to around 50% among offspring groups of more than twelve. The distribution of the number of offspring in Bimoba women was similar to the distribution in the whole population suggesting that the maternal fertility pattern between tribes is not different. The mean number of offspring was 6.3 (SE 0.05) for all women and 7.7 (SE 0.07) for women aged 45 years and over. The socioeconomic status of the households of these women differed slightly, with a trend of decreasing socioeconomic status in the women with an increasing number of offspring. The number of offspring decreased with increasing wealth from 6.35 (SE 0.10) in the lowest wealth quintile to 5.98 (SE 0.10) in the highest wealth quintile (p for trend = 0.007). The proportional survival of offspring increased with increasing wealth from 0.74 (SE 0.01) in the lowest quintile to 0.78 (SE 0.01) in the highest quintile (p for trend = 0.009).

Table 1. Demographic and fertility characteristics of the 2,461 women included in the study

Number of offspring	Number of women (n)	Proportional survival (SE)	Mean age (St. dev.)	Percentage of postmeno-pausal women	Percentage of Bimoba women	SES in US$ (St. dev.)
0	18	-	41.8 (14)	44.4	70.6	1,898 (1,753)
1	56	0.95 (0.03)	28.3 (9)	7.1	60.7	2,027 (1,703)
2	120	0.92 (0.02)	30.0 (10)	8.3	62.5	1,917 (1,219)
3	196	0.87 (0.02)	31.0 (10)	9.2	65.1	1,982 (1,757)
4	220	0.86 (0.01)	35.0 (12)	17.3	61.4	1,629 (1,450)
5	344	0.83 (0.01)	40.4 (14)	30.5	64.2	1,590 (1,374)
6	362	0.81 (0.01)	43.0 (13)	40.5	65.8	1,622 (1,379)
7	387	0.74 (0.01)	48.5 (14)	58.1	65.4	1,747 (1,460)
8	253	0.69 (0.01)	48.7 (14)	58.5	70.8	1,762 (1,537)
9	238	0.65 (0.01)	53.4 (14)	75.2	69.7	1,803 (1,631)
10	165	0.59 (0.02)	54.6 (12)	81.2	73.2	1,559 (1,258)
11	58	0.56 (0.03)	57.7 (12)	86.2	67.2	1,458 (1,643)
12	22	0.51 (0.04)	63.0 (16)	86.4	68.2	1,820 (1,214)
13	12	0.48 (0.06)	59.5 (17)	81.3	91.7	1,568 (553)
14	3	0.57 (0.12)	58.3 (16)	66.7	66.7	987 (399)
15	7	0.40 (0.08)	66.6 (19)	100	71.4	1,878 (1,520)

SES = socioeconomic status. An age of 45 years and over was considered post-menopausal.

The observation of declining proportional survival with an increasing number of offspring, however, has to be adjusted for various potentially confounding variables. Using multivariate regression we adjusted for these factors using several models. Table 2 shows the different analyses of the relationship between number and proportional survival of the offspring for the 2,443 women who had had at least one delivery. In the unadjusted analysis the proportional survival of offspring decreased 4.0% (95%CI 3.7%-4.3%, p<0.001) for each additional child. However, as among older women the number and the age of offspring will be higher, adjusting for age of the mother is critical to adjust for the different accumulated mortality risks of the offspring. Because different tribes could have different fertility patterns and different survival probabilities, an adjustment for tribe is also necessary. Finally, we adjusted for socioeconomic status, because wealthier families have both higher proportional survival, more wives per compound and less offspring per wife. To further minimize the effect of tribe and age, we also performed two restricted analyses. All models show that even after correcting for the various confounders, and when performing the restricted analyses, the association between the number of offspring and proportional survival persisted.

Table 2. Different analyses of the relation between number of offspring and proportional survival of offspring. Reported values are percentages with 95% confidence intervals

Model	n	Decrease in proportional survival for each increase in offspring number (95%CI)	p
1 Unadjusted	2,443	4.0% (3.7%-4.3%)	<0.001
2 Adjusted for age	2,443	2.4% (2.1%-2.8%)	<0.001
3 Adjusted for age, SES	2,443	2.3% (2.0%-2.7%)	<0.001
4 Adjusted for age, SES, tribe	2,443	2.3% (1.9%-2.6%)	<0.001
5 Model 3 restricted to the Bimoba tribe	1,623	2.5% (2.1%-2.9%)	<0.001
6 Model 4 restricted to post-menopausal	957	2.3% (1.6%-2.9%)	<0.001

SES = socioeconomic status. An age of 45 years and over was considered post-menopausal.

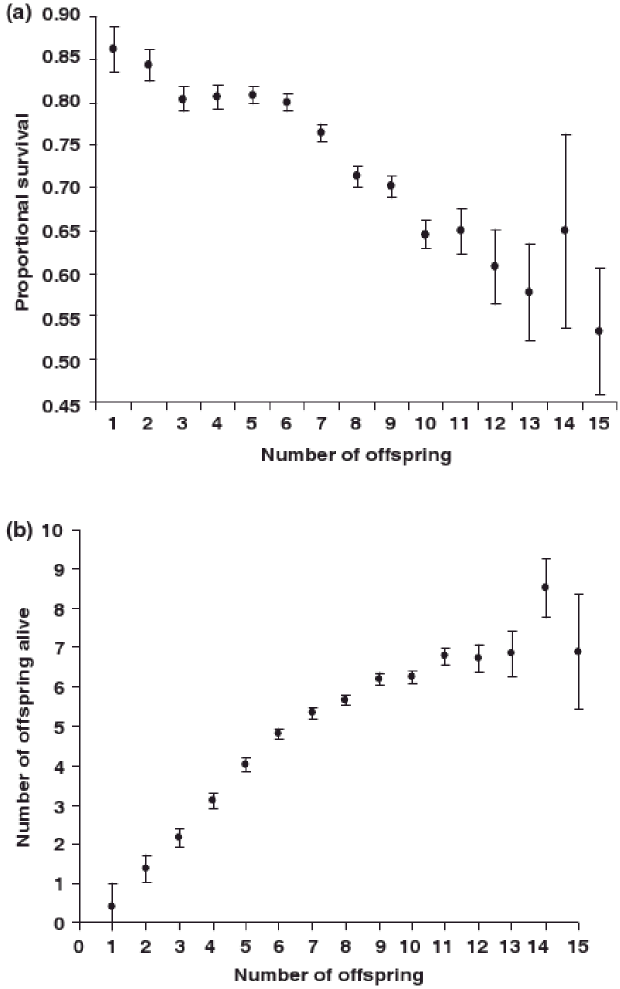

Figure 1. Relation between quality and quantity of offspring
(a) Proportional offspring survival dependent on the number of offspring. Data presented as means with standard error from linear regression models, adjusted for age of the mother, tribe of the mother and socioeconomic status. (b) Relation between number of offspring and number of offspring alive. Estimates from a linear regression model adjusted for age of the mother, tribe of the mother and socioeconomic status.

Using the regression models, we could plot the adjusted proportional survival for the groups with different numbers of offspring. Figure 1a is a graphical representation of the regression model adjusted for age of the mother, tribe of the mother and socioeconomic status. Here, each additional child resulted in a 2.3% (95%CI 1.9%-2.7%, $p<0.001$) lower proportional survival of the offspring.
Figure 1b shows the relation between the number of offspring and the number of offspring alive for all 2,461 women, as obtained from the same regression model. Going from lower offspring numbers to higher offspring numbers, the number of offspring alive reached a plateau around seven life offspring. These data show that with an increasing number of offspring the reproductive succes is maximized at about seven offspring alive.

When fitting the observed fertility patterns using regression, we found that a quadratic model ($r2=0.49$, $p<0.001$) described our data better than a linear model ($r2=0.44$, $p<0.001$). A quadratic model has often been used in animal species and assumes that at higher clutch sizes almost no offspring will survive. This may not apply to humans who increase the number of offspring with sequential births. Therefore, a plateau model was fitted and it was found that this described the data equally well as the quadratic model ($r2=0.49$, $p=<0.001$). The three different models are depicted in figure 2.

To further study the quality-quantity tradeoff we made use of the polygamous structure of the population. We compared different offspring groups from pairs of co-wives of the same compound or household, who share the same environmental conditions. A graphical representation of a compound is shown in figure 3a, the critical observation being that all children of various women within the compound share the same resources. All children are collectively raised, food at the compound is shared during communal meals and all children share the same hut. In this way we made use of an experiment by nature, studying two offspring groups with a different family background but sharing the same environment.

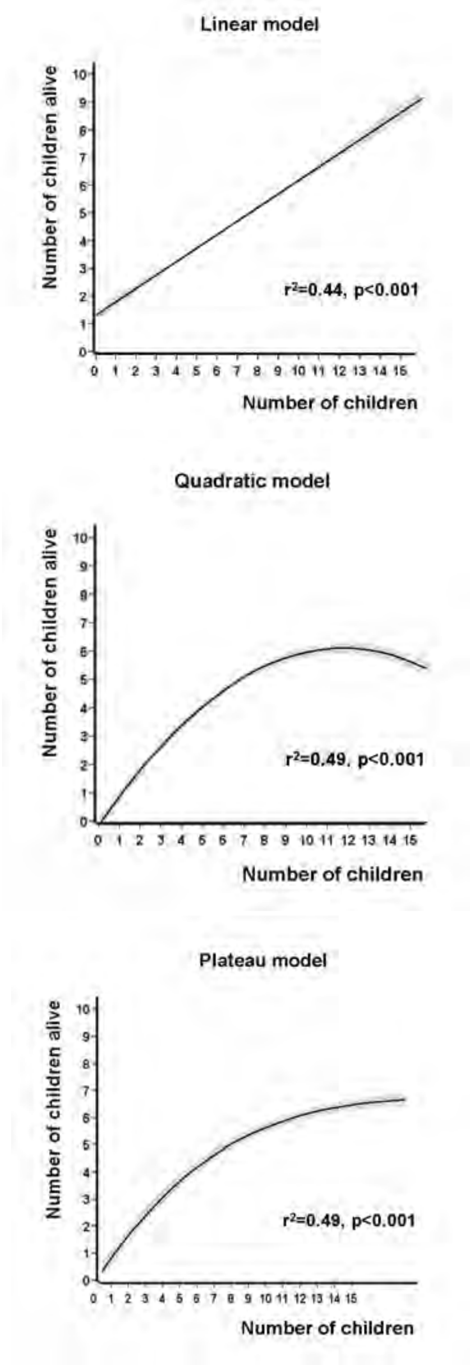

Figure 2. Different models of the relation between number of offspring and number of offspring alive. Grey area indicates 95% confidence interval.

Within compounds we have selected pairs of co-wives within an age band of ten years at a maximum; the mean difference in age between co-wives was 3.9 years (SE 0.11). Figure 3b shows the differences in offspring survival comparing the offspring groups of pairs of co-wives within one compound. The offspring group with the larger number is compared to the one with the smallest number, categorized as +1, +2, +3, etc. based on the number of extra offspring when compared to the offspring group with the smallest number. The figure shows that within pairs of co-wives of the same compound, proportional offspring survival is significantly lower among the larger offspring groups (p for trend <0.001).

The pair-wise analysis within compounds can also be employed in a linear mixed model including all women with at least one offspring. When adjusted for age of the mother and tribe of the mother and clustered on compound we calculated a 2.8% (95%CI 2.3%–4.0%, p<0.001) decrease in proportional offspring survival for each increase in offspring number.

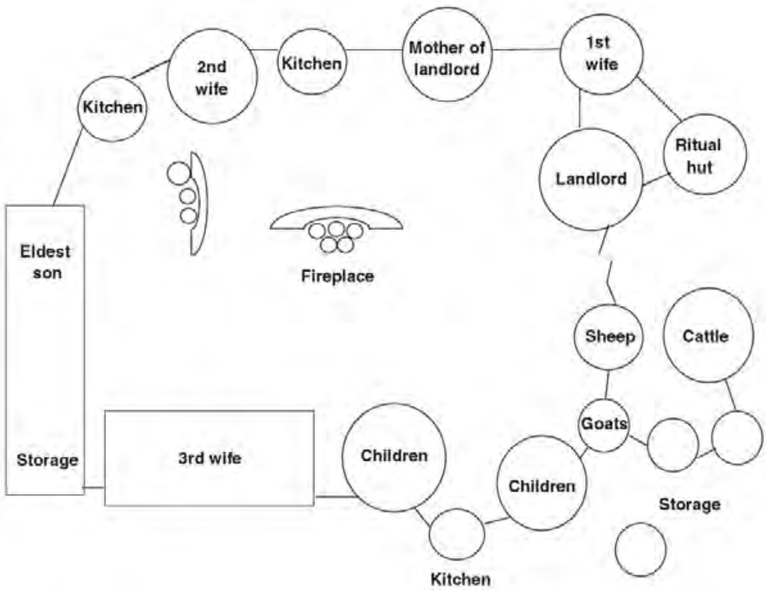

Figure 3. Pair-wise analysis of co-wives within one compound.
a) Typical example of a Bimoba Compound. The land lord and his three wives live in separate huts. First, second and third wife denote the order of marriage and not esteem or position. All women have their private kitchen but the food is shared. All children over four years of age live in the same hut, separated from their mother. Upon puberty children obtain their individual hut.

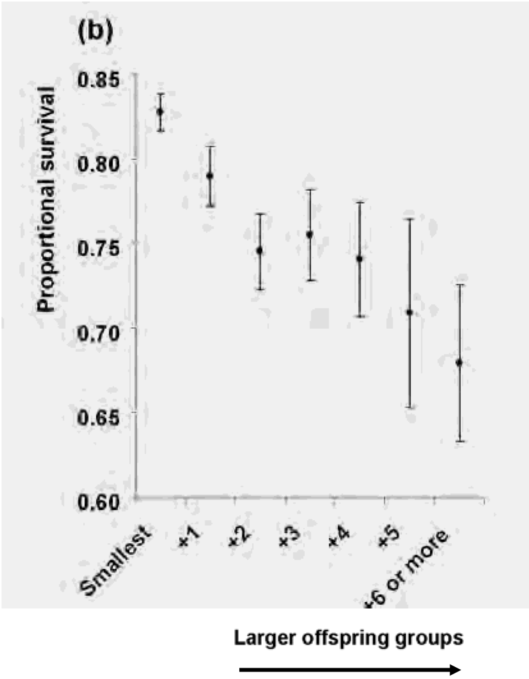

Figure 3. Pair-wise analysis of co-wives within one compound.
b) Offspring survival within polygamous compounds, comparing offspring groups of 388 pairs of co-wives within an ageband of ten years. Data present the difference in offspring survival (means with standard errors) among women with the largest offspring group when compared to the co-wife with the smallest number of offspring, categorized as +1, +2, +3 etc.

However, several alternative explanations for the outcomes of our study need to be considered. First, the observed association between the number and survival of offspring might better be explained by differences in social position within the compound. An observation of this kind was made among the Kipsigis in Kenya, where women with more inherited land had higher esteem and better offspring survival[29]. Also in our research area, larger families are regarded as a marker of esteem. As the wife with the highest social status would be expected not only to have more offspring but also to have better living conditions, it can thus be expected that their numerous offspring would have a higher proportional survival. We have observed the opposite: within large families survival of offspring was lowest. If anything, the observed survival cost would be an underestimation of the effect. It is therefore unlikely that our observed association is caused by differences in social status. Second, another possible confounding variable was identified when studying polygyny among the Dogon. Child mortality in polygynous households was higher than in monogamous households[38]. Since we still found evidence for the tradeoff when comparing pairs of co-wives, all living in polygynous compounds, it can not account for the observed association. Third, early mortality, especially neonatal mortality, is far less likely among breast-fed infants when compared to formula-fed infants[39,40]. As the habit of formula-feeding in our research area is virtually absent, this is unlikely to have influenced our results. Fourth, our results might have been biased because of vertical transmission of the HIV virus. In this reasoning, women with more offspring would have had more sexual contact and would have been more likely to have contracted the HIV virus. Vertical transmission to the child would have consequentially lowered offspring survival, creating the association between number of offspring and offspring survival. However, the sero-prevelance of HIV in the region of the research area is very low. According to the 2003 Ghana Demographic and Health Survey, the sero-prevalence of HIV among pregnant women in the whole region is 0.8% and among sexually active men it is 2.2%[33,40]. It is therefore unlikely that mother to child transmission of the HIV virus can explain for the present data. Finally, the higher proportional offspring survival among women who had a smaller number of offspring could be the result of survival-based family planning. This would be the case if a mother would become pregnant earlier when one of her offspring has died. While this is a phenomenon seen in other societies[40,41], we do not think that this explains the findings presented here. All interviewed women expressed the wish to have as many offspring as possible, independent of the individual survival of the offspring. Therefore, the effect of survival-based family planning is likely to be limited. In line with this reasoning, we found the number of offspring alive being maximized at around seven. Also, only 40% of the under fifteen mortality is between birth and the age of two, the estimated average breastfeeding time. Therefore, only in a minority of the deaths, the birth interval would be reduced by shortening the lactation period. However, when children die at a young age, duration of lactation can be reduced and birth intervals could be shorter which may partly account for our findings. We think, however, that the impact of this effect is small and cannot fully account for the relation we have found.

It is allways possible that external, unmeasured, determinants or factors also influence the observed relation between number of offspring and proportional survival of offspring. Parents might consider economic, social or cultural determinants, even unconsciously, in family planning matters[42]. Different life history tradeoffs could also be at play, for example the tradeoff between parental care and fecundity, as some studies in birds have also shown[43].

When we modelled our data using three different models, a quadratic model fitted our data better then a linear model. Such a quadratic relationship between offspring number and offspring alive is found in different animal studies, for example in birds, from which an optimum clutch size can be inferred. A plateau model however, fitted the data as well as the quadratic model and we would propose this model as an alternative model to describe the human situation. This model reflects the human fertility patterns since human children are not born simultaneously, but at average intervals of two to three years. Since children are at greatest survival risk in the first five years, additional newborns mainly influence the survival chances of their youngest sib. A quadratic model, in contrast, implies that at higher numbers of offspring, the additional offspring also diminish the survival chances of their older sibs. In the human situation, with sequential births, this seems unlikely. It appears that environmental constraints limit the number of offspring alive to a maximum of about seven. One could question why the observed mean number of offspring is lower than the optimum number of offspring as inferred from the models. We hypothesize that a higher number of offspring goes with a cost of reproduction to the mother. With the declining return with increasing numbers of offspring, the effort for the mother could be too great. The risk from child birth or the weakness from subsequent pregnancies could result in the death of the mother which would also put the younger children at risk. The best strategy could therefore be to limit the number of offspring to around seven, when the returns of increasing numbers of offspring diminish strongly and no longer outweigh the risks and costs of reproduction.

We further studied the tradeoff making use of the polygamous family structure of the research population. Hereby, we were able to compare offspring groups from co-wives of one compound who share exactly the same socioeconomic environment. Even when comparing these offspring groups, larger offspring groups had lower proportional survival than the smaller offspring groups of the same compound. Because the environmental conditions are the same for all offspring in the compound, an additive biological mechanism seems to be at play.

Different explanations are possible for this residual difference within one compound. A first possibility is that there is still a difference in the resources available to the offspring. In this reasoning the children from smaller offspring groups would still have better access to care and resources. We think that this could partly explain for the residual differences. However, we think that we have maximally controlled for the (micro) socioeconomic differences using the polygamous structure of this population and question whether the effect is large enough to account for the observed survival differences. A second explanation for the residual differences in proportional survival could be persisting differences not in the children but in the mothers. These persisting differences could be quality differences of the mother which are caused by a non-shared environmental determinant or by other life history characteristics. A second possibility is that next to environmental factors genetic factors also play a role in the tradeoff. These genetic factors could influence both the fertility of the mother, i.e. the offspring number and also offspring survival. Others have also found that certain women carry a fertile fenotype, independent of their health-status[44,45]. One could think of genetic factors that account for efficient food storage, which would not only give children a higher survival chance but also allow mothers to quickly rebuild resources after giving birth. This would allow them to have shorter birth intervals and therefore more children. Another possible genetic mechanism that could influence both the quality and the quantity of offspring is the innate immune system[46]. Accumulating evidence exists on the role of the innate immune system on both survival and fertility. As over thousands of years human survival has been highly dependent on resistance to infectious diseases, genetic adaptations resulting in inflammatory responses were favored. An inflammatory host response is critical to fight infection necessary to survive up to reproductive age. An inflammatory host response however, is also negatively associated with fertility because immunotolerance for the paternal antigens of the fetus is required for pregnancy to proceed successfully. It has been shown that sub-fertile women with concurrent abortions have higher pro-inflammatory markers[47]. One could hypothesize on the existence of an 'anti-inflammatory' and therefore vulnerable but fertile fenotype, and a 'pro-inflammatory' and therefore resistant but less fertile fenotype. Earlier we have provided evidence that specific inflammatory signaling cytokines associated with survival to infectious diseases[48,49] are negatively associated with[47,50,51]. Since the innate immune system is highly genetically determined, these characteristics would cross generations and could lead fertile – but vulnerable –

mothers to give birth to vulnerable – but fertile - offspring. These genetic mechanisms, however, are hypothetically only and are presented here as an alternative explanation to the environmental explanations of the residual differences within co-wives of one compound. The biological mechanisms behind the quality-quantity tradeoff have yet to be fully unraveled. Note also that life history tradeoffs are often presumed to be resource allocation tradeoffs, while hard empirical evidence that these tradeoffs are actually resource allocating tradeoffs is scarce.

One of the strengths of our study is that we studied the tradeoff under adverse conditions. This is reinforced as we based our inference on the fertility histories of the women, i.e. making use of data that reflect the environmental past of the last 80 years, which was even more adverse. Another strong point is that we were able to control for socioeconomic differences, which can easily mask the quality-quantity tradeoff as wealthier women could have both less offspring and higher proportional offspring survival. A stratified analysis of the tradeoff in different wealth categories showed that with increasing wealth the effect of the tradeoff reduces. This could explain why other studies did not show evidence for the tradeoff because they studied contemporary data, that are likely to originate from a less adverse environment. Finally, we could make use of the unique polygamous family structure in the area. Thus, we were able to compare offspring groups from co-wives from the same compound, who share the same socioeconomic environment, allowing us to maximally control for (micro) socioeconomic differences.

An important consideration is the observational nature of the study. In animal studies, more experimental methods have been used, sometimes giving strong arguments for the existence of a quality-quantity tradeoff. In humans, however, it is not possible to experimentally alter the number of offspring. In any observational study, there is always the problem of unmeasured factors. This should also be noted in this study. However, we tried in two ways to overcome this limitation. First we corrected for socioeconomic status, an important determinant of quality differences. Second we used the polygynous familystructure to compare co-wives of one compound and in this way matched women on as many unmeasured factors as posssible. With both different approaches we still found a negative relation between number of offspring and proportional survival. It is however always possible that other non-shared environmental or heritable factors influence the 'quality' of the mother.

Alltogether, our data show a strong negative association between number of offspring and survival of offspring in humans. This is in line with findings from studies in plants and animals. We interpret our data as consistent with a quality-quantity tradeoff in humans under adverse conditions. Despite the general validity of the theory, the biological mechanism that accounts for this tradeoff has yet to be unraveled.

Declarations

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Conflict of interest

We have no conflict of interest.

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