The cost of reproduction in the Gambia: does investment in reproduction decrease women's survival rates?

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Abstract

Life history theory predicts that where resources are limited, investment in reproduction will cause a decline in body condition and ultimately may lower survival rates. We investigate the relationship between reproduction and mortality in women in rural Gambia. We use a number of different measures of reproductive investment: the timing of reproduction, intensity of reproduction and cumulative reproductive investment (parity). Though giving birth is clearly a risk factor for increased mortality, we find limited evidence that the timing, intensity or cumulative effects of reproduction have a survival cost. Instead, there is some evidence that women who have invested heavily in reproduction have higher survival rates than women with lower reproductive investment. The one exception is that women who have given birth to twins (considered to be a marker of heavy investment in reproduction) have higher mortality rates than other women, after the age of 50 years. A potential confounding factor may be differences in health between women: particularly healthy or robust women may be able to invest substantially in both reproduction and their own survival, leading to the correlation we observe. To control for differences in health between women, we re-analyse the relationship between reproduction and mortality but include anthropometric variables in our models (for height, BMI and haemoglobin level). Even when controlling for health, the positive correlation between investment in reproduction and survival remains unchanged.

Introduction

Life history theory predicts that where resources are limited, investment in reproduction will cause a decline in body condition and ultimately may lower survival rates (Reznick 1985; Roff 1992; Stearns 1992). This is because energy allocated to reproduction cannot simultaneously be used for repair and maintenance of somatic (i.e. non-reproductive) tissues. Reproductive effort should therefore be negatively correlated with survival rates. It has been possible to demonstrate costs of reproduction using experimental manipulation of reproductive effort in non-human species. For example, some bird species show a decline in immune response if their brood size is artificially increased (Gustafsson 1994; Moreno *et al.* 1999). This suggests a proximate mechanism through which reproductive effort could lead to higher mortality rates, and a correlation between increased reproductive effort and higher mortality has also been observed among bird species (Daan *et al.* 1996). However, identifying these costs is problematic in observational studies (the only option when studying our own species), because of variation in resource levels between individuals (e.g. Wendeln and Becker 1999). Individuals with relatively high levels of resources may be able to invest relatively heavily in reproduction but still maintain good body condition, leading to a positive association between reproductive and survival.

Previous research on human populations on the relationship between reproductive effort and survival risks has given mixed results (the following discussion relates to women only: women are predicted to suffer greater costs of reproduction than men given their greater energetic investment in reproduction, and consequently there is a larger literature on costs of reproduction in women rather than men). A recent thorough review of the evidence for a relationship between number of births and mortality risk in post-reproductive women found inconsistent results (Hurt *et al.* 2006). There was some evidence that mortality decreased with increasing parity in natural fertility populations, suggesting that individual variation in resources may be leading to a positive correlation between reproduction and survival and masking potential costs of reproduction. In contrast, there were indications that in contemporary populations women with many children did suffer higher mortality rates. These findings are somewhat counter-intuitive given that the costs of reproduction are predicted to be more obvious in populations with limited resources, rather than well nourished contemporary populations. Overall, these authors concluded that the evidence for costs of reproduction was weak: there were few statistically significant results, and different methods of analysis resulted in inconsistent outcomes. A global analysis of the relationship between longevity and fertility, however, came to the opposite conclusion. Thomas et al (2000) conducted an analysis of 153 populations worldwide, and found the negative correlation between fertility and longevity predicted by life history theory.

Total fertility is one measure of reproductive effort, but several studies have investigated the impact of other components of reproduction on mortality risk. A number of studies have found that women who have a relatively late age at last birth tend to have lower mortality risks in later life than those who finish reproducing earlier (Doblhammer 2000; Muller *et al.* 2002; Smith *et al.* 2002; Grundy and Tomassini 2005; Helle *et al.* 2005). Again, this suggests that observational studies are more likely to find positive correlations between reproductive effort and survival, than any costs of reproduction. However, several studies have also shown that a late start to reproduction also leads to lower mortality in later life (Doblhammer 2000; Korpelainen 2000; Smith *et al.* 2002; Grundy and Tomassini 2005). This may indicate that a strategy of delayed reproduction leads to the lowest mortality risks. The proximate mechanisms by which these relationships are brought about are not yet clear, though the greater longevity of women with late births may reflect slow ageing among these women.

As well as the timing of reproduction, the intensity of reproduction may also be important. The intensity of reproductive effort is less well studied than either cumulative effort (parity) or scheduling of reproduction, but various authors have found that mortality rates are increased by short inter-birth intervals (Grundy and Tomassini 2005), giving birth to twins (Helle *et al.* 2004) and to sons (Helle *et al.* 2002). All three are thought to be indicators of particularly intensive reproduction. However, as with parity, the relationship between these alternative components of reproductive effort (both timing and intensity) and mortality is not always clearcut. It is always possible to find studies which observe no effects of these measures of reproductive investment on mortality risk: see, e.g., Helle (2005) for age at first birth, Mueller (2004) for age at last birth, and Menken et al (2003) for the pace of reproduction. Overall, therefore, there is some evidence for costs of reproduction in women, but this is by no means universal, and several studies observe positive correlations between reproductive investment and mortality rather than evidence that reproduction is detrimental to survival chances.

The aim of this study was to investigate the impact of all components of reproductive effort on women's mortality risk in a natural fertility population: intensity of reproduction, timing and cumulative reproductive investment. In addition, this analysis attempted to control for differences between women in access to resources, by including variables for anthropometric status in the models. The measures of anthropometric status used here (height, BMI and haemoglobin level) should correlate with women's resource availability. Relatively tall, well nourished women with high haemoglobin levels should be those with relatively plentiful access to resources, or women of high 'quality'. By including variables which correlate with individual 'quality', trade-offs between reproduction and survival may be revealed which would otherwise be masked by differences in resource access between women.

Data

The data were obtained from four villages in rural Gambia. The UK Medical Research Council has been funding research in this region of the Gambia since 1950. Research in this area was established by Ian A McGregor, who set up a demographic surveillance system in 1950, which continues to operate today (see McGregor 1991 for a full description of the study and study site). McGregor also systematically collected anthropometric data from these villagers, collecting data on height, weight and haemoglobin level from all villagers during anthropometric surveys which were conducted at least annually between 1950 and 1980. McGregor (a medical doctor) offered villagers medical treatment as necessary during his visits to the area, and in the early years of his study attempted village-wide treatments to eradicate certain parasitic infections. Overall, however, this population was without systematic access to medical care and contraception until 1975, when the MRC set up a permanent medical clinic in one of the villages, as part of a permanent research station which continues to operate in the village today. This clinic had a significant impact on the demography of these villages: child mortality dropped rapidly, and fertility has also declined, although at a slower rate than mortality (Lamb *et al.* 1984; Weaver and Beckerleg 1993; Sear 2001).

This analysis was confined to the period between 1950 and 1980, during the period when anthropometric data was collected systematically. Adult mortality patterns and fertility were slower to change than child mortality due to the influence of the clinic, so including 5 years of data after the clinic was established is unlikely to affect the results substantially. During most of this period, both fertility and child mortality were high: women gave birth to around 7 children on average, but more than 40% of these children died before the age of 5 years (Billewicz and McGregor 1981). The economy of these villages was largely based on subsistence agriculture. Women were responsible for a substantial proportion of the subsistence farming; men also contributed to this subsistence work and did a little cash-cropping of groundnuts. It was a very seasonal environment. Individuals tended to lose weight during the rainy season, when high workloads were combined with food scarcity and high disease loads, but gained weight again during the dry season (McGregor 1976). Adults were not well nourished by Western standards, but the majority of individuals had BMI measurements within the range that the WHO considers to indicate adequate nutritional status. Average BMI for adults of both sexes was approximately 20. More than 80% of women had an average BMI between 18.5 and 24.9 (considered to indicate adequate nutritional status); 13% of women were malnourished (BMI<18.5), but very few were overweight (only 4% had an average BMI of 25 or greater).

Methods

The aim of this research was to investigate the impact of reproductive investment on adult female mortality risk. Discrete-time event-history analysis was used to analyse the probability of an adult women dying over time. This technique has the dual advantages of being able to include both censored cases, and time-dependent variables, such as parity (Allison 1984; Singer and Willett 2003). The sample included all women who survived to at least age 15 by 1980. All births have been systematically recorded in these villages since 1950. Attempts were made to reconstruct birth histories for women who began their reproductive careers before 1950, but the fertility histories of older women are unlikely to be complete. The impact of reproductive investment may also differ in younger women, who are still experiencing reproductive events, and older women, whose physiological investment in reproduction has ended (though they are likely to be still caring for children and grandchildren). We therefore divided the sample into two groups: reproductive-aged women (defined as those aged between 15 and 49) and post-reproductive women (aged 50 and older). For the younger sample, we excluded any women born before 1920, in order to only include women with the most accurate birth histories. We also excluded childless women from both samples. In a strongly pro-natal society such as this, where all women marry and contraception is not used, childless women are likely to be those who are physiologically incapable of reproducing and therefore a rather unusual group of women.

Women were included in the analysis from the age of 15 (for the younger sample) or from age 50 (for the older sample) until they died, or were censored. All women with no recorded date of death were given a right-censoring date of either the last occasion they were reported to have been alive in the population, or in 1980 if they were known to have survived beyond 1980. Additionally, for the younger sample, women who were known to have survived until the age of 49 were censored at that age. All women who reached the age of 15 before 1950 were left-censored at the age they were in 1950. All models controlled for both village and birth cohort, as there were slight differences between villages and cohorts in mortality rates.

Reproductive-aged women

We ran two models of the effects of reproduction on the probability of dying for reproductive-aged women. The first model included all women who ultimately gave birth at least once during their reproductive lives. The two measures of reproductive investment we included in this model were: whether the woman gave birth in a particular year, and her parity. Both variables were coded as time-varying covariates. Parity was defined as the number of maternities a women had experienced (i.e. twins were counted as a single birth). Stillbirths were included in the number of maternities because, physiologically, a stillbirth is little different from a neonatal death. Dummy variables were used to indicate parity, in order to test for a non-linear relationship between parity and risk of dying.

The second model included only women who had had at least two births. This model included both reproductive variables used in the first model, and also measures of the timing and the intensity of a woman's reproductive investment. Age at first birth was included as a time-constant measure of reproductive timing. Three variables of intensity were included: whether a woman had ever given birth to twins, whether her previous birth had been a son, and the length of the interbirth interval between her two preceding births (this last variable necessitated restricting the second model to women who had had at least two births). All intensity variables were time-varying. Early first births, twins, sons and short interbirth interval are all assumed to indicate relatively heavy investment in reproduction. Table 1 shows descriptive statistics for the variables used in both models.

Post-reproductive women

Again, we ran two models of the probability of dying for post-reproductive women. The first included all parous women aged 50 and older, and tested whether a measure of cumulative reproductive investment (completed fertility) affected mortality risk. Because some of these older women do not have complete fertility histories, instead of using absolute family size we constructed a relative measure of family size. There are differences in the total number of births reported by women according to their birth cohort: older women report smaller completed family sizes than younger women (suggesting they have incomplete birth histories). We therefore calculated whether women had below average, average or above average completed fertility *for her birth cohort*, by dividing each 10-year birth cohort of women into three roughly equal groups according to their completed family size. Dummy variables for below average and above average parity were then included in the model.

The second model was restricted to those women who had had at least 2 births, and tested for the effects of timing and intensity of reproduction. For the timing of reproduction, relative measures of age at first and last birth were used, rather than absolute age at first and last birth. For each birth cohort, women were coded into three categories of age at first birth: younger than average age, average age and above average age at first birth. Age at last birth was similarly divided into three groups by birth cohort. Dummy variables for below and above average age at first birth, and for below and above average age at last birth were then included in the model. Three measures of reproductive intensity were included in the model: whether the woman had ever given birth to twins, the proportion of her children that were male, and her pace of reproduction. Pace of reproduction was calculated by dividing a women's reproductive span (the difference between her ages at first and last births) by her total number of maternities. This was then coded as a relative measure by dividing women into birth cohorts and assigning women a status of below average, average of above average pace of reproduction for her birth cohort. Table 2 shows descriptive statistics for the variables used in both models.

Controlling for 'quality'

As discussed in the Introduction, a number of studies have found it difficult to find convincing evidence for costs of reproduction, perhaps because women vary in 'quality'. If women who are high 'quality' are able to both produce many children, and maintain good body condition, then a positive, rather than the predicted negative, correlation may be seen between reproductive effort and mortality. To attempt to control for 'quality' between women, we ran each model in two versions. The first version included only the reproductive measures described above (with controls for village and birth cohort). The second included the reproductive measures and three anthropometric variables.

The measures of anthropometric status used were: height, BMI (weight/height^2) and haemoglobin level. Height is a measure of energetic availability during childhood. Relatively high energetic availability in childhood may also indicate relatively high availability during adulthood. Height has also been shown to correlate with some measures of fitness in this Gambian community, such as child mortality, suggesting it may be a measure of the 'quality' of a woman (Sear *et al.* 2004). BMI and haemoglobin level are short-term measures of energy availability. BMI should indicate available energetic reserves. Haemoglobin is affected by both nutritional status and disease load, so may be an indicator of the overall health of the woman.

BMI and haemoglobin were included in the models as time-varying covariates. Few individuals were surveyed in every year between 1950 and 1980, so a mean BMI or haemoglobin measurement was calculated for each individual for 5-year age blocks (for the ages 21-24, 25-29, 30-34 *etc*, up to the age groups 70-74, 75 and over), assuming the individual had more than one measurement in the 5-year age block. These mean BMI and haemoglobin measurements were then entered into the model as time-varying in 5-year age blocks. If no measurements were taken in a particular age block, the mean of the 2 measurements in the immediately younger and older age blocks was calculated and included in the model for the age block with missing data. BMI and haemoglobin measurements taken during pregnancy were excluded, as were measurements taken within three months after a birth for the haemoglobin analysis (haemoglobin declines during pregnancy and takes a few months after birth to return to pre-pregnancy levels).

Height is clearly less variable with age than either BMI or haemoglobin, though does show a decline in older adults. Height was therefore included as time-constant until the age of 49 years, and time-varying for older individuals. A mean height was calculated for each individual using all measurements collected between the ages of 15 and 49, and this measurement was included as the individual's height for ages under 50 years. From the age of 50 onwards, height was included as a time-varying covariate. These time-varying height measures were constructed using the same method as for BMI and haemoglobin.

Results

Reproductive-aged women

Table 3 shows the results of the first model for reproductive-aged women. For these women, giving birth is clearly a risk factor for increased mortality (women who give birth in a particular year have higher risks of dying than those who had not given birth in that year). Parity is also correlated with mortality risk, but we do not see the linear positive relationship that might be expected if costs of reproduction were in evidence. There is a broadly negative relationship between parity and mortality risk. Women of parity 1 or 2 have a significantly higher risk of dying than women of all higher parities. Inspection of the odds ratios suggests this negative relationship is reverse J-shaped rather than strictly linear. Figure 1 shows the odds of dying for women of various parities. This figure suggests the risks of dying decrease from parity 1 to 2 up to parity 7 to 8 but then increase for women of very high parity (9 and above). Controlling for health variables appears to make little difference to this relationship between parity and risk of dying (Table 3). Figure 1 also shows the odds ratios calculated from the same model but including variables for height, BMI and haemoglobin. This figure shows there may be some slight attenuation of the effects of parity when health is controlled for (as the odds ratios are slightly closer to 1), but this effect is very slight: the relationship between risk of death and parity is very similar whether health is controlled for or not.

Table 4 shows the results of the second EHA model for reproductive-aged women, including only women of party 2 and higher. Again, we see that giving birth is a risk factor for dying, and that there is a reverse J-shaped relationship between parity and the risk of death. However, no other measure of reproductive investment appears to affect mortality rate: there is no correlation between age at first birth and the probability of dying, nor are mortality risks affected by whether the women had recently given birth to twins, to a son, or had had a short interbirth interval between her two preceding births. Again, controlling for health makes little difference to the results.

Post-reproductive women

For post-reproductive women, the evidence for any costs of reproduction is similarly inconclusive. In the first model, including all parous women over the age of 50, there is little evidence that completed family size (relative to birth cohort) has any effect on the risks of dying (Table 5). Including anthropometric variables in the model makes no difference to the results: the odds ratios are virtually identical when health is included in the model. In the second model, including post-reproductive women who had had at least two births, two reproductive variables appear to be significantly related to mortality risk (Table 6). Women who gave birth at a relatively late age have lower mortality risks than those who stopped reproducing earlier, again suggesting a negative relationship between reproductive investment and the risk of mortality.

However, mothers of twins did have significantly higher mortality risks than women who had only given birth to singletons. Once more, controlling for health made no difference to the results.

Discussion

This analysis has shown that while giving birth is clearly a risk factor for mortality, there is little evidence that reproduction is costly in the long-term in this population. For reproductive-aged women the association between parity and mortality risk is actually negative, with women of higher parity having lower mortality risks than those of lower parity. Women of very high parity may suffer slightly higher mortality risks than those of medium parity, but this effect is small. The only reproductive variable to correlate with mortality in post-reproductive women is age at last birth: women with later last births have lower mortality risks after the age of 50 than those with earlier last births. This finding has been replicated in several other studies. It may be that this correlation results from the correlation of reproductive senescence and somatic senescence (women who can achieve late last births are those who age slowly and are therefore relatively long-lived).

The only women who appear to suffer costs of reproduction, in terms of higher mortality rates, are mothers of twins. After the age of 50, women who have given birth to twins have significantly higher mortality rates than those who have only given birth to singletons. We have previously shown that twin mothers in this population are particularly heavy investors in reproduction (Sear *et al.* 2001). Not only is a twin birth energetically costly in itself, but twin mothers also have shorter birth-intervals and a larger total number of births than mothers of singletons. Twin mothers on average had 10 maternities in this population (counting a twin birth as a single maternity); singleton mothers only around 7. This analysis suggests these mothers are paying the price for heavy reproductive effort in terms of higher mortality risk during their post-reproductive period. Similar results have also been found in historical Finland and contemporary Britain (Helle *et al.* 2004; Grundy and Tomassini 2005). In Finland, the higher mortality of twin mothers appeared to be due to a higher probability of dying from infectious disease. This suggests that the costs of reproduction are mediated by an impairment in immune function, as has been observed for several bird species.

But twin mothers are scarce in this population. For the majority of Gambian women, reproduction appears to have relatively few long-term costs. However, reproduction clearly has short-term costs in the higher risk of death in the year that a woman gives birth i.e. maternal mortality. Maternal mortality is not widely discussed in the life history literature on costs of reproduction, perhaps because it is rather lower in non-human species than in humans. The two human characteristics of bipedal location and large brains combine to cause human females particular problems during childbirth. The narrow pelvis required for bipedal location means that the birth canal is rather a tight fit for a large-brained baby, resulting in relatively difficult labours (Rosenberg 1992). In terms of the probability of dying per birth, a maternal death is relatively rare even in our species. Using data from the Gambia in the 1980s, Graham et al (1989) estimated the probability of dying in childbirth to be around 1% per birth. In high fertility populations the lifetime risk of maternal mortality is, of course, much higher. In the 1980s Gambia study, the lifetime risk of dying in childbirth was estimated to be 1 in 17. In relative terms, maternal mortality does cause a high proportion of deaths to reproductive-aged women. In certain populations up to a half of all deaths to reproductive-aged women may be caused by pregnancy and childbirth (AbouZahr and Wardlaw 2003). This significant risk of maternal mortality is a very real cost of reproduction.

Finally, the results of the analyses presented here were virtually identical whether or not measures of anthropometric status were included in the models. This suggests that the negative relationship between reproduction and mortality is not mediated by the measures of health included in the model. This is somewhat surprising given that BMI is thought to be a good indicator of nutritional status, and should correlate with the energetic reserves available for both reproduction and somatic maintenance. Haemoglobin should also be a good indicator of the health of the women, given that it is affected by disease load. It may be that costs of reproduction are most obvious under conditions of more extreme resource stress (Tracer 1991). These women are mostly within the range of nutritional status considered to be adequate by international standards. They may therefore be able to devote energy to reproduction without sacrificing their own body condition too much. Women do appear to have a number of adaptations which allow them to optimally manage the allocation of energy between reproduction and survival. There is a negative correlation between BMI and length of interbirth intervals in this population, for example, suggesting that women only attempt a reproductive bout when they are in sufficiently good condition to bear the costs (Sear *et al.* 2003). This careful allocation of energetic reserves, together with adequate food resources in this population, may mean that any long-term costs of reproduction are not sufficiently severe enough to show up as increased mortality rates. Alternatively, it may be that the measures of anthropometric status used are not good proxies of individual 'quality'. There may be other factors which underlie the positive correlation between reproductive investment and adult survival chances.

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References

AbouZahr, C. and Wardlaw, T. (2003) Maternal Mortality in 2000: Estimates Developed by the WHO, UNICEF and UNFPA. Geneva, World Health Organisation.

Allison, P. D. (1984) Event History Analysis: regression for longitudinal event data. Newbury Park, Sage Publications.

Billewicz, W. Z. and McGregor, I. A. (1981) The demography of two West African (Gambian) villages, 1951-75. *Journal of Biosocial Science* **13:** 219-240.

Daan, S., Deerenberg, C. and Dijkstra, C. (1996) Increased daily work precipitates natural death in the kestrel. *Journal of Animal Ecology* **65** (5)**:** 539-544.

Doblhammer, G. (2000) Reproductive history and mortality later in life: A comparative study of England and Wales and Austria. *Population Studies-a Journal of Demography* **54** (2)**:** 169-176.

Graham, W., Brass, W. and Snow, R. W. (1989) Estimating maternal mortality: the sisterhood method. *Studies in Family Planning* **20:** 125-135.

Grundy, E. and Tomassini, C. (2005) Fertility history and health in later life: a record linkage study in England and Wales. *Social Science & Medicine* **61** (1)**:** 217-228.

Gustafsson, L. (1994) Infectious disease, reproductive effort and the cost of reproduction in birds. *Philosphical Transactions of the Royal Society London Series B* **346:** 323-331.

Helle, S., Lummaa, V. and Jokela, J. (2002) Sons reduced maternal longevity in preindustrial humans. *Science* **296** (5570)**:** 1085-1085.

Helle, S., Lummaa, V. and Jokela, J. (2004) Accelerated immunosenescence in preindustrial twin mothers. *Proceedings of the National Academy of Sciences of the United States of America* **101** (33)**:** 12391-12396.

Helle, S., Lummaa, V. and Jokela, J. (2005) Are reproductive and somatic senescence coupled in humans? Late, but not early, reproduction correlated with longevity in historical Sami women. *Proceedings of the Royal Society of London Series B-Biological Sciences* **272** (1558)**:** 29-37.

Hurt, L. S., Ronsmans, C. and Thomas, S. L. (2006) The effect of number of births on women's mortality: systematic review of the evidence for women who have completed their childbearing. *Population Studies* **60** (1)**:** 55-71.

Korpelainen, H. (2000) Fitness, reproduction and longevity among European aristocrats and rural Finnish families in the 1700s and 1800s. *Proceedings of the Royal Society, London, Series B, Biological Sciences* **267:** 1765-1770.

Lamb, W. H., Lamb, C. M. B., Foord, F. A. and Whitehead, R. G. (1984) Changes in maternal and child mortality rates in three isolated Gambian villages over ten years. *Lancet* **2 (8408):** 912-914.

McGregor, I. A. (1976) Health and communicable disease in a rural African environment. *Oikos* **27:** 180-192.

McGregor, I. A. (1991) Morbidity and mortality at Keneba, the Gambia, 1950-75. In: Disease and Mortality in Sub-Saharan Africa (eds. R. G. Feacham and D. T. Jamison). Oxford University Press for the World Bank, Oxford. pp. 306-324.

Menken, J., Duffy, L. and Kuhn, R. (2003) Childbearing and women's survival: New evidence from rural Bangladesh. *Population and Development Review* **29** (3)**:** 405-+.

Moreno, J., Sanz, J. J. and Arriero, E. (1999) Reproductive effort and T-lymphocyte cell-mediated immunocompetence in female pied flycatchers Ficedula

hypoleuca. *Proceedings of the Royal Society of London Series B-Biological Sciences* **266** (1424)**:** 1105-1109.
Mueller, U. (2004) Does late reproduction extend the life span? Findings from European royalty. *Population and Development Review* **30** (3)**:** 449-+.
Muller, H. G., Chiou, J. M., Carey, J. R. and Wang, J. L. (2002) Fertility and life span: Late children enhance female longevity. *Journals of Gerontology Series a-Biological Sciences and Medical Sciences* **57** (5)**:** B202-B206.
Reznick, D. (1985) Costs of reproduction: an evaluation of the empirical evidence. *Oikos* **44:** 257-267.
Roff, D. A. (1992) The Evolution of Life Histories. New York, Chapman and Hall.
Rosenberg, K. R. (1992) The evolution of modern human childbirth. *Yearbook of Physical Anthropology* **35:** 89-124.
Sear, R., Allal, N. and Mace, R. (2004) Height, marriage and reproductive success in Gambian women. *Research in Economic Anthropology* **23:** 203-224.
Sear, R., Mace, R. and McGregor, I. A. (2003) A life-history approach to fertility rates in rural Gambia: evidence for trade-offs or phenotypic correlations? In: The Biodemography of Human Reproduction and Fertility (eds. J. L. Rodgers and H. P. Kohler). Kluwer Academic Publishers, Boston. pp. 135-160.
Sear, R., Mace, R., Shanley, D. and McGregor, I. A. (2001) The fitness of twin mothers: evidence from rural Gambia. *Journal of Evolutionary Biology* **14:** 433-443.
Sear, R. S. (2001) *Evolutionary Demography of a Rural Gambian Population*. PhD thesis, University College London.
Singer, J. D. and Willett, J. B. (2003) Applied Longitudinal Data Analysis: Modeling Change and Event Occurrence. Oxford, Oxford University Press.
Smith, K. R., Mineau, G. P. and Bean, L. L. (2002) Fertility and post-reproductive longevity. *Social Biology* **49** (3-4)**:** 185-205.
Stearns, S. C. (1992) The Evolution of Life Histories. Oxford, Oxford University Press.
Thomas, F., Teriokhin, A. T., Renaud, F., De Meeus, T. and Guegan, J. F. (2000) Human longevity at the cost of reproductive success: evidence from global data. *Journal of Evolutionary Biology* **13** (3)**:** 409-414.
Tracer, D. P. (1991) Fertility-related changes in maternal body composition among the Au of Papua New Guinea. *American Journal of Physical Anthropology* **85:** 393-405.
Weaver, L. T. and Beckerleg, S. (1993) Is health sustainable? A village study in the Gambia. *Lancet* **341:** 1327-1330.
Wendeln, H. and Becker, P. H. (1999) Effects of parental quality and effort on the reproduction of common terns. *Journal of Animal Ecology* **68** (1)**:** 205-214.

Table 1: reproductive variables used in the models for reproductive-aged women (figures are percentage of cases)

	All women	Women of parity 2 or greater
Birth year:		
Yes	28	29
No	72	71
Parity:		
1-2	40	24
3-4	26	34
5-6	18	23
7-8	10	12
9+	6	7
Age at first birth:		
<18		31
19-20		30
21+		33
Missing		6
Woman has ever given birth to twins:		
Yes		4
No		96
Last birth was:		
Male		46
Female		48
Missing		6
Previous interbirth interval:		
<3 yrs		55
>3 yrs		35
Missing		10

Table 2: reproductive variables used in the models of post-reproductive women (figures are percentage of cases)

	All women	Women of parity 2 or greater
Completed fertility:		
Below average	34	
Average	35	
Above average	31	
Age at first birth:		
Younger than average		35
Average		37
Older than average		28
Age at last birth:		
Younger than average		22
Average		37
Older than average		40
Woman has ever given birth to twins:		
Yes		2
No		98
Proportion of sons:		
<0.5		40
0.5		19
>0.5		41
Pace of reproduction:		
Less than average		30
Average		32
Greater than average		38

Table 3: results of the event history analysis modelling the relationship between reproductive investment and mortality risk in parous reproductive-aged women[1]

Variable	Model I			Model II		
	Parameter estimate	SE	**Odds ratio**	Parameter estimate	SE	**Odds ratio**
Constant	-6.87	0.69*		7.52	3.63*	
Age	0.08	0.02**	**1.12**	0.08	0.02**	**1.09**
Birth year	0.97	0.24**	**2.61**	0.85	0.27**	**2.35**
Parity:						
1-2			**1.00**			**1.00**
3-4	-0.73	0.27**	**0.48**	-0.52	0.30	**0.59**
5-6	-1.25	0.35**	**0.29**	-0.92	0.37*	**0.40**
7-8	-1.88	0.51**	**0.15**	-1.60	0.53**	**0.20**
9+	-1.30	0.50*	**0.27**	-0.89	0.52	**0.41**
Height				-0.05	0.02*	**0.95**
BMI				-0.16	0.06**	**0.85**
Haemoglobin				-0.30	0.07**	**0.74**
Number of women	999			983		
Deaths	90			77		

* p<0.05, ** p<0.01

[1] All models control for village and birth cohort

Table 4: results of the event history analysis modelling the relationship between reproductive investment and mortality risk in reproductive-aged women of parity 2 or greater

Variable	Model I			Model II		
	Parameter estimate	SE	**Odds ratio**	Parameter estimate	SE	**Odds ratio**
Constant	-7.10	0.91**		1.51	4.20	
Age	0.08	0.02**	**1.08**	0.09	0.02**	**1.10**
Birth year	0.89	0.28**	**2.43**	0.94	0.30**	**2.57**
Parity:						
1-2			**1.00**			**1.00**
3-4	-0.72	0.31*	**0.49**	-0.49	0.35	**0.61**
5-6	-1.21	0.40**	**0.30**	-0.90	0.43*	**0.40**
7-8	-1.86	0.56**	**0.16**	-1.60	0.58**	**0.20**
9+	-1.32	0.57*	**0.27**	-0.98	0.60	**0.37**
Age at first birth:						
<18	-0.15	0.39	**0.86**	-0.20	0.41	**0.82**
18-19			**1.00**			**1.00**
21+	0.31	0.32	**1.36**	0.18	0.33	**1.17**
Twin birth	0.35	0.55	**1.43**	0.39	0.56	**1.45**
Male birth	0.03	0.25	**1.03**	0.11	0.27	**1.11**
Length of preceding IBI	-0.01	0.01	**0.99**	-0.01	0.01	**0.99**
Height				-0.02	0.02	**0.98**
BMI				-0.14	0.07*	**0.87**
Haemoglobin				-0.34	0.08**	**0.71**
Number of women	954			885		
Deaths	68			61		

* p<0.05, ** p<0.01

Table 5: results of the event history analysis modelling the relationship between reproductive investment and mortality risk in parous post-reproductive women

Variable	Model I			Model II		
	Parameter estimate	SE	**Odds ratio**	Parameter estimate	SE	**Odds ratio**
Constant	-8.29	0.83**		-1.23	3.64	
Age	0.07	0.01**	**1.08**	0.07	0.01**	**1.08**
Completed fertility:						
Below average	-0.28	0.27	**0.76**	-0.24	0.28	**0.78**
Average			**1.00**			**1.00**
Above average	-0.44	0.26	**0.65**	-0.45	0.27	**0.64**
Height				-0.02	0.02	**0.98**
BMI				-0.08	0.05	**0.92**
Haemoglobin				-0.23	0.09*	**0.79**
Number of women	317			310		
Deaths	93			87		

* p<0.05, ** p<0.01

Table 6: results of the event history analysis modelling the relationship between reproductive investment and mortality risk in post-reproductive women of parity 2 or greater

Variable	Model I			Model II		
	Parameter estimate	SE	**Odds ratio**	Parameter estimate	SE	**Odds ratio**
Constant	-8.67	0.93**		-0.93	4.45	
Age	0.07	0.01**	**1.08**	0.08	0.02**	**1.09**
Age at first birth:						
Below average	0.07	0.29	**1.08**	0.26	0.31	**1.30**
Average			**1.00**			**1.00**
Above average	0.11	0.32	**1.11**	0.22	0.33	**1.25**
Age at last birth:						
Below average	0.05	0.29	**1.05**	0.01	0.31	**1.02**
Average			**1.00**			**1.00**
Above average	-0.82	0.31**	**0.44**	-0.82	0.32**	**0.44**
Twin mother	2.26	0.67**	**9.61**	2.25	0.69**	**9.51**
Proportion male	-0.02	0.49	**0.98**	-0.01	0.52	**0.99**
Pace of reproduction						
Below average	0.30	0.31	**1.36**	0.45	0.35	**1.57**
Average			**1.00**			**1.00**
Above average	-0.10	0.31	**0.91**	0.06	0.34	**1.06**
Height				-0.02	0.02	**0.98**
BMI				-0.08	0.06	**0.92**
Haemoglobin				-0.35	0.10**	**0.70**
Number of women	275			269		
Deaths	78			73		

† p<0.1, * p<0.05, ** p<0.01

Figure 1: odds ratios for the probability of dying by parity, for reproductive-aged women (solid line shows results of model with only reproductive variables, dotted line the same model but including controls for anthropometric status)