

A life history approach to fertility rates in rural Gambia: evidence for trade-offs or phenotypic correlations?

by

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Abstract

Life history theory predicts that a trade-off will occur between investment in current and future reproduction. We test this hypothesis in a rural Gambian population by determining whether women who have invested heavily in reproduction in the past have lower reproductive rates in the present. We find the opposite: women of high parity for a given age have higher reproductive rates than those of lower parity. We also find no differences in fertility rate between women who began reproducing early and those who began reproducing later, nor does the sex of the child at the start of the birth interval affect subsequent fertility rate. These results suggest that phenotypic correlations are prevalent in this population. Women of high quality are able to reproduce at a high rate throughout their reproductive careers, women of low quality are only able to devote relatively little effort to reproduction throughout their lives. We have tried to control for this heterogeneity among women by including variables for phenotypic condition in our model. Condition was measured by adult height, weight and haemoglobin level. Weight (controlling for height) and haemoglobin were positively correlated with fertility rate, which reinforces the view that phenotypic correlations are prevalent. Even controlling for these variables, a positive correlation was still observed between investment in past and present reproduction. This suggests the heterogeneity between women that leads to these phenotypic correlations is not adequately captured by these measures of female body condition. In this population, some of this unexplained heterogeneity may be related to genetic variance in the ability to resist disease.

Introduction

The rate of giving birth is an important determinant of a woman's completed fertility and hence her Darwinian fitness. Life history theory has much to say about such an important determinant of fitness and much to add to the traditional 'proximate determinants of fertility' approach of classic demography (Bongaarts, Frank, & Lesthaeghe, 1984; Stover, 1998; Wood, 1994). The central tenet of life history theory is that all organisms have finite amounts of energy that they must allocate to somatic functions (growth, development and body maintenance) and reproduction (Roff, 1992; Stearns, 1992). All organisms therefore face trade-offs when allocating resources between these functions. As life history theory is a branch of evolutionary theory, life history theorists predict that these trade-offs will be resolved in a manner that maximises Darwinian fitness. Iteroparous organisms must make decisions about how to allocate reproductive effort between temporally spaced bouts of reproduction. The primary aim of this analysis is to determine whether a trade-off between effort expended on reproduction in the past and current reproductive effort can be detected among women in this population.

This trade-off is usually formulated as a conflict between investment in current and future reproduction. If females have high expectations of reproduction in the future, then it may pay them to invest relatively little in current bouts of reproduction in order to have some reserves left to reproduce later. Conversely, as the expectation of future reproduction recedes, investment in the current reproductive bout should increase, as there is little point in reserving energy for reproduction which may not take place. Induced abortion rates have been found to decrease with advancing maternal age in Western populations, which has been attributed to women making decisions about their fertility based on their expectation of future reproduction (Hill & Low, 1992; Lycett & Dunbar, 1999; Tullberg & Lummaa, 2001). In this analysis, we intend to investigate this trade-off between reproductive bouts by determining whether investment in past reproduction has an impact on present reproduction. If women have only finite resources to expend on reproduction over their lifetimes, then women who have expended considerable effort in the past should have fewer reserves left to use for reproductive purposes in the present.

Some research in both the demographic and evolutionary ecology literature has suggested the opposite. In some populations, women of high parity for a given age have been found to have

higher fertility than those of lower parity (Hill & Hurtado, 1996; Pennington & Harpending, 1993; Strassmann & Warner, 1998). Positive correlations have also been found between age at first reproduction and subsequent fecundity: women who begin reproducing early have higher fecundity throughout their reproductive lives than those who begin reproducing late (Borgerhoff Mulder, 1989; Hill & Hurtado, 1996; Komura, Miyake, Chen, Tanizawa, & Yoshikawa, 1992; Udry, 1979; Udry & Cliquet, 1982, but see Otor & Pandey, 1998). This may be an example of an expected life history trade-off being obscured by individuals' differential access to resources. Positive phenotypic correlations between two energetically expensive functions occur when individuals with plentiful resources at their disposal are able to devote sufficient resources to both functions so that a positive correlation is seen between the two traits, rather than the negative correlation expected from the theory of trade-offs. Women in good condition may both be able to start reproducing early and reproduce at a rapid rate throughout their fertile years, whereas women in poor condition must wait for longer until they are capable of producing their first live birth and reproduce at lower rates throughout their reproductive lifespans.

Clearly, differences in 'quality' between women may be reflected in body condition. Phenotypic correlations may be seen because some women are of higher anthropometric status than others. If anthropometric status is correlated with reproductive efficiency, then controlling for body condition in the analysis may reduce these phenotypic correlations. Evidence is steadily accumulating that anthropometric status does affect female fecundity and ultimately lower fertility. This has been demonstrated both by analysing how nutritional status affects levels of female reproductive hormones (Bentley, 1999; Ellison, 1994; Jasienska & Ellison, 1998), and by observing the effects of nutritional status on the length of post-partum amenorrhoea or birth intervals (Aguirre, Palloni, & Jones, 1998; Delgado, Martorell, & Klein, 1982; Huffman, Ford, Allen, & Streble, 1987; Popkin et al., 1993; Tracer, 1996). We use a longitudinal dataset from rural Gambia, that consists of both demographic and anthropometric data, to determine whether women who have previously expended considerable effort on reproduction have lower current fertility than women who have expended little reproductive effort in the past. We control for body condition, in an attempt to reduce the presence of phenotypic correlations, as well as a number of other factors which are known to affect female fertility rates.

Data

The data used in this analysis were collected by Ian McGregor between 1950 and 1974 from four villages in rural Gambia – Keneba, Manduar, Kanton Kunda and Jali. Demographic data have been collected continuously by literate village recorders in all villages since 1950. Between 1950 and 1980, McGregor returned to these villages at least once a year to conduct anthropometric surveys (McGregor, 1991). Information on height, weight and haemoglobin level was collected from all villagers during these surveys. McGregor went to considerable lengths to trace individuals seen in previous surveys, and collected data on demographic events that were known to have occurred to individuals temporarily absent from the villages. Though data was collected in this way until 1980, we have restricted our analysis to the period between 1950 and 1974. During 1974 the MRC Dunn Nutrition Unit (DNU) began research in this area and established a permanent medical clinic as part of their research station in Keneba. The constant availability of modern methods of medical care and contraception, as well as the economic opportunities opened up by the DNU, have affected the demography of these villages considerably (Lamb, Lamb, Foord, & Whitehead, 1984; Sear, 2001; Weaver & Beckerleg, 1993). Mortality underwent a sharp decline after the arrival of the DNU. Fertility rates have also declined, though more slowly. We have restricted our analysis to the period when these villages were a natural fertility and natural mortality population, in order to exclude any potential biases introduced by the availability of modern medicine.

Before the introduction of the DNU, both mortality and fertility rates were high (Billewicz & McGregor, 1981). Women averaged slightly more than 7 births during their reproductive careers, but 43% of these children died before they reached the age of 5 years. The majority ethnic group were the patrilineal Mandinka, but there was a minority of matrilineal Jola origin (Thompson, 1965). This was an agricultural society. Rice and millet were the most important staples, farmed largely by women. Other subsistence crops and groundnuts, some grown for sale, were the responsibility of men. The environment was extremely seasonal. The rainy season lasted between mid May and mid November and was the time of heaviest agricultural labour, when food was short and disease, particularly malaria, prevalent. This resulted in considerable seasonal fluctuations in weight for both adults and children (Billewicz & McGregor, 1982). Over the entire study period, adult women averaged a body mass index (BMI) of 20.7 kg/m², and adult men 20.4 kg/m².

Methods

This analysis modelled the probability of birth over time, thereby analysing the fertility of women in this population. Multilevel discrete-time event history analysis was used to analyse the probability of birth. Event history analysis is useful for analyses such as this as it allows the inclusion of censored data. All individuals in this dataset without a known date of death were given a censoring date. This was the date at which they were last seen alive: either the date of their last survey, the date of birth of their last born child or their date of permanent migration from the villages. As the demographic data collection has continued to the present day, many individuals were known to be alive after 1974 and, for the purposes of this analysis, were given a date of censoring of 1st January 1975. Discrete-time methods were used because time is measured here in months, which are relatively large units of time. This results in many ‘ties’ (events occurring in the same time interval), which continuous time methods find hard to deal with (Yamaguchi, 1991).

A multi-level approach is used because there is known to be considerable heterogeneity between women in fertility (Larsen & Vaupel, 1993; Wood, 1994). Many women in this dataset contribute more than one interval to the analysis. If the lengths of birth intervals of any one woman are correlated, then the assumption of independent observations made by standard regression analysis is violated. Multi-level models overcome this problem by the inclusion of a mother-specific random effect (Goldstein, 1995). These models take the form:

$$\log \left(\frac{h_{ij}}{1 - h_{ij}} \right) = \alpha_t + \beta \mathbf{x}_{ij} + u_j$$

where h_{ij} is the hazard of birth in time interval t after child i in family j ; α_t is a function of time; \mathbf{x}_t is a vector of covariates, which may be either time-constant or time-varying, with associated parameters β and u_j is the mother-level random effect which is assumed to follow a normal distribution with zero mean and variance σ_u^2 . MLwiN 1.01 software was used to run all models. A useful measure that may be used to evaluate the extent of family-level variation due to unobserved factors is the intra-family correlation. For the binary logit model, this may be defined as:

$$\rho = \frac{\sigma_u^2}{\sigma_u^2 + \frac{\pi^2}{3}}$$

where $\pi^2/3$ is the variance of a standard logistic distribution (Snijders & Bosker, 1999).

Only women who have had at least one birth were entered into the analysis, as the birth of a child is taken to be the starting point of the time interval during which women are at risk of giving birth. Both stillbirths and livebirths were included in the analysis. Fertility is usually defined by demographers as the production of livebirths, but biologically the maternal costs of giving birth to a full-term but dead child are likely to be similar to the costs associated with a child that is born alive but dies shortly after birth. Intervals between marriage and first birth were not included as few dates of marriage are available for this dataset. This also has the advantage of excluding women with primary sterility. Women of reproductive age rarely remained unmarried for long in this polygynous population, so we have included intervals where women were widowed or divorced (n=43 for intervals during which woman was widowed and n=39 for divorce). Though marital disruption did increase the length of birth intervals (by approximately 9 months in the case of both widowhood and divorce: Sear, Mace, & McGregor, in press), controlling for marital disruption did not affect the relationship between fertility and the variables considered in this analysis. All intervals which were opened by the birth of a singleton child between 1950 and 1974 for Keneba and Manduar, between 1960 and 1974 for Kanton Kunda and between 1957 and 1974 for Jali were included in the analysis (demographic data during the early years of the study period was known to be under-recorded for the latter two villages). Intervals which did not end in a birth were censored when the mother died or was lost to follow-up or after 6 years, as intervals longer than this may be affected by sterility or pathological sub-fecundity. In addition, any intervals still open on 1st January 1975 were censored at that date, to exclude any effects of the medical clinic on birth interval length. This resulted in a total of 2533 birth intervals from 765 women, of which 1780 were closed by a birth within 6 years and before 1975.

Variables considered in the analysis

This analysis modelled the probability of a birth occurring per unit time. The dataset was expanded into one month periods and the relationship between time since last birth and probability of giving birth was modelled using a quadratic function. Table 1 lists the variables

included in the model, together with sample sizes and mean birth interval lengths. These models make the assumption of proportional hazards, *i.e.* that the shape of the relationship between fertility and time since last birth is identical for all values of the covariate, though the curves may be shifted vertically relative to one another if there is a difference in fertility risks between values of the covariate (Singer & Willett, 1993). Interaction terms between each covariate and time since last birth were therefore also included in initial models, to check the assumption of proportional hazards. Non-significant interaction terms were removed from the final model. To avoid losing information because of missing data, a 'missing' dummy variable was constructed for each of the covariates that follow. These missing variables were included in initial models to control for any biases that may have been introduced by this missing data. Non-significant missing dummies were dropped from the final model.

Child death, maternal age, season and cohort of birth

These variables were included in the analysis because they are known to affect fertility rates. Survival status of the index child (the child at the start of the interval) is an important determinant of the length of birth intervals, because of the inhibitory effect of lactation on ovulation (Aguirre et al., 1998; Fink et al., 1992; Jain, Hermalin, & Sun, 1979; Lunn, 1992; Nath, Singh, Land, & Talukdar, 1993). Women breastfed their children exclusively for 4-6 months after birth in this society. Children were not fully weaned until at least 18 months and usually not until around the age of 2 years (Thompson, 1965). The survival status of the index child is likely, therefore, to have a large impact on the probability of becoming pregnant again. The survival status of the index child was entered as a time-varying covariate. A dummy variable indicating whether the child was stillborn was also included in initial models, to determine whether birth intervals after stillbirths were any different from those after livebirths where the child died very early in life. There was no additional effect of having a stillborn child so this variable was removed from the final model.

One of the strongest determinants of a woman's fertility is her age (Dew, Don, Hughes, Johnson, & Steigrad, 1998; O'Connor, Holman, & Wood, 1998; Wood & Weinstein, 1988). Fertility tends to show an inverse J-shape with age, rising from menarche to peak in the early 20s and then beginning to decline in the late 20s until menopause in the fifth decade of life

(see Figure 1). Terms for both maternal age and maternal age squared were included in the model to control for this non-linear relationship.

As subsistence agriculturalists, residents of these villages are sensitive to both seasonal and annual fluctuations in food availability, prevalence of endemic and epidemic disease *etc.* Seasonal variation in reproductive function has been reported for several populations, and may be particularly pronounced in agricultural communities, where there is marked seasonal variation in both food availability and workload (Bailey et al., 1992; Bantje, 1988; Panterbrick, Lotstein, & Ellison, 1993, but see Madrigal, 1993). Dummy variables for both season and cohort of birth were included to control for any effects these fluctuations might have on birth rate. Year of birth was grouped into 5-year periods and dummy variables entered for four of these five periods. Season was entered as a time-dependent variable, coded into early rainy (June-August), late rainy (September-November), early dry (December-February) and late dry (March-May) seasons.

Previous reproductive investment

Parity was included as a covariate because this analysis is concerned with potential trade-offs between past and current reproduction. Women with many children at a given age have already invested heavily in reproduction and may have fewer reserves to invest in reproduction in the present. Parity was measured as total number of children born including stillbirths. The woman's age at her first birth was also included as a measure of past reproductive effort. Women were usually married before puberty in this population, and began to have intercourse with their husbands at menarche (Thompson, 1965). Most of the variation in age at first birth should therefore be due to variation in physiological capacity to conceive, rather than variation in age at marriage. Both variables were included as continuous variables.

Sex of children

The sex of the child both at the start and the end of the interval has been shown to affect birth interval length. Though many reports find no differences in the length of birth intervals after boys and girls (Korpelainen, 2000; Strassmann & Warner, 1998; Zaldivar, Lizarralde, & Beckerman, 1991), it is not uncommon for boys to be followed (Blanchard & Bogaert, 1997; Larsen, Chung, & Das Gupta, 1998; Mace & Sear, 1997; Swenson & Thang, 1993) and

occasionally preceded (Low, 1991; Nath, Leonetti, & Steele, 2000) by longer intervals than girls. Male foetuses are larger than female, and male infants have higher energetic intakes than females while breastfeeding (Hoffmans, Obermann-de Boer, Florack, van Kampen-Donker, & Kromhout, 1988). Sons are therefore more energetically costly to raise than daughters, and women may take longer to recover from the birth of a son than a daughter. Some Gambian women consider that giving birth to a boy ‘cuts two muscles’ whereas giving birth to a girl cuts only one muscle because of the greater difficulty in expelling large male foetuses (Bledsoe, Banja, & Hill, 1998). The sex of the index child may therefore be considered an indication of previous reproductive investment if giving birth to sons is more costly than giving birth to daughters.

Variation in the length of birth intervals could also result from parental sex preferences. If parents value sons over daughters they may breastfeed them for longer periods or deliberately shorten post-partum abstinence after the birth of a girl in the hope of becoming pregnant again sooner with a male child. Not all parents prefer sons, however. Daughter preference has been documented in several African populations (Clark, Colson, Lee, & Scudder, 1995; Cronk, 2000; Pennington & Harpending, 1993), and birth intervals after daughters were observed to be longer than those after sons in a Hutterite population in north America (Margulis, Altmann, & Ober, 1993). Sex of the index child has been entered into the model as a dummy variable.

Maternal phenotypic condition

Three indicators of maternal phenotypic condition – height, weight and haemoglobin level – were included in the analysis. Height is a measure of the resources available to a women during childhood and adolescence. While weight (controlling for height) measures nutritional status, haemoglobin level may be a better indicator of overall body condition as it is sensitive to both nutritional and disease status (Kent, 1992). Women in these populations not only suffered periods of nutritional stress, compounded by heavy workloads, at certain times of year but also suffered high rates of disease. Many sexually transmitted diseases clearly have the capacity to reduce fertility by directly damaging the reproductive tract, but non-sexually transmitted diseases may also have an impact on both male and female fertility. Malaria is particularly prevalent in these villages and febrile illnesses such as malaria are known to reduce sperm counts in men and increase rates of spontaneous abortion and stillbirth in

women (Mascie-Taylor, 1992; McFalls & McFalls, 1984). Interactions between nutrition and disease may exacerbate the effects of both factors on fecundity: poorly nourished individuals tend to be at higher risk of disease, and disease may increase malnutrition by reducing appetite (Beisel, 1982). Measurements of maternal height, weight and haemoglobin level within the inter-birth interval were entered into the models. Measurements taken after the index birth and before any subsequent pregnancy were used, excluding measurements of haemoglobin within 3 months of the index birth (when women were still recovering from the index pregnancy). All maternal condition variables were included as continuous variables.

Three separate models were run on this dataset. Model 1 included all variables described above except for maternal anthropometric status variables, to determine the relationship between parity and current fertility without controlling for maternal body condition. We then ran two models which included variables for maternal body condition. Model 2 included maternal height and weight as measures of body condition, Model 3 included haemoglobin level. Separate models were run because in non-pregnant, reproductive aged women haemoglobin is correlated with both height and weight (Pearson's correlation coefficient for weight and haemoglobin=0.041, $p<0.01$; for height and haemoglobin 0.060, $p<0.01$).

Results

Figure 2 shows the probability of birth over time since last birth. Separate lines are plotted for women whose child died within the first six months of life (including stillbirths) and those whose child survived for at least 6 months. For those women who lost their children in early life, the probability of birth begins to rise rapidly after the 9 months required for full-term gestation and peaks just over a year after their previous birth. The second peak around 4 years after the index birth is based on a very small number of births and may be an artifact of small sample size. For women whose children survived for at least 6 months, the pattern is markedly different. Few of these women gave birth within 2 years of the index birth. The probability of birth begins to rise around the end of the second year and peaks around 3 years after the birth of the index child. There are also discernible secondary and tertiary peaks at 48 and 60 months for women with surviving children, which are unexpected. These peaks may be a problem with data quality. They might have resulted from the birth dates of a few

previously unrecorded 3 or 4 year old siblings being entered into the database with reference to the subsequent birth in whole year values.

Over all intervals the mean closed birth interval length was 31.59 months (32.06 and 19.29 months for live and stillbirths respectively). Tables 2, 3 and 4 show parameter estimates with standard errors from the multilevel analysis for each of the three models. Interaction terms are indicated in the tables by an asterisk *e.g.* death*month indicates the interaction term between death of the index child and time since last birth.

Child death, maternal age, season and birth cohort

The parameter estimates for all these variables were similar whether maternal condition variables were included in the model or not. As expected, the death of the index child had a highly significant effect on the subsequent probability of birth. There was also a highly significant interaction between child death and time, suggesting the effects of the death of the child were not constant over the whole time period. This is intuitively obvious, as women who lose their children soon after birth are likely to resume ovulating much sooner than women who are still lactating. The loss of the child after weaning will have a much smaller effect on the woman's fertility, as most women (with or without living children) will have resumed ovulating by this point. Both maternal age and maternal age squared had highly significant effects on the hazard of giving birth, confirming the non-linear relationship of maternal age and fertility.

There were significant differences in the probability of birth between seasons. Compared to the late dry season (odds ratio 1.00), births are less likely in both the early and late rainy seasons (odds ratios around 0.82 and 0.72 respectively). Births in the early rainy season correspond to conceptions in the late rainy season, when agricultural labour and lack of food reduced energetic balance and disease was prevalent. Births in the late rainy season correspond to conceptions in the early dry season. Energetic conditions improve during the early dry season, as this is when the harvest occurs, but the effects of disease and malnutrition during the late rainy season may linger into the early dry to affect conception rates (infant mortality rates were also highest in the late rainy and early dry seasons: Sear, 2001). Fertility rates appear to have been similar for all birth cohorts before 1970. Fertility rates for the 1970-

74 cohort were elevated, but all birth intervals were censored in 1975 and only the shortest completed birth intervals will be included in these fertility rates.

Previous reproductive investment

Parity had a significant, positive relationship with the probability of giving birth: women with many previous births had a higher probability of giving birth per unit time than women with few previous births. There was a statistically significant interaction with time, indicating that the effects of birth order were particularly pronounced during the earlier part of the time period under study (*i.e.* soon after the index birth). Higher order terms did not significantly improve the fit of the model, suggesting the relationship is linear. There was no relationship between the woman's age at first birth and her subsequent fertility rate. There was no evidence for a non-linear relationship between these two variables, as higher order terms were also not significant. These conclusions are identical whether maternal body condition was controlled for or not.

Sex of children

There was no difference in the probability of giving birth by sex of the index child. The length of closed birth intervals by the sex of the children opening and closing the interval was also compared. There were no significant differences in the lengths of the four different types of interval (boy-boy, boy-girl, girl-boy, girl-girl: $F=0.43$, $p>0.05$) though intervals bounded by two girls were marginally longer (32.3 months) than those which began and/or ended with a male birth (31.6 months).

Maternal phenotypic condition

Model 2 shows that there was a significant relationship between weight within the birth interval and probability of birth: heavier women (controlling for height) had a higher probability of birth per unit time than lighter women. This model suggests the relationship between maternal height and the probability of birth may have been similarly positive. The main effect of height was not significant, but there was a significant interaction between height and time. Though the parameter estimate for the main effect of height is negative, the positive interaction with time means that overall the effects of height on fertility are positive, and slightly more pronounced during the latter part of the period under study. Model 3

indicates that haemoglobin level was also highly significantly related to the probability of birth. Again, the relationship was positive: increasing haemoglobin level resulted in an increased probability of birth. For both weight and haemoglobin, these effects appear to have been rather small, but highly statistically significant.

Unobserved heterogeneity

The multilevel model estimates that there was significant variance at the level of the individual woman not accounted for by the variables included in the model. This effect is estimated to account for approximately 8% of the total variance in the probability of giving birth.

Discussion

This analysis has found no evidence for any life-history trade-off between previous and current reproductive investment in this Gambian population. On the contrary, women of high parity for a given age had higher fertility rates than those of lower parity. Higher fertility of women of high parity has also been observed in life history studies of other natural fertility populations: the Ache, hunter-gatherers in Paraguay (Hill & Hurtado, 1996), Herero pastoralists in southern Africa (Pennington & Harpending, 1993) and Dogon agriculturalists in West Africa (Strassmann & Warner, 1998). This is likely to be at least partly due to a selection bias: only women of high fertility reach high parities, less fertile women take a longer time to have a smaller number of births and are selected out of the high parity sample. We have attempted to control for unobserved differences between women in fertility by including a random variable which is allowed to vary between women. We might therefore predict that controlling for this unobserved heterogeneity should eliminate the positive relationship between parity and fertility rate. A similar analysis of the effects of parity on fertility in contemporary Sweden found that the positive relationship between parity and fertility that was observed in a single-level analysis disappeared when unobserved heterogeneity was statistically controlled for (Andersson, 1999). However, in this analysis we still find a positive relationship between parity and current fertility rate even when we control for unobserved heterogeneity. Two explanations are possible. Firstly, it should be noted that we are controlling for unobserved heterogeneity in a relatively crude way. We lump together all unobserved factors into one variable, and make certain assumptions about this variable.

The model assumes, for example, that this random variable is normally distributed. If these assumptions do not hold, then our model may not be adequately specified.

Secondly, our random variable only controls for those factors which affect current fertility. When we control for unobserved heterogeneity in this way, we do not necessarily control for the phenotypic correlations which act to both increase current fertility and increase parity, thus leading to a positive relationship between these two variables. Though high parity women are likely to be those of high fertility who have many births in quick succession, other factors may play a role in the attainment of high parity that are not correlated with fertility. Women may reach high parity, for example, if they have suffered a large number of infant deaths among their children. Our random variable includes all factors which affect current fertility only, not just those that are correlated with both parity and current fertility, and so we do not find that controlling for unobserved heterogeneity makes our positive relationship disappear. These results may differ from those of the Swedish study because the selection processes which result in a positive correlation between parity and current fertility are likely to be very different in an environment where advanced medical technology and contraception are widely available, compared to the rural Gambian population studied here. Social considerations (such as active preferences for large family size) are likely to play a more important role in the attainment of high parity in modern Sweden. Differences in biological fecundity, while they may still be present, are likely to be far less important in such a medically sophisticated environment.

We have also attempted to circumvent the problem of positive phenotypic correlations by including variables which are good candidates for those factors which both increase parity and increase current fertility rate: maternal anthropometric status. Women in good physical condition are likely to be able to reproduce rapidly, and have a larger number of births than women in poor condition. Introducing these variables into the model was therefore predicted to reduce or eliminate the positive relationship between parity and fertility. This relationship remains unchanged, however, when maternal condition variables are entered into the model. Though differences in physical condition clearly result in differential fertility between women, it seems that differences in anthropometric status cannot adequately explain why some women both reach high parity and reproduce rapidly at high parity.

We are left with two explanations for this positive relationship between previous and current investment in reproduction. Firstly, that there are factors which act to both increase parity and current fertility that are not included in our model and not covered by our control for unobserved heterogeneity between women in fertility. Currently, new statistical techniques are being developed which may help us to determine whether such variables are obscuring the trade-off between past and present reproduction. Future analysis of this dataset will use these multiprocess models to further investigate this trade-off. The second possibility is that women of high parity do have higher reproductive rates than women of low parity and that there is no life history trade-off between past and present reproduction in this society.

Although the random variable we have included in our multilevel model does not eliminate the positive relationship between parity and fertility, we do find significant heterogeneity between women in fertility that is not explained by the variables in our model. What causes this heterogeneity between women is unclear. This variance may be related to observable characteristics of women which we do not have data on. For example, we have no information on socio-economic status for individuals in this database. This may be an additional source of variation between women causing phenotypic correlations between previous and present reproductive effort. However, the effects of socio-economic status are likely to act mainly through their effects on anthropometric status, and we have controlled for this in our models. In this environment, where modern medical care is almost non-existent, this heterogeneity between women in fertility may well be due to differences in biological fecundity. Part of the explanation may lie in genetic differences between women in reproductive efficiency (*i.e.* successful ovulation, implantation and carrying the foetus to term). Previous research on this database suggest that mothers of twins have faster reproductive rates and higher completed fertility than women who have only given birth to singletons (Sear, Mace, Shanley, & McGregor, 2001). This higher fertility of twin mothers has been suggested to be due to higher levels of polyovulation among twin mothers, which increases the probability of a successful birth resulting from a single ovulatory cycle (Anderson, 1990). Dizygotic twinning is known to be heritable, though the environment may also play a role in determining whether a twin conception survives to term. This result suggests that genetic differences between women in certain aspects of their reproductive capabilities, of which being a twin mother may be one of the few observable signs, may be responsible for heterogeneity in fertility. Recent research on the heritability of fertility in

contemporary populations, using twin studies, has found evidence of genetic contributions to fertility (Kirk et al., 2001; Rodgers, Kohler, Kyvik, & Christensen, 2001).

Fisher's fundamental theorem of natural selection states that genetic variation in fertility should not exist in stable populations (Fisher, 1930). The significant relationship between maternal haemoglobin level and fertility may point to an explanation for why variation in fertility appears to be heritable. Haemoglobin is an indicator of the overall health of an individual, which includes not just nutritional status but also disease load (Kent, 1992). It is a measure known to be sensitive to malaria parasite load in the blood, for example (McGregor, Williams, Billewicz, & Thomson, 1966). The existence of pathogens and parasites means that stable environments are a rarity in the real world. Pathogens and their hosts are constantly engaged in an arms race: pathogens continually evolve new strategies to evade host defences, and hosts must develop new resistance strategies against their pathogens. If genetic differences in ability to resist disease confer reproductive benefits, then this provides a mechanism whereby variation in fertility may have a genetic basis. The relationship between disease resistance and fertility is an area relatively unexplored in the demographic literature, though medical science has been aware of the link between reproductive hormones and immune function for some time (Grossman, 1985; Pathak & Mathur, 1988). Interactions between immune function and reproduction have become an active area of research for biologists interested in life history theory (Lochmiller & Deerenberg, 2000; Møller, 1997; Norris & Evans, 2000; Sheldon & Verhulst, 1996). Evolutionary biologists working on nonhuman vertebrates have shown that reproductive effort correlates negatively with level of infectious disease, and that experimental manipulations which cause these animals to increase their reproductive effort have detrimental effects on their ability to resist disease (*e.g.* Gustafsson, 1994; Johnsen & Zuk, 1999; Moreno, Sanz, & Arriero, 1999; Saino, Calza, & Moller, 1997; Skarstein, Folstad, & Liljedal, 2001). This analysis suggests that investigation of the relationship between disease resistance and reproduction may also be a profitable line of enquiry in the human sciences.

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Table 1: sample sizes, percentage of closed intervals and mean length of birth intervals for all variables entered into models (all variables relate to status of index child)

Variable	Mean (SD)	N ¹	Percentage of intervals closed	Mean length of closed IBIs (months)
Index child:				
Died		827	81	26.88
Alive		1603	65	34.55
Censored		49	41	34.57
Season of birth:				
Early dry		662	69	31.78
Late dry		639	75	32.14
Early rainy		577	69	31.98
Late rainy		655	68	31.99
Year of birth:				
1950-54		221	80	34.35
1955-59		332	83	33.07
1960-64		529	84	32.33
1965-69		638	87	32.09
1970-74		813	40	30.58
Maternal age (years):				
< 20	26.75	456	75	31.21
20-29	(7.14)	1176	78	31.31
30-39		776	64	33.57
>40		112	22	33.55
Parity:				
1	3.70	481	77	32.11
2-3	(2.31)	878	72	32.02
4-6		839	71	31.95
7+		334	53	31.65
Maternal age at first birth (yrs):				
<17	18.62	431	71	30.73
17-19	(2.47)	968	70	31.57
>19		731	71	32.18
Sex of index child:				
Male		1267	71	31.73
Female		1251	69	32.29
Height (cm):				
135-154.95	157.57	684	70	33.37
154.96-159.38	(5.37)	737	71	33.65
159.39-178		715	70	33.06
Weight (kg):				
14-19.88	51.85	711	70	32.92
19.89-21.54	(6.40)	712	69	33.79
21.55-30		707	71	33.41
Haemoglobin (g/dl):				
3-10.95	11.52	707	71	34.38
10.96-12.35	(1.87)	677	72	33.43
12.36-17		753	68	32.39

¹ Sample sizes do not always add up to 2533 because of missing data

Table 2: parameter estimates and standard errors from Model 1 (excluding maternal anthropometrics)

Variable	Estimate	SE	Sig.
Constant	-14.7804	0.5210	<0.001
Month	0.4930	0.0191	<0.001
Month ²	-0.0055	0.0003	<0.001
Index child dead†	7.6218	0.3852	<0.001
Dead*month	-0.3423	0.0229	<0.001
Dead*month ²	0.0037	0.0003	<0.001
Season†:			
Early dry	-0.0503	0.0663	NS
Early rainy	-0.3297	0.0722	<0.001
Late rainy	-0.1957	0.0688	<0.001
Year of birth†:			
1950-54	-0.0780	0.1098	NS
1955-59	-0.0040	0.0867	NS
1965-69	0.0788	0.0733	NS
1970-74	0.3521	0.0885	<0.001
Maternal age	0.2079	0.0282	<0.001
Maternal age ²	-0.0053	0.0005	<0.001
Parity	0.2151	0.0374	<0.001
Parity*month	-0.0040	0.0010	<0.001
Mother's age at first birth	0.0028	0.0049	NS
Male child†	0.0868	0.0549	NS
Between woman variance	0.3002	0.0394	<0.001
Intra-class correlation	0.0836	-	-

†For categorical variables omitted category is reference category

Table 3: parameter estimates and standard errors from Model 2 (including maternal height and weight)

Variable	Estimate	SE	Sig.
Constant	-15.0312	1.2412	<0.001
Month	0.4681	0.0197	<0.001
Month ²	-0.0057	0.0002	<0.001
Index child dead†	6.9563	0.3922	<0.001
Dead*month	-0.3034	0.0234	<0.001
Dead*month ²	0.0032	0.0003	<0.001
Season†:			
Early dry	-0.0386	0.0665	NS
Early rainy	-0.3405	0.0724	<0.001
Late rainy	-0.1981	0.0690	<0.001
Year of birth†:			
1950-54	-0.0427	0.1105	NS
1955-59	0.0228	0.0874	NS
1965-69	0.1012	0.0737	NS
1970-74	0.3000	0.0892	<0.001
Maternal age	0.2000	0.0278	<0.001
Maternal age ²	-0.0052	0.0005	<0.001
Parity	0.2146	0.0375	<0.001
Parity*month	-0.0041	0.0005	<0.001
Mother's age at first birth	0.0006	0.0049	NS
Male child†	0.0836	0.0551	NS
Maternal height	-0.0053	0.0082	NS
Height*month	0.0003	0.0001	<0.001
Maternal weight	0.0188	0.0070	<0.01
Between woman variance	0.2987	0.0394	<0.001
Intra-class correlation	0.0832	-	-

†For categorical variables omitted category is reference category

Table 4: parameter estimates and standard errors from Model 3 (including maternal haemoglobin)

Variable	Estimate	SE	Sig.
Constant	-15.7260	0.5518	<0.001
Month	0.5001	0.0192	<0.001
Month ²	-0.0056	0.0003	<0.001
Index child dead†	7.3577	0.3884	<0.001
Dead*month	-0.3258	0.0231	<0.001
Dead*month ²	0.0035	0.0003	<0.001
Season†:			
Early dry	-0.0461	0.0665	NS
Early rainy	-0.3354	0.0724	<0.001
Late rainy	-0.1983	0.0690	<0.001
Year of birth†:			
1950-54	-0.0356	0.1110	NS
1955-59	0.0588	0.0885	NS
1965-69	0.0692	0.0741	NS
1970-74	0.2688	0.0898	<0.001
Maternal age	0.2144	0.0275	<0.001
Maternal age ²	-0.0054	0.0005	<0.001
Parity	0.2045	0.0376	<0.001
Parity*month	-0.0038	0.0010	<0.001
Mother's age at first birth	0.0018	0.0049	NS
Male child†	0.0877	0.0552	NS
Maternal haemoglobin	0.0737	0.0178	<0.001
Between woman variance	0.3171	0.0406	<0.001
Intra-class correlation	0.0879	-	-

†For categorical variables omitted category is reference category

Figure 1: yearly probability of livebirth for women in Keneba and Manduar between 1950-74 (3 point moving average)

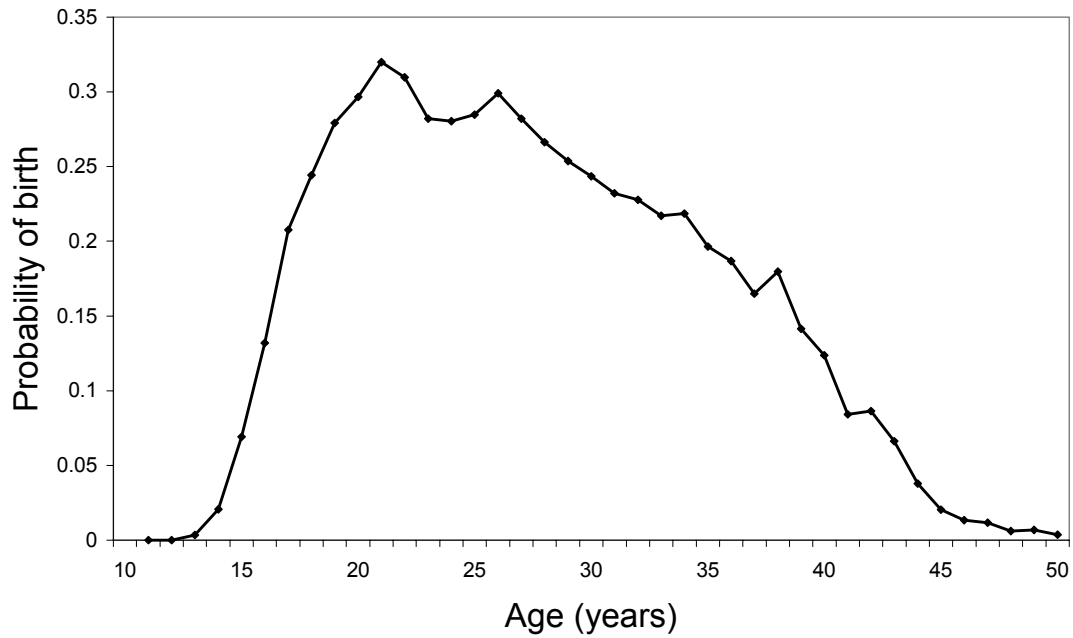


Figure 2: monthly probability of birth over first 6 years after birth of index child (3 point moving average) for cases where index child survived at least 6 months (solid line) and those where index child died before the age of 6 months (dashed line)

