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– these preliminary analyses are currently being augmented with slightly more data and will be submitted shortly.

Determinants of fertility in rural Gambia: an evolutionary ecological approach

by

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Abstract

A longitudinal database from rural Gambia collected between 1950 and 1974 was analysed to identify the determinants of fertility. Multilevel discrete-time event history analysis identified the following variables as having a significant effect on fertility: maternal age, marital duration, parity, haemoglobin levels, being a twin mother, sex of first child, and disrupted marital history. No effects were found of paternal age, sex of child or sex composition of previous children, age at first birth, polygyny, or the presence of the woman's or her husband's kin. The results are interpreted in the light of evolutionary theory and it is concluded that no evidence for any life-history trade-offs was observed. Instead, women in good body condition and those who had previously invested heavily in reproduction had the highest fertility in the present, suggesting that phenotypic correlations were prevalent. Women who gave birth to many children in these villages also had greater numbers of children surviving childhood, indicating that rapid reproductive rate more than compensates for the higher mortality of closely spaced children.

The rate of reproduction is an important determinant of a woman's fertility and hence her Darwinian fitness. Factors determining the pace of reproduction have received much attention from both demographers and evolutionary ecologists, although the two disciplines often adopt different approaches to the same phenomenon. Demographers tend to be concerned with the proximate determinants of fertility (Bongaarts et al. 1984; Gray et al. 1993; Wood 1989; Wood 1994), i.e. the physiological and behavioural factors which influence a woman's probability of giving birth. Evolutionary ecologists are more interested in explaining fertility as an adaptation to a particular environment, which includes the ecological, social and historical contexts in which particular reproductive patterns evolved (see Voland 1998, Mace 2000 for reviews). One branch of evolutionary ecology – life history theory – is concerned with how individuals allocate their resources between the various activities that allow them to survive and reproduce. The application of life-history theory to the study of human populations is a relatively new field of enquiry, which has the potential to provide new insights into human reproductive behaviour (Hawkes et al. 1997; Hill 1993; Hill and Hurtado 1996; Hill and Kaplan 1999).

We use evolutionary theory to inform this analysis of fertility in a natural fertility population. In particular, we are interested in testing the following hypotheses:

1. That women who have invested heavily in reproduction in the past will suffer lowered fertility in the present.
2. That fertility will be positively correlated with maternal body condition.
3. That the presence of relatives will increase reproductive rate.

Previous versus present reproduction

The first hypothesis is derived from life-history theory. 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 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. Three trade-offs have received particular attention: that between somatic investment and investment in reproduction; between investment in current and future reproduction; and between quality and quantity of offspring. We are particularly interested in determining whether we can detect trade-offs between past and present reproduction in this database. The timing of expenditure on reproductive effort is an important determinant of fitness. Decisions on reproductive scheduling are influenced by future mortality rates, rate of population growth and also the costs of reproduction. If rapid reproduction entails an equally rapid deterioration in health and body condition then it may be better to reproduce more slowly thereby extending the reproductive lifespan. In human populations there may also be social considerations. For example, Gambian women in unstable marriages may deliberately attempt to avoid childbearing so that they still have reserves of ‘faso’ (strength) left over should their marriage break down and they need to forge a new relationship (Hill 1997). Life history theory would predict that individuals who invest in reproduction heavily in early life have few remaining resources to invest in reproduction at older ages. However, research in the demographic literature has suggested the opposite: women who begin reproducing early have higher fecundity throughout their reproductive lives than those who begin reproducing late (Udry 1979 but see Otor and Pandey 1998). This may be an example of a phenotypic correlation. Women in good condition may both be able to start reproducing early and reproduce at a rapid rate during 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 lifespan.

Phenotypic condition

Another life history trade-off to have been the focus of much research is that between reproduction and survival. Both these functions are vital to the fitness of an organism but are in competition for the same resources. When resources are scarce, therefore, life history theory predicts that trade-offs will be seen between reproduction and somatic maintenance. But again these studies are plagued by phenotypic correlations. Individuals with many resources should use their resources both to reproduce and to maintain good body condition, individuals with few resources may be forced to reproduce at a lower rate while still being unable to devote much energy to somatic maintenance.

Most of the research on how resources affect reproduction and the health of women in human populations has been done by demographers. They have long been interested in how nutritional status and energy balance affects reproduction, and how reproduction affects the health of women under conditions of energetic stress. Whether nutritional status has a significant impact on female fertility is a subject of some controversy. Some authors argue that human reproduction is remarkably well buffered against poor nutritional status, and only has a significant effect on fertility under extreme conditions such as famine (e.g. Bongaarts 1980). Evidence is steadily accumulating, however, that both low nutritional status and heavy workloads affect female fecundity and ultimately lower fertility. This has been demonstrated both by analysing how nutritional status and workload affect levels of female reproductive hormones (Bentley 1999; Ellison 1994; Jasienska and Ellison 1998), and by observing the effects of nutritional status on the length of post-partum amenorrhoea or birth intervals (Aguirre et al. 1998; Delgado et al. 1982; Huffman et al. 1987; Popkin et al. 1993; Tracer 1996). Some studies have even carried out intervention trials by providing women with high energy supplements during pregnancy and/or lactation. These studies observed a shortening of the period of post-partum amenorrhoea in supplemented (Lunn et al. 1984; Lunn et al. 1981). Studies of human populations, then, suggest that reproduction suffers during times of limited resources. This has been proposed to be an adaptive mechanism to ensure survival until a better time for reproduction presents itself (Ellison 1994). During periods of scarce resources it may be too risky to attempt an energetically expensive bout of reproduction if it means diverting resources away from somatic maintenance, which could mean death. We would therefore expect to see a slowing down of reproductive rate among women in poor body condition.

Kin effects on fertility

The reproductive rate of human females may also be affected by the social nature of our species. Humans have a number of unusual life-history characteristics compared to other apes, including a faster reproductive rate during their fertile period. Inter-birth intervals in humans tend to average around 3 years, whereas chimpanzees have birth intervals of around 5.5 years, gorillas of 4 years and orang-utans of 8 years (Galdikas and Wood 1990). One hypothesis for this rapid reproduction is that the human females receive assistance from their kin in raising offspring. If some of the costs of child-rearing are borne by individuals other than the mother, then women should be able to speed up their reproductive rate compared to other apes where females are solely responsible for raising their offspring. Analysis of the determinants of child mortality in this population has shown that the presence of a child's maternal grandmother or elder sisters improves the survival probabilities of that child, indicating that maternal kin invest in children in this community (Sear et al. 2000). We test whether this investment in child care allows women to shorten their inter-birth intervals. If maternal grandmothers and elder sisters are taking over some responsibility for their grandchildren at weaning then it may be that women with this help from matrilineal kin are able to wean their children earlier than those without these kin, and so concentrate on getting pregnant again more quickly. Nath et al (2000) have shown that the presence of a 'grandmother' in the household shortens birth intervals in scheduled caste populations in India. Although males could effect child nutrition or survival, we found no evidence that male or paternal relatives, even the paternal grandmother, had any effect, so would not predict that patrilineal relatives have any influence on reproductive rate.

We also test whether marital status affects reproductive rate. Reproduction tends to occur within a socially acknowledged union in most populations and reproduction outside these unions may be frowned upon. Age at first reproduction and subsequent reproductive rate may therefore be limited by age at marriage and stability of marriages. In addition, type of marriage may affect fertility. Polygyny clearly increases fertility for males, but it has been suggested that polygynously married women reproduce at lower rates than monogamous women. We therefore analyse the effects of marriage type and marriage stability on female fertility in this population.

Data

The data come from an agricultural community in the West Kiang region of the Gambia. The data form part of an ongoing project funded by the Medical Research Council (MRC) that was initiated by Sir Ian McGregor in 1950. The villages were visited at least annually between 1950 and 1980 by McGregor to collect data on heights, weights and the health status of individuals (see McGregor 1991 for a more detailed description of the study). To complement this biomedical data a system of demographic data collection was set up in 1950 whereby data on all births and deaths that occurred in the villages were continuously recorded by literate village recorders. This data was supplemented by information on marriages, migration and residence collected during the annual surveys. Genealogical trees were then created using this demographic data. These trees, as well as listing the basic demographic events in each individuals’ life, also linked each individual with their parents, grandparents, spouses, children *etc*. The continual recording of events as they happened and the presence at least once a year of MRC researchers has resulted in an unusually detailed and high quality dataset from a natural fertility and mortality population.

This is a patrilineal, patrilocal, agricultural community. Between 1950 and 1974 the area was remote and little developed. Educational services were not supplied by the government of the Gambia until the mid 70s, and medical care, except that provided by McGregor during his visits, was limited. No modern methods of contraception were available to women in these villages during the period under study. Between 1950 and 1974 both fertility and mortality were high: women gave birth to about 7 children on average but 40% of these children failed to reach their fifth birthday (Billewicz and McGregor 1981). In 1974 a permanent medical centre was set up in one of the villages (Keneba) by the MRC Dunn Nutrition Unit. This has changed the demography of these villages by dramatically reducing mortality and making contraception available (Lamb et al. 1984; Weaver and Beckerleg 1993). We have therefore restricted our analysis to the period between 1950-74 when these villages were under a natural fertility-natural mortality regime.

For women marriage occurs early and is universal in this polygynous population. Divorce and remarriage are not infrequent so that women as well as men may have a number of spouses during their reproductive years. Women are responsible for much of the subsistence work, while men are involved both in subsistence work and do a little cash cropping of groundnuts. The intensive subsistence work, together with their domestic duties, mean that women are under considerable energetic stress at certain times of the year. It is a very seasonal environment and the wet season is particularly energetically challenging. It is not only the most physically demanding time of the agricultural calendar, but is also the season of greatest food shortage and disease prevalence. Morbidity and mortality are highest at this time of year. Both adults and children regularly lose weight during this season, though they tend to regain this weight during the dry season, when workloads are lighter and food is more readily available (Billewicz and McGregor 1982).

Methods

All birth intervals which were opened by the birth of a child between 1950 and 1974 were included in our analysis (intervals between marriage and first birth were not included). Stillbirths are often excluded from analyses such as this partly because of the difficulty of collecting data on stillbirths, but also because of the difficulty of distinguishing between miscarriages and stillbirths. We have included stillbirths in our analysis, because 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. Stillbirths are clearly distinguished from miscarriages in our dataset. Our sample consists of all intervals where the date of the birth was known to the month. Births between 1950 and 1974 are included for two of the four villages (Keneba and Manduar). For the other two villages (Jali and Kanton Kunda) only births after 1957 and 1960 respectively are included, as mortality in these villages before then is known to be under-recorded. Intervals which did not end in a birth were censored when the mother died or was lost to follow-up, or after 6 years (the probability of a birth after this time was low and may have been affected by sterility). 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 2410 birth intervals from 718 women, of which 1813 were closed within 6 years and before 1975.

We use multilevel discrete-time event history analysis to analyse birth intervals in this population, using MlwiN software (Goldstein et al. 1998). Event history analysis models the duration until a particular event occurs, in this case a birth (Allison 1984). These models are used because they can easily accommodate two common features of event histories: censored data and time dependent variables. A discrete-time approach is favoured over a continuous time approach because here birth intervals are measured in months. This results in a number of tied observations which continuous models find difficult to deal with. A discrete-time logit model is used to overcome this problem. A multilevel approach is used because some women in this dataset contribute a number of intervals. There is likely to be an association between the length of birth intervals of any one women (Larsen and Vaupel 1993), which means that the events in the model are not independent, violating an assumption of regression analysis. The multilevel model controls for this unobserved heterogeneity by incorporating a random effect which varies across families (see e.g. Goldstein 1995).

The random effects discrete-time logit model takes the form:

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

where h_{tij} is the hazard that birth i to woman j is followed by another birth at time t; α_t is a function of time; $\mathbf{x}_{tij}$ is a vector of covariates (which may be constant over time or time-varying) with associated parameters $\boldsymbol{\beta}$; and u_j is the family-level random effect which is assumed to follow a normal distribution with zero mean and variance σ_u^2. Here, the effect of the time since the last birth on the probability of another birth (represented by α_t) is modelled by inclusion of a set of dummy variables, one for each time point t.

Variables used in analysis

This analysis models the probability of a birth occurring per unit time. The data has to be expanded into a time-based file rather than an individual based file for this type of analysis. Data on these covariates was divided into 6 month periods (rather than single months, which would have resulted in a very large dataset). Table 1 lists the variables included in the model. One factor analyses of fertility have to control for is the survival status of the index child (the child opening the birth interval). Lactation suppresses ovulation so that in a community such as this where infants are breast-fed for at least 18 months (Thompson 1965) women with a surviving infant may not resume cycling after their last birth for many months. There are also cultural taboos against becoming pregnant while still lactating that may serve to lengthen birth intervals after surviving children. Women whose child has died will not experience suppression of ovulation induced by lactation, and will not suffer censure for becoming pregnant again rapidly. 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, to determine whether birth intervals after stillbirths were any different from those after livebirths where the child died very early in life.

Maternal age, paternal age and marital duration

One of the strongest determinants of a woman’s fertility is her age. Fertility tends to show an inverse U-shape with age, rising from menarche to the mid 20s and then beginning to decline in the late 20s before decreasing quite rapidly after the age of 30 to menopause in the fifth decade of life (see Fig. 1). Older women may be less susceptible (because of menopause, sterility or terminal abstinence), less fecund (because of age-related decline in physiological capacity to conceive or decreasing coital frequency) and have a decreased ability to bring a pregnancy to term. Both maternal age and maternal age squared were entered into the analysis to model this nonlinear relationship effectively. Paternal age and marital duration have also been observed to affect fertility: coital frequency declines with both age and marital duration which reduces the probability of conception per fertile cycle (Goldman and Montgomery 1989; Mineau and Trussell 1982), and men may also suffer age-related fertility decline (Murray and Meacham 1993).

Previous reproductive investment

Parity was included as a covariate because we are interested in 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. We have measured parity as total number of children born including stillbirths. The age at the mother's first birth was also included in the model to test whether women who invest in reproduction early in life differ in reproductive characteristics from those who begin reproduction later. Only first births that occurred in 1950 or later and where the woman was under 25 years at her first birth were included. In these villages women are married before puberty and start to have intercourse with their husbands at menarche, though they usually continue to reside in their natal household until after the birth of at least one or two children. Variation in age at first birth should therefore reflect physiological differences in capacity to conceive rather than differences at age at marriage. Women who apparently gave birth to their first child after the age of 24 may be suffering from physiological difficulties in conceiving or have missing data on earlier births so were given a missing value code for this variable.

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 in a number of studies. Where the sex of the child is found to influence its length, the most common finding is for boys to be followed (Blanchard and Bogaert 1997; Larsen et al. 1998; Mace and Sear 1997; Swenson and Thang 1993) and occasionally preceded (Low 1991; Nath et al. 2000) by longer intervals than girls. Sons are more energetically costly to raise than daughters. Male foetuses are larger than female, and male infants have higher energetic intakes than female while breastfeeding (Hoffmans et al. 1988). 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 male foetuses (Bledsoe et al. 1998). The sex of the index child and existing children may therefore be considered an indication of previous reproductive investment if giving birth to sons is more costly than giving birth to daughters. We have also included a variable for the sex of the woman’s first child because this may be an indicator of her condition at the start of her reproductive career.

Birth interval variation 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 girls in the hope of becoming pregnant again sooner with a preferred male child. This is not a universal pattern, however, some studies find no difference in the length of birth intervals by sex of child (Korpelainen 2000; Strassmann and Warner 1998; Zaldivar et al. 1991) and intervals after daughters have been observed to be longer than those after sons (Margulis et al. 1993). This was interpreted as mothers’ preference for daughters in this community where daughters ‘paid back’ their mothers’ investment directly by helping with domestic tasks whereas sons ‘paid back’ the community as a whole. The sex composition of all a woman’s previous births has also been shown to affect birth interval length. Women with no sons have been observed to have shorter birth intervals and a lower probability of stopping childbearing than those with at least one son (Bairagi and Langsten 1986; Nath and Land 1994). The most common preference seems to be for a combination of sons and daughters, rather than a straightforward son preference, as often women with both sexes have the longest intervals and highest probability of stopping reproduction (Arnold 1997; Rahman and DaVanzo 1993; Yamaguchi and Ferguson 1995). We have entered the sex of the index child into the model. We also created two dummy variables for sex of the woman's previous children: one coded 1 if the woman has no sons and 0 for all other cases and the other coded 1 if the woman has no daughters and 0 for all other cases. The reference category is therefore women who have both sons and daughters.

Phenotypic condition

For two of these villages we have data on both heights and weights from the anthropometric surveys conducted each year. We have calculated body mass index (wt^2/ht) from these measurements, which we have entered into the model as an indicator of maternal nutritional status. We also have data on haemoglobin levels. While BMI 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 suffer periods of nutritional stress, compounded by heavy workloads, at certain times of year but also suffer high rates of disease. Many sexually transmitted diseases clearly have the capacity 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 and 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).

For each birth interval we included only the measurement taken most recently after the index birth. Measurements taken when the woman was pregnant with her subsequent birth were discarded. We also included a variable for the length of time since the birth that the measurement was taken, to control for any confounding effects of pregnancy on anthropometric status.

Marriage and kin variables

We have entered variables for the survival status of the woman’s mother and father (i.e. the index child’s maternal grandmother and grandfather) and the husband’s mother and father (i.e. the index child’s paternal grandmother and grandfather). All four variables are entered as time-varying covariates as the survival status of any of these relatives may change during the birth interval. We have included an additional variable which codes for the reproductive status of the maternal grandmother (no paternal grandmothers were still reproductively active in this population). Reproductively active maternal grandmothers are defined as those who had a birth in the year of their grandchild’s birth or later. Non-reproductively active grandmothers are those who had completed reproduction before the index child’s birth. Whether the grandmother is occupied with small children of her own may be an important determinant of the amount of investment she can give to her adult children and grandchildren. In support of this argument, child nutritional status was found to be higher in children whose maternal grandmothers were non-reproductive than those with reproductively active grandmothers (Sear et al. 2000).

We included variables which indicate whether the women was polygynously married at the time of the index birth, and whether she remarried within the interval. Polygyny has attracted considerable attention as a factor which may affect female fertility but no consensus has yet been reached on whether it does directly influence birth rates. Some authors have found that polygynously married women have lower fertility than monogamous women (Garenne and van de Walle 1989; Hern 1992; Pebley and Mbugua 1989) but a number of confounding variables, such as selection of sub-fecund women into polygynous marriages, variation in socio-economic status, ducation etc, may be influencing these relationships. Many studies find no fertility differences between polygynous and monogamous women (Borgerhoff Mulder 1989; Chojnacka 1980; Sembajwe 1979; Strassmann and Warner 1998), and others find that there is variation among polygynous women themselves, with first and later wives having different levels of fertility (Bean and Mineau 1986). This is a highly polygynous society: more than 80% of births occur within a polygynous marriage and we have included a variable for polygyny to test the hypothesis that women in polygynous marriage do have lower fertility than monogamously married women. The woman’s marital status may also have an impact on her fertility. Divorce and remarriage are not uncommon for women in this part of the Gambia, nor is widowhood (as husbands tend to be considerably older than their wives). Though women do tend to remarry relatively rapidly they must wait a minimum of five months before they do so to ensure that they are not carrying their previous husband’s child. Any breaks in her marital history may therefore decrease a woman’s fertility.

Twins and twin mothers

We have included a variable for whether the index birth was a twin or singleton birth. Gestating, giving birth and lactating for two children is likely to be more energetically costly than having a single birth and so we might expect intervals following twin births to be longer than those after singletons. We have also included a variable which distinguishes mothers who have ever given birth to twins from mothers whose children are all singletons. Previous research on the fertility of twin mothers in this population has shown that twin mothers tend to have higher fertility than singleton mothers. This may be because twin mothers have higher rates of polyovulation than singleton mothers. Polyovulation (releasing more than one egg at ovulation) is likely to increase a woman's fecundity because it increases the probability that at least one egg will be fertilised and survive to term as a viable foetus. Anderson (1990) has suggested twinning is maintained within human populations, despite the high mortality associated with twin births both for the infants and the mother, because twin mothers have high rates of polyovulation and therefore higher fertility than mothers without a tendency to have twins.

Results

Figure 2 shows the distribution of the probability of birth over time since last birth. Few women give birth within 18 months of the index birth, but the probability of birth begins to rise after about 20 months to reach a peak in the 34th month before beginning a more gradual decline. There are discernible secondary and tertiary peaks at 48 and 60 months, which are unexpected. Such peaks could be generated by a very strong seasonality in month of giving birth, but there is no evidence that seasonality is strong enough to generate such precise peaks (Figure 2), and in any case there is no peak at 24 months, which might be expected. We can only assume these peaks are 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 31.49 months (31.96 months if stillbirths are excluded). Table 2 gives the results of the multilevel model. As expected the death of the index child had a highly significant effect on the subsequent probability of birth, increasing the hazard of another birth by 5.81 for each six month period after the start of the interval. Intervals opened with a stillbirth were significantly different from those opened with a livebirth. If the index birth was stillborn then the probability of a birth increased by 1.84 for each six month period. This may be because stillbirths were more likely to be premature, reducing the cost of the pregnancy to the mother and/or because lactation, even if only for a few days, increases the costs of that pregnancy to the mother resulting in a longer subsequent interval.

Maternal age, paternal age and marital duration

Both maternal age and maternal age squared have highly significant effects on the hazard of giving birth, confirming the inverse U-shaped relationship of maternal age and fertility. Wood has suggested that one of most important factors influencing the age-related decline in fertility for women may be increased foetal loss. Our data demonstrates that the stillbirth rate does increase at high maternal ages in this population (Fig. 3). Martial duration also appears to have a non-linear relationship with fertility as both marital duration and marital duration squared have a significant effect on the probability of a birth. From table 1 it appears that marital duration may make little difference to mean birth interval length during the first 15 or 20 years of marriage, but that the probability of another birth after 20 years of marriage may decrease considerably. Though the effect of marital duration was small compared to the effect of maternal age, it was highly statistically significant. There was no additional effect of paternal age over and above maternal age and marital duration.

Previous reproductive investment

Parity has a significant, positive relationship with the probability of giving birth: women with many previous births have a higher probability of giving birth per unit time than women with few previous births. Age at first reproduction had no effect on current fertility.

Sex of children

There was no difference in the probability of giving birth by sex of the index child, nor by the sex composition of the woman's previous children. We also compared the length of closed birth intervals by the sex of the children opening and closing the interval. There were no significant differences in the lengths of the four different types of interval (boy-boy, boy-girl, girl-boy, girl-girl) though intervals bounded by two girls were slightly longer (32.8 months) than those which began or ended with a male birth (31.8 months). However, women whose first child was male were significantly more likely to give birth per unit time than women whose first child was a daughter. When an interaction term between age at first birth and sex of first birth was entered into the model the size and significance of the effect increased. Women whose first child was a daughter tend to have earlier first births than those whose first child was a son (age at first birth was 212.7 months if first child was female compared to 221.4 if first child was male: $F=0.048$, $p<0.05$, $n=62$ and 84 respectively).

Phenotypic condition

Overall this is a poorly nourished and mildly anaemic population compared to Western standards. The mean haemoglobin level for non-pregnant women in this sample was 11.6 g/dl, below the cut-off point of 12 g/dl for anaemia given by the World Health Organisation. 5% of measurements were taken from women who were severely anaemic, with haemoglobin levels below 8 g/dl. Mean BMI was also rather low at 20.74, with 12% of measurements taken from women with BMIs under 18.5, indicating very low body mass. There is a highly significant relationship between haemoglobin and probability of birth: women with lower levels of haemoglobin have a lower probability of birth per unit time than those with higher levels (Fig 5). This appears to be a linear relationship. There is no additional effect of BMI on the probability of birth. Haemoglobin levels are correlated with indicators of nutritional status (Tracer 1997) but even when haemoglobin is removed from the model BMI has no relationship with probability of birth.

Marriage and kin variables

There were no significant effects of the survival or reproductive status of mother's mother, mother's father, father's mother or father's mother. Women who are polygynously married at the time of the index birth do not have longer birth intervals than those who are monogamously married, thus providing no support for the hypothesis that fertility is lower for women in polygynous marriages. Women who remarry within the birth interval do have longer birth intervals than those who remain married to the same man. Table 1 suggests that the birth intervals of women who remarry may be increased by 10 months compared to those who remain married to the same man. This suggests that, despite rapid remarriage, women who have a disrupted marital history either through widowhood or divorce may suffer costs relative to those who remain married to the same man throughout their reproductive years.

Twins and twin mothers

There was no difference in the length of intervals after the birth of twins or singletons, despite the expectation that giving birth to two children would be more energetically costly than giving birth to a single child. Twin mothers did have significantly higher probability of giving birth than singleton mothers. This is compatible with the ‘insurance ova hypothesis’, which suggests that twins are a side-effect of polyovulation which increases fertility by compensating for high levels of embryo mortality. Additional research carried out on this data indicates that mothers of twins also have higher age-specific fertility and slightly later age at last reproduction than mothers of twins (Sear et al. 2001). Our analysis of twin mothers further suggests that these women may be of particularly high quality, in that their nutritional status is slightly higher than that of singleton mothers and they are slightly more likely to give birth to sons among their singleton children.

Between woman variance

The multilevel model estimates that there is significant variance at the level of the individual woman not accounted for by the variables included in the model. We estimate that this effect accounts for approximately 32% of the total variance in the probability of giving birth. This is a substantial proportion of the variation in fecundity that is unaccounted for. Sterility may be one factor which is causing unexplained variation between women. Primary sterility is fairly low in these villages but secondary sterility is higher, between 13-19%, which may indicate some prevalence of STDs (Billewicz and McGregor 1981). When conducting analyses such as this on the probability of birth we are actually including two sub-populations of women. The first is a sub-population of fertile women who will conceive at some future date, the problem to model is how long it will take them to conceive. The second is a sub-population of sterile women who will never conceive, so a second issue is the probability of becoming sterile in any particular interval. Work is in progress in developing mixture models which can model these two problems simultaneously (McDonald and Rosina 1998). We have attempted to reduce the problem of 'long-term survivors' by excluding all intervals longer than 6 years. Other possible causes of this unexplained variation may be variability in socio-economic status. Nutritional status and overall health tend to be highly correlated with socio-economic status (Tracer 1997), but there may be some impact of SES which is not captured by our health variables. Although female fecundity is the focus of much demographic research, it may be that variation in the husband's fecundity, which is also affected by disease, energetic balance and environmental factors (Campbell and Leslie 1995), is causing some of this unobserved heterogeneity.

Discussion

This analysis has found no evidence for a life-history trade-off between previous and current reproductive investment in this Gambian population. On the contrary, a positive relationship was found between previous reproductive effort and reproductive effort in the present i.e. women of a given age had faster birth intervals if they were of higher parity. This was also observed in a life history study of the Ache, hunter-gatherers in Paraguay (Hill and Hurtado 1996). The Ache show a positive correlation between previous and current reproductive investment, even when access to resources is partially controlled for.

That women who have male first births have faster reproductive rates than those who have female first births indicates that sex of child may be related to a woman's phenotypic condition. There is little evidence for sex-biased parental investment in this population. There were no significant differences in the probability of birth by sex of child opening or closing intervals, nor by the sex composition of a woman's existing children. Mortality rates in childhood also show little difference between sons and daughters. Overall approximately equal proportions of males and females survive childhood, though female children die at lower rates than males in the first year and higher rates than males during the second year of life (Sear et al. in press). These results do not suggest any active son preference; rather physiology may determine whether women have many boys or girls. As male children are more energetically costly to raise than female, women in poor condition may be more likely to give birth to daughters rather than sons. A male first child may be an indicator of particularly good phenotypic condition, which allows a more rapid reproductive rate throughout the reproductive lifespan. There was also some suggestion that the intervals of women with many girls, or intervals bounded by girls, were particularly long, compared to intervals which involved male children. This may also indicate that women in particularly poor condition are likely to give birth to many girls, perhaps because the probability of pregnancy loss in women in poor condition is greater for male foetuses (Nonaka et al. 1998)??.

Women with higher reproductive rates will tend to have higher completed fertility (in terms of total number of births or livebirths), but there is a cost to this strategy for the children. Short birth intervals are known to increase the risks of mortality of both the child at the start and the child at the end of the interval (Cleland and Sathar 1984; Curtis et al. 1993; Hobcraft et al. 1985; Madise and Diamond 1995; Muhuri and

Menken 1997; Palloni and Millman 1986). In this Gambian population children born after intervals less than 48 months have mortality rates almost double those of children born after longer intervals in the first year of life. Children whose subsequent sibling is born within 22 months or less of their own birth suffer mortality rates three times higher than those who are followed by longer birth intervals (Sear et al. in press). Women with short birth intervals may therefore not have higher fitness (in terms of number of children reaching adulthood) than those with longer birth intervals even if they suffer high rates of mortality among their children. Studies which have investigated this question have found that women with short birth intervals tend to have high Darwinian fitness despite this cost of high child mortality (Crognier 1998; Hobcraft et al. 1983). Though early work on the modelling of optimum birth intervals suggested that long birth intervals in !Kung foragers may increase the mother's fitness (Blurton Jones 1986), this research has been criticised for methodological flaws (Pennington and Harpending 1993). Hill and Hurtado (1997) find that Ache women with the shortest birth intervals have the highest. In this Gambian population, women who give birth to many children also have more surviving offspring than those with fewer births, despite the higher mortality associated with rapid reproductive rate (Fig. 6). Rapid reproduction more than compensates for the higher infant mortality, and there is no evidence that women are reproducing too fast in terms of maximising their Darwinian fitness.

The question then becomes why do women have such long intervals? The answer may lie in the correlation between reproductive rate and body condition, as measured by haemoglobin levels. Maternal body condition is likely to be a constraint on reproduction. The suppression of reproduction observed in women of poor nutritional status is adaptive in that it allows them to conserve their energy until a more appropriate moment for reproduction comes along (Ellison 1994). When women are in poor health because of low nutritional status, negative energy balance, disease or some combination of these factors, they cannot afford to devote scarce energy reserves to reproduction without a high risk of death. They are therefore forced to wait until one or more of these factors improve and they have sufficient energy, once necessary survival functions are taken care of, to reproduce. Mammals have sophisticated immune systems that are energetically expensive to maintain and there may be a trade-off between reproductive effort and effort allocated to maintaining good defences against parasites (Norris and Evans 2000; Sheldon and Verhulst 1996). Evolutionary biologists working on birds have shown that reproductive effort correlates negatively with immune response and 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; Moreno et al. 1999; Saino et al. 1997). Conversely, individuals who must expend considerable effort in fighting disease may have few resources left over for reproduction. We might thus predict that women with high birth rates would have higher mortality. However, simulations we have conducted elsewhere suggest that only very high rates of maternal mortality can offset the fitness advantages of rapid reproduction (Sear et al 2001).

Intrinsic aspects of body condition, many of which may be hidden to simple anthropometric or haematological measures, may influence physiological mechanisms that determine whether ovulation occurs, whether embryos implant, or whether male or twin foetuses are carried to term. Only in women who are phenotypically fit will such costly pregnancies be observed. Interaction between nutrition, disease and early history are all likely to play a role. In short, some women are just of higher phenotypic quality than others, and this variation between women is masking the majority of the life history trade-offs that she may, nonetheless, be experiencing.

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Table 1: sample sizes, percentage of closed intervals and mean length of birth intervals for single variables in model. (Age and body condition variables are shown here as categorical variables for illustrative purposes, and were entered into the model as continuous variables.)

	N	Percentage of closed intervals	Mean length of IBI (months)
Stillborn	93	72	19.28
Liveborn	2317	75	31.96
Index child dead	763	87	26.50
Index child alive	1146	81	34.41
Keneba	1167	79	31.45
Manduar	371	75	31.41
Kanton	187	64	32.03
Jali	685	71	31.47
Maternal age (years):			
< 20	441	77	30.87
20-29	1159	80	30.99
30-39	710	72	32.69
>40	90	29	32.46
Paternal age (years):			
< 30	262	79	29.78
30-49	1561	79	31.24
>50	425	68	33.23
Marital duration (years):			
0-9	1727	77	31.35
10-14	328	76	31.59
15-19	165	56	31.30
20+	44	29	30.69

Haemoglobin (g/dl):			
<10.6 g/dl	290	75	33.72
10.6-11.8	290	82	32.17
11.9-12.9	279	79	32.19
>12.9	286	75	31.08
BMI (kg/m^2):			
<19.42	290	74	31.12
19.42-20.48	286	79	32.56
20.49-21.84	280	78	32.99
>21.84	291	80	32.35
Parity:	470	82	31.95
1	852	76	31.70
2-3	780	77	31.39
4-6	308	60	30.12
7+			
Age at first birth (years):			
<17	411	74	30.53
17-19	944	74	30.72
>19	693	77	31.60
Male first birth	1186	75	30.75
Female first birth	1166	75	32.23
Index child male	1207	76	31.48
Index child female	1188	75	31.59
All sons	431	79	31.67
All daughters	432	77	33.05
Both sons and daughters	1531	74	31.06
Index birth twin	40	70	26.89

Index birth singleton	2370	75	31.56
Twin mother	282	79	29.80
Singleton mother	2128	75	31.73
Maternal grandmother non-reprod	873	77	30.95
Maternal grandmother reprod	109	72	29.00
Maternal grandmother dead	201	65	31.32
Maternal grandfather alive	808	76	30.60
Maternal grandfather dead	264	62	29.90
Paternal grandmother alive	667	80	29.51
Paternal grandmother dead	283	68	30.92
Paternal grandfather alive	273	80	29.44
Paternal grandfather dead	354	67	28.97
Polygynous	1859	77	31.29
Monogamous	396	72	31.93
Mother remarried	123	84	40.06
Continuously married	2056	83	30.97

Table 2: parameter estimates, standard errors and odds ratios obtained from the multivariate multilevel model of birth interval

Variable	Estimate	SE	Odds ratio[1]
Constant	-4.255	0.827*	
Stillbirth	0.611	0.240*	1.84
Livebirth	0	0	1
Index child dead	1.760	0.094*	5.81
Index child alive	0	0	1
Keneba	0	0	1
Manduar	-0.272	0.140	0.76
Kanton	-0.122	0.202	0.88
Jali	-0.288	0.144*	0.75
Maternal age	0.231	0.047*	1.26
Maternal age squared	-0.006	0.001*	0.99
Paternal age	-0.002	0.004	1.00
Marital duration	0.064	0.027*	1.07
Marital duration squared	-0.005	0.002*	0.99
Maternal haemoglobin	0.142	0.033*	1.15
Maternal BMI	0.002	0.015	1.00
Parity	0.233	0.036*	1.26
Mother’s at age first birth	0.013	0.007	1.01
Male first birth	0.682	0.244*	1.98
Female first birth	0	0	1
Interaction with age at first birth	-0.026	0.014	0.97
Index child male	-0.031	0.111	0.97
Index child female	0	0	1
All sons	-0.092	0.146	0.91

All daughters	-0.117	0.146	0.89
Both sexes	0	0	1
Index birth twin	0.200	0.383	1.22
Index birth singleton	0	0	1
Twin mother	0.400	0.146*	1.49
Singleton mother	0	0	1
Maternal grandmother non-reprod	0	0	1
Maternal grandmother reprod	0.073	0.224	1.07
Maternal grandmother dead	-0.063	0.149	0.94
Maternal grandfather alive	0	0	1
Maternal grandfather dead	-0.323	0.299	0.72
Paternal grandmother alive	0	0	1
Paternal grandmother dead	-0.006	0.132	0.99
Paternal grandfather alive	0	0	1
Paternal grandfather dead	0.133	0.125	1.14
Polygynous	-0.041	0.100	0.95
Monogamous	0	0	1
Mother remarried	-0.889	0.184*	0.41
Continuously married	0	0	1
Mother level effect	1.528	0.113*	

* $p < 0.05$

[1] The odds ratio gives the relative probability of a birth per unit time (6 months) compared to the reference category (reference category has odds ratio of 1)

Figure legends

Figure 1: Yearly probability of a live birth for women in Keneba and Manduar (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)

Figure 3. Number of birth per calendar month (open bar: live births, black bar: still births)

Figure 4: Proportion of births that were stillborn by maternal age (1950-74)

Figure 5: effect of haemoglobin level on length of birth intervals. Only intervals where index child survived the interval are shown. Haemoglobin level divided into quartiles: 1 = lowest quartile, 4 = highest quartile

Figure 6: number of children born that survived at least 5 years by total number of births for women aged at least 45 years old. Only women born in 1930 or later included (only one woman had 19 births)

Figure 1

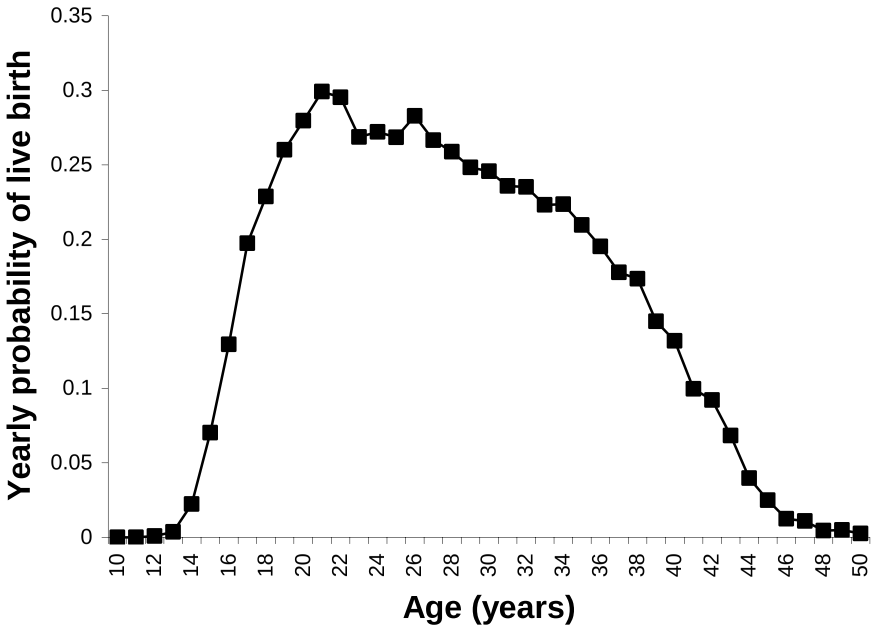

Yearly probability of live birth
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44
46
48
50
Age (years)

Figure 2

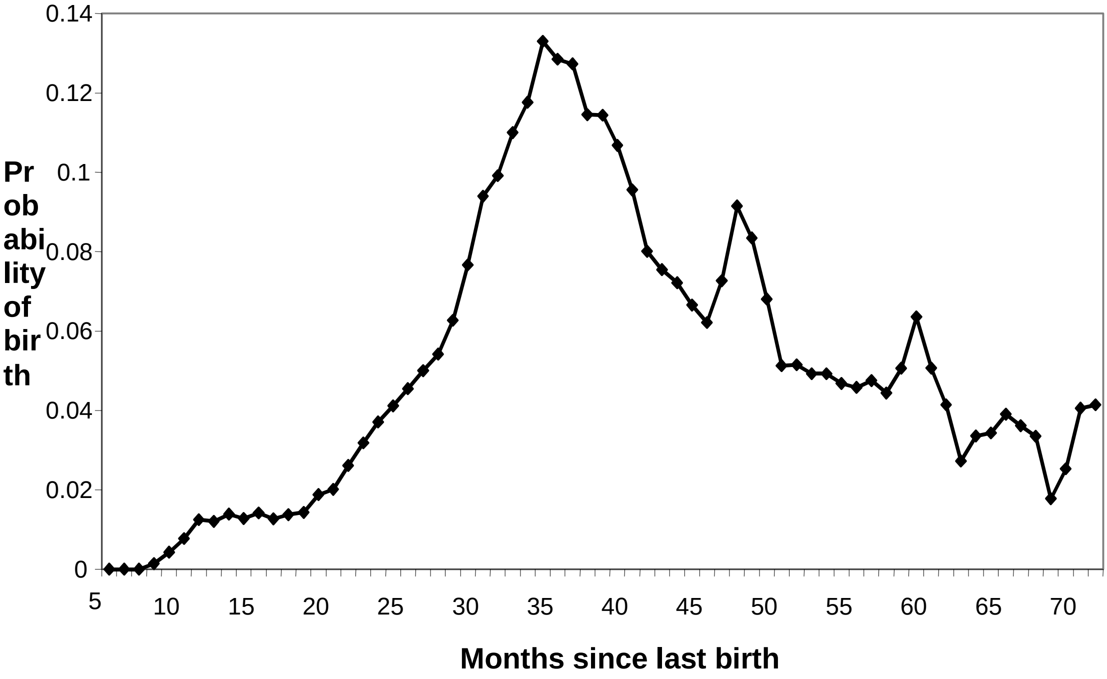
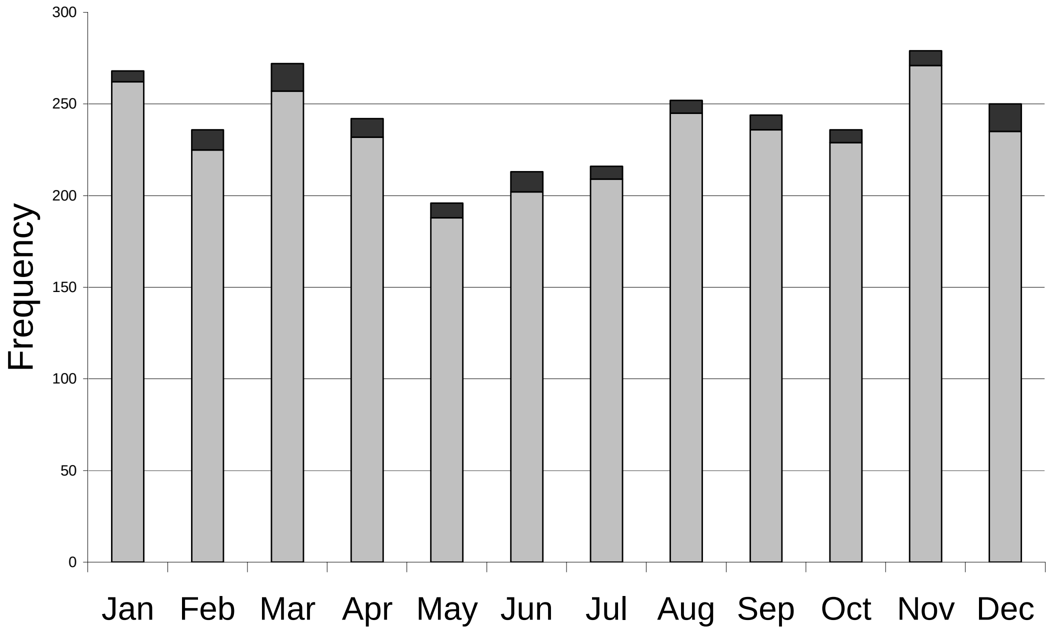

0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
Probability of birth
5
10
15
20
25
30
35
40
45
50
55
60
65
70
Months since last birth

Figure 3



Frequency
300
250
200
150
100
50
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Figure 4.

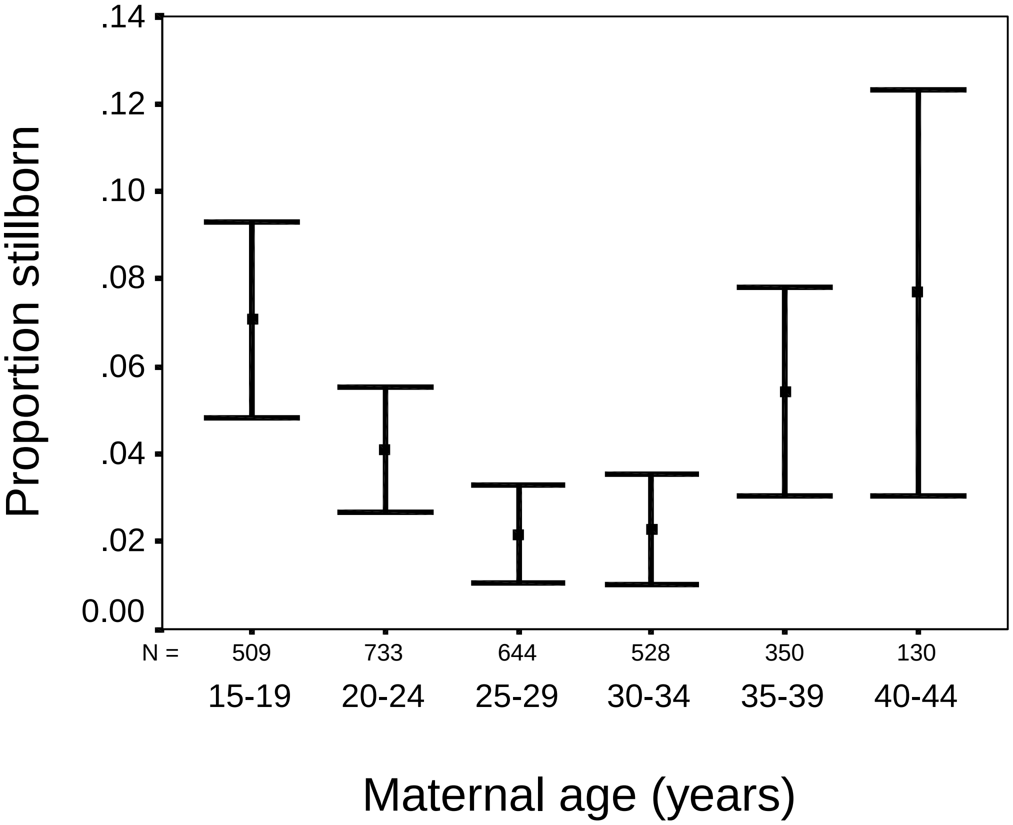
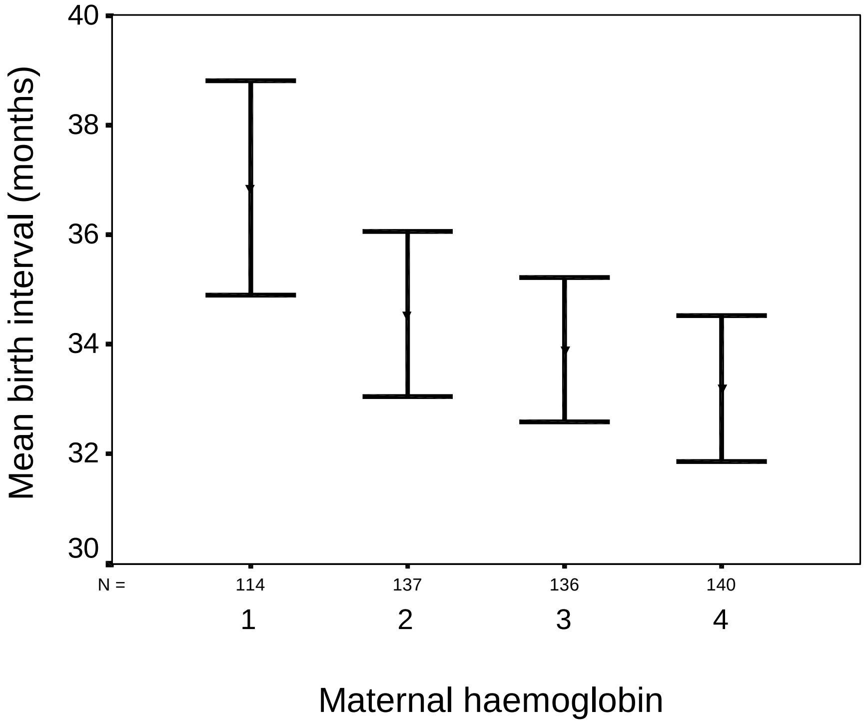
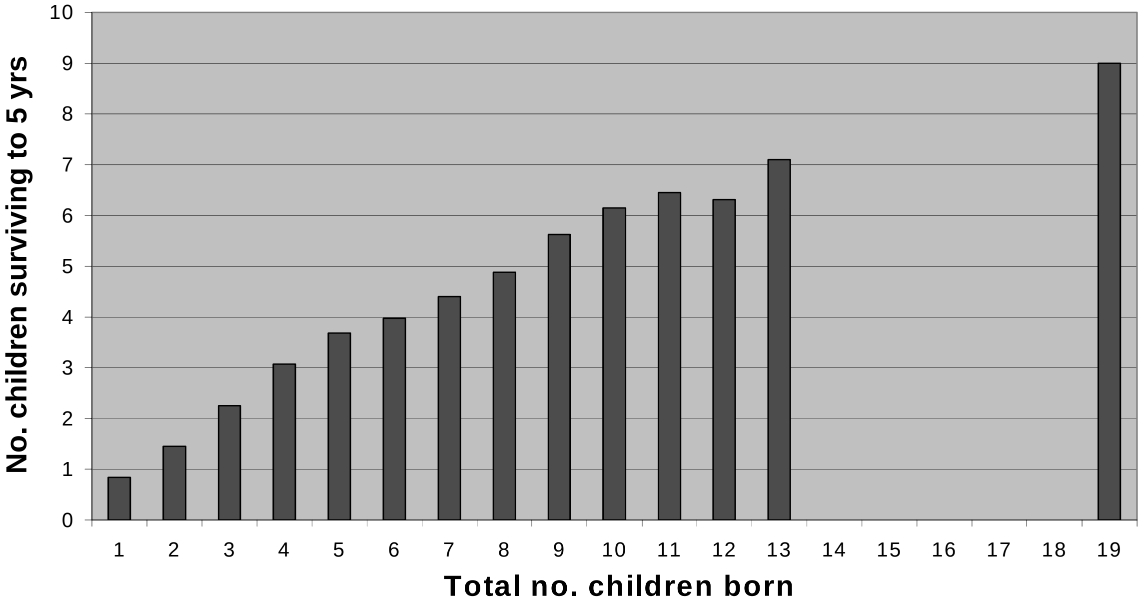

Proportion stillborn
.14
.12
.10
.08
.06
.04
.02
0.00
N =
509
733
644
528
350
130
15-19
20-24
25-29
30-34
35-39
40-44
Maternal age (years)

Figure 5



Mean birth interval (months)
40
38
36
34
32
30
N =
114
137
136
140
1
2
3
4
Maternal haemoglobin

Figure 6


10
9
8
7
6
5
4
3
2
1
0
No. children surviving to 5 yrs
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
Total no. children born