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Abstract

Human females reproduce relatively rapidly throughout their reproductive years compared to the other great apes. It has been suggested that women are able to sustain this rapid pace by co-opting family members to help raise their children. We tested the hypothesis that the presence of kin will increase the reproductive rates of women using a longitudinal database collected from rural Gambia. We found that both the husband's mother and, to a lesser extent, the husband's father increased the probability that a woman would give birth. A woman's parents, however, had no effect on her fertility rate, nor did her elder sisters or co-wives. The presence of a woman's elder brothers even decreased her probability of giving birth. There was no evidence that elder children acted as 'helpers at the nest', as the existence of living elder children slowed down rather than increased birth rates. We suggest that the increased fertility in the presence of mothers-in-law may be due to these women helping out their daughters-in-law with domestic and subsistence duties. Given that it is paternal, rather than maternal, relatives who increase fertility, social pressures on women from older kin to bear many children may also be important.

Keywords: kin, fertility, evolutionary demography, Gambia

Introduction

In humans, reproduction does not occur in a social vacuum. Most births occur within a socially sanctioned union, and reproduction outside of these unions may be frowned on or prohibited. In traditional societies, marriage and childbearing may be heavily influenced by family members, as well as the couple's own motivations (Locoh, 1988). The aim of this analysis was to examine female fertility rates in a traditional, agricultural population in rural Gambia to determine which, if any, relatives affected the rate of giving birth. In addition, the effects of marital status on fertility were examined. This paper was stimulated by the prediction from evolutionary theory that individuals should have a vested interest in the reproductive behaviour of their close genetic relatives.

Humans are a group-living species, characterised (in females, at least) by relatively long pre- and post-reproductive stages. This means that there is potential for mothers to receive considerable assistance from pre-reproductive girls and post-reproductive grandmothers in raising offspring. Humans are also unusual amongst mammals in that males are often involved in provisioning females and offspring, though the degree of male help varies considerably across cultures (Hill, 1982). Both male involvement in raising children and help from female kin may underlie the evolution of a number of human life history patterns (Hill, 1993; Hawkes et al., 1997, 1998; Kaplan et al., 2000). For example, help from kin may be responsible for the relatively short inter-birth intervals of human females, compared to the other great apes (Hawkes et al., 1998). The females of other ape species must ensure that their offspring are relatively self-sufficient by the time they are weaned. Human infants can be weaned while they are still heavily dependent on adults for provisioning and protection, if individuals other than the mother will take over some of this responsibility. This early weaning allows the mother to resume ovulation and become pregnant again sooner, than if she was solely responsible for raising her offspring to independence.

We have already demonstrated that maternal, but not paternal, grandmothers were beneficial in that they improved the nutritional status and survival probabilities of children in this population (Sear et al., 2000, 2002). We now intend to determine whether the presence of older female relatives also increased women's fertility rates.

We extend our analysis of the effects of kin on fertility beyond that of older women, however. Elder siblings are often assigned as nursemaids to younger children in West African societies (Thompson & Rahman, 1967; Whittemore & Beverly, 1989). We found that the presence of a woman's elder daughters increased the survival chances of her children (Sear et al., 2002) and their nutritional status (unpublished data). A recent study of a Moroccan Berber population has shown that probable helpers (*i.e.* older siblings) improved not only child survival rates but also fertility rates of women (Crognier et al., 2001). Other studies have suggested that the siblings of the woman herself may affect her fertility rates (Hill & Hurtado, 1996; Bereczkei, 1998; Draper & Hames, 2000), though siblings may not necessarily be beneficial. In this analysis, we have included all a woman's close relatives – her mother, father, husband's mother, husband's father, elder sons and daughters, and her own brothers and sisters – to determine whether the presence of any of these categories of kin affected her fertility rates.

The effects of marital status on fertility rate are also investigated. Marital disruption is clearly likely to affect fertility if women who are not in stable unions are at lowered risk of conception (Isiugo-Abanihe, 1998). Women invariably remarried after widowhood or divorce in this population but had to wait a minimum of 4 months and 10 days before remarrying to ensure they were not pregnant with their previous husband's child (Thompson, 1965). Any breaks in marital history are therefore likely to have reduced a woman's fertility.

Some research has suggested that polygyny may lower female fertility, through its effect of reducing coital frequency (Pebley & Mbugua, 1989; Hern, 1992, but see Sembajwe, 1979; Borgerhoff Mulder, 1989; Strassmann & Warner, 1998). From an evolutionary point of view, polygyny is not necessarily expected to be costly for women. The polygyny threshold model predicts that women (or their families) will choose husbands based on the resources that will be available to the woman during her marriage (Orians, 1969; Borgerhoff Mulder, 1990). Wealthy men become polygynous because they can provide each of multiple wives with a similar amount of resources to those that a poorer man can offer a single wife. If polygyny involved such high costs as decreased fertility, women should be reluctant to marry polygynously. However, if women of low mate value are forced to marry men who

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are already married, then fitness costs of polygynous marriages may be observed, particularly in second and later wives (Bean & Mineau, 1986; Sellen et al., 2000). In addition, polygyny brings such reproductive benefits to males, it is in their interests to persuade women into polygynous marriages, even if it brings a fitness cost to women (Chisholm & Burbank, 1991; Marlowe, 2000).

Data

The data used in this analysis were collected from four villages in rural Gambia between 1950 and 1974 by Ian McGregor (McGregor, 1991). Data on all births and deaths in the villages were recorded as they happened by literate village recorders. Unique personal identification numbers allow us to identify members of each individual's extended family in the database. Though demographic data recording is still ongoing in these villages, we have restricted our analysis to the period between 1950 and 1974. During 1974 the MRC Dunn Nutrition Unit (DNU) established a permanent medical clinic in one of the study villages. The availability of modern medicine caused a sudden drop in mortality, and a slower decline in fertility (Lamb et al., 1984; Weaver & Beckerleg, 1993). Between 1950 and 1974, this population had no access to contraception and little medical care. As a result both child mortality and fertility were high: 43% of children died before their 5th birthday, and women averaged over 7 births during their reproductive lifetimes (Billewicz & McGregor, 1981).

The community was a patrilineal, patrilocal and Muslim society. The majority of villagers were Mandinka, with a minority of Jola origin (Thompson, 1965). Women married early, and transferred to their husbands' compounds after marriage, but often not until after the birth of a child or two. Most women married within their own villages or a village nearby, and remained in close contact with their mothers after marriage. Polygyny was the ideal, and divorce was not uncommon so that both men and women may have had a number of spouses over their lifetimes. Women were responsible for much of the subsistence farming of the staple crops, millet and rice. Men were also involved in subsistence farming, but combined this with a little cash cropping of groundnuts.

Methods

This analysis modeled the probability of birth over time. All birth intervals which were opened by the birth of a singleton child between 1950 and 1974 were included in the analysis. 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 have been affected by sterility or missed births. 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 2532 birth intervals from 765 women, of which 1780 were closed by a birth within 6 years and before 1975.

Multilevel discrete-time event history analysis was used to analyse the probability of birth, using MLwiN 1.1 (Rasbash et al., 2000). Event history analysis models the time until an event occurs (Allison, 1984). Event history models are useful for analysing demographic data because they are able to accommodate two common features of demographic data that standard statistical techniques find hard to deal with: censoring and time-dependent variables (Yamaguchi, 1991). The ability to include time-dependent variables is particularly useful in analysis such as this as some relatives will die during the period of interest.

A multi-level approach is used because there is known to be considerable heterogeneity amongst women in fertility (Larsen & Vaupel, 1993; Wood, 1994). 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 can be used to overcome this problem by allowing variation at the mother level, with the inclusion of a mother-specific random effect (Goldstein, 1995).

Variables considered in the analysis

A single model was built which included all kin variables discussed below and a number of non-kin variables known to affect fertility, in order to determine the partial effects of the kin variables. The dataset was expanded into one month periods and both time since last birth and time squared were entered into the analysis to model the

probability of birth over time. Survival status of the index child (*i.e.* the child born at the start of the birth interval) was included in the model because this variable is known to have strong effects on the probability of giving birth. Maternal age and parity were also included because they are likely to be correlated both with the probability of birth, and with the survival status of many of the categories of kin entered into the analysis.

These event history 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). This assumption was tested by including interactions between time and each covariate in the model. Non-significant interactions were dropped from the final model.

Kin variables

Table 1 lists all kin variables with sample sizes and Kaplan-Meier estimates of mean length of birth intervals for each kin category. Variables coding for the survival status of the woman's husband, her mother and father and the husband's mother and father were included in the model. For each relative, we constructed four categories of survival status: living, dead, censored and missing. Censored kin were those who disappeared from the dataset but had no known date of death, and were therefore likely to have moved away from the villages. A code of missing was given to all those kin for whom no information exists in our database. This category is likely to include kin who either died before the study began, or who never lived in the study villages during the period of data collection. Though we have no data on residence patterns, we consider that the 'living' category of kin is likely to be a good approximation of those kin who were available to women during their marriages, as it only includes kin who were known to be alive *and resident in one of the four study villages*. The vast majority of these individuals are likely to be living in the same village as their kin. During the 1960s, Thompson observed that 80% of Keneba residents married within their natal village and only a further 9% came from one of the other three study villages (Thompson, 1965). In initial models, we tested whether the censored and

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missing categories differed from the dead category for each kin variable. In no case were there significant differences between these categories. In the final model, we entered the 'living' variable for each category of kin, so that the reference category included those kin who were dead, censored or missing.

All five variables were entered as time-varying covariates as the survival status of any of these relatives may change during the birth interval. An additional variable was included which coded for the reproductive status of the maternal grandmother at the birth of the child (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.

Variables were included for whether the mother had any elder brothers or sisters who survived to adulthood (coded as dichotomous time-constant variables). Finally, two time-varying variables which coded for whether the index child had any living elder brothers and sisters at least 10 years older than the child were included (again as dichotomous variables). This indicates whether the mother had any children who would have been old enough to contribute to childcare and domestic tasks. A variable for the index child's sex was also included in the model, as were interactions between child's sex and the presence of elder brothers of sisters.

Marriage variables

A dummy variable which indicated whether the woman was polygynously married at the time of the index birth was included in the model. A variable coding for whether the mother had divorced within the interval was also included. As there are few dates of marriage available for this dataset, these variables were constructed from the dates of birth of children of the marriages. A man is considered to be polygynously married if he is recorded as simultaneously having children with more than one wife, and monogamous if only one wife is recorded for him or if the dates of birth of his children with each of his wives do not overlap. Mothers are recorded as divorced if they had children with two different fathers but there was no record of the first husband's death in the interval between the two births. These definitions are therefore a conservative estimate of the prevalence of polygyny and divorce.

Results

Table 2 gives parameter estimates and standard errors for all covariates in the model. Interactions are indicated by an asterisk (*i.e.* mother*month indicates the interaction term between the 'mother' variable and time since last birth). The survival status of the index birth, mother's age at birth and parity all had significant effects on the probability of birth (the effects of non-kin variables are not discussed extensively here as these issues are covered in detail in Sear et al., in press and Sear et al., submitted).

Kin variables

Unsurprisingly, the death of the woman's husband significantly decreased fertility. Table 1 suggests that widowhood may have increased the length of the birth interval by only about 9 months compared to women who remain married to the same man during the birth interval. This is indicative of rapid and universal remarriage after widowhood.

Husbands' mothers significantly increased fertility (Figure 1). There is little convincing evidence for an effect of the woman's mother on the probability of giving birth, though there were significant interactions between the survival status of the woman's mother and time since last birth. This indicates that the effects of mothers vary over time but that, overall, there is no main effect of the woman's mother. Figure 2 suggests that the effects of mothers were only positive in the case of children who had died. In cases where the index child survived, the effects of mothers seem to be negative. The reproductive status of mothers was unimportant, as the effect of reproductively active mothers was not significant.

Having a living father had no effect on the probability of birth, but the husband's father did have a significant effect on fertility. The parameter estimate is negative but again there is a significant interaction between this variable and time since last birth, which changes the interpretation of the main effect. Figure 3 suggests that, in the majority of cases, the husband's father increased fertility. Having elder sisters had no

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effect on a woman's fertility, but having elder brothers who survived to adulthood appeared to decrease the probability of giving birth.

The model suggests that elder daughters did not act as 'helpers at the nest' in this population (Figure 4). The odds ratio for the probability of birth after a female child is 0.61 for those girls with elder sisters, compared to an odds ratio of 1.00 for those without elder sisters. In comparison, the odds ratio for the probability of birth after a boy is 0.97 for those with and 1.02 for those without elder sisters. Rather than any helping effect of elder sisters, these results suggest that parental investment strategies may have been more important. Women with existing daughters slowed down reproduction after another daughter, perhaps trying to avoid the birth of yet another girl. The effect of elder sons on the probability of birth is also negative. There is a significant interaction between this variable and time, but the effect is not altered by the sex of the index child (Figure 5). That the presence of living elder siblings of both sexes reduced the probability of another birth may suggest that women start to slow down their reproductive rate once a desired family size and composition is achieved.

Marriage variables

There is no evidence that polygyny decreased fertility: the birth rates of polygynously married women were not statistically different from those of monogamously married women. Rather, this analysis suggests there were no costs to women of polygynous marriages in terms of lowered fertility, as predicted by the polygyny threshold model. Though a few studies have found a negative effect of polygyny on fertility (Pebley & Mbugua, 1989; Hern, 1992; Josephson, 1993), polygyny takes many forms and is confounded by a number of variables which also affect fertility (such as socio-economic status, age of husband *etc.*). This makes it difficult to generalise such findings across populations. In this society, any benefits polygyny might bring, such as co-operation between co-wives or marrying into a wealthy household, may be counterbalanced by its disadvantages, such as competition between co-wives and over-crowding in the 'women's house' of the compound.

Divorce did decrease fertility. Table 1 suggests that, as with widowhood, divorce added an extra 9 months onto the birth interval.

Discussion

This analysis indicates that there were relatively small but significant influences of certain relatives on female fertility rates in this population. In contrast to the analysis of child mortality (Sear et al., 2000, 2002), the effects of the husband's mother were more important than those of the woman's mother. Somewhat unexpectedly, the husband's father also had a slight positive effect on female fertility.

The exact mechanisms by which mothers-in-law increased the fertility of their daughters-in-law are not clear. We suggested in the introduction that fertility rates may increase in the presence of kin if women are able to wean children early by passing over some of their care to other relatives, thus allowing them to resume ovulation more rapidly. Ethnographic reports indicate that women's mothers did take over some childcare duties around the time of weaning (Thompson, 1965), and our earlier analysis of child mortality suggests this assistance was of sufficiently high quality to improve child survival rates. However, there was no overall positive effect of mothers, and where they did appear to increase fertility rates, it was only in the cases of children who died. The effects of mothers-in-law were equally strong whether the child lived or died. These results make it unlikely that early weaning of children in the presence of kin is the explanation for increased fertility rates.

A similar explanation may be that older women are able to help younger relatives out with domestic and subsistence duties, thus reducing her workload. Nutritional status and workload are known to affect fecundity (Popkin et al., 1993; Tracer, 1996; Gibson & Mace, 2002; Sear et al., in press), so this lightened energetic burden may enable women to conceive again sooner. The presence of mothers-in-law was still beneficial even when variables for anthropometric status were included in the model (results not shown). This suggests that the higher fertility was not solely due to higher nutritional status of women with living mothers-in-law (though this analysis does not

control for workload, which has been shown to have independent effects on fecundity: Jasienska & Ellison, 1998). In this patrilocal community, women tend to live with their mothers-in-law rather than their mothers so mothers-in-law may be able to share domestic work with their daughters-in-law. However, subsistence work may be shared with either matrilineal or patrilineal female relatives. The women of a household tend to work together on farms belonging to that household but rice fields are inherited matrilineally in this area (Thompson, 1965, N. Allal, pers.comm.). Matrilineally inherited farms tend to be worked on by matrilineally related kin. And we have already described how mothers, rather than mothers-in-law, help women out with childcare. Women with living mothers-in-law may have been slightly better off in terms of work burden than those without, but mothers also appear to have had the opportunity to affect the energetic burden of their daughters. A reduction in energetic expenditure in the presence of older women may not, therefore, be the whole explanation for the observed effect of mothers-in-law.

Social pressures can also affect a woman's decision about when and how many children to have (Adongo et al., 1997). In patrilineal populations, a husband and his family often desire a wife to bear many children, particularly sons, to increase the size of their patriline. These social pressures may explain why paternal and not maternal relatives increased fertility rates in these villages. In this patrilineal society, men can rely on their brothers for economic support. Men (and their wives) may therefore be keen to see their compounds increase in prosperity by the addition of many children. The husband's relatives may also be more likely to exert pressure on women to have many children, even if this exceeds the woman's own desire for children, because the husband's kin are not genetically related to his wives. A woman's family may be concerned with the welfare of both her children and the woman herself, whereas the husband's family may be keen to see their extended family increase in size even at the expense of the woman's health.

It should be emphasised that relationships between kin are not exclusively characterised by mutually beneficial behaviour. Relatives tend to live in close proximity and utilise the same resource base in traditional societies, so interactions may be characterised by competitive rather than co-operative behaviour (Dunbar et al., 1995). Detrimental effects of elder siblings on the fertility of younger same-sex

siblings have been reported, and have been explained by competition between siblings of the same sex for parental resources (Low, 1991; Mace, 1996; Borgerhoff Mulder, 1998). The mechanism to account for the dampening effect of elder brothers on their sisters' fertility is less clear, as brothers and sisters usually do not compete for similar resources. Ache hunter-gatherer women in Paraguay also suffer lowered fertility rates if they have living adult brothers (Hill & Hurtado, 1996). Male fertility is increased in the presence of adult sisters, however, and it was suggested that women were improving their brother's fertility at some cost to their own. Whether a similar phenomenon is occurring in the Gambia must await an analysis of male fertility.

Finally, both the raw data and the model predictions suggest that the effects of relatives on fertility were rather small. Women undergo a number of birth intervals during their reproductive careers, however, and the cumulative effects of kin across a number of birth intervals will be larger than that reported here for a single birth interval. Nevertheless, the effect of maternal grandmothers on child mortality was considerably larger than the effects of any kin on fertility rates (survival rates of children were increased by roughly 10% in the presence of maternal grandmothers). A similar analysis of the effects of kin on female fertility and child mortality using historical German data found larger effects of the presence of grandmothers on child mortality than on fertility (Voland & Beise, in press). There is growing evidence that, in natural fertility societies, variation in child mortality may be more important than variation in fertility in determining reproductive success (Pennington, 1992; Strassmann & Gillespie, 2002). The analyses of the effects of relatives on child mortality and fertility in this population suggest that any effects kin have on the reproductive success of women is likely to act more strongly through child mortality rates than fertility rates.

Acknowledgements

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Table 1: kin and marriage variables included in model

Variable	N	Percentage of intervals closed	Kaplan-Meier estimate of mean birth interval length (months)
Husband:			
Dead	43	81	40.34
Alive and stayed married	2054	82	31.75
Alive but divorced	39	74	40.87
Mother:			
Dead	206	63	33.90
Alive:	1005	72	32.67
Reproductive	107	72	31.13
Non-reproductive	898	72	32.75
Father:			
Dead	276	58	32.77
Alive	830	73	32.36
Husband's mother:			
Dead	293	64	33.09
Alive	722	75	30.81
Husband's father:			
Dead	369	64	31.74
Alive	283	75	30.33
Elder brothers:			
Yes	594	71	33.27
No	1106	70	32.99
Elder sisters:			
Yes	537	70	32.55
No	1163	71	33.32
Sons at least 10 yrs older than index child:			
Yes	360	58	36.75
No	2174	72	32.86
Daughters at least 10 yrs older than index child:			
Yes	343	57	36.50
No	2191	72	32.94
Polygynous	403	70	32.91
Monogamous	1968	72	33.14

Table 2: parameter estimates and standard errors from multi-level model

| Variable	Estimate	SE
Constant	-9.864	0.273**
Kin variables		
Husband:		
Alive and stayed married	0.442	0.106**
Alive but divorced	-0.647	0.214**
Mother:		
Alive and reprod	-0.010	0.152
Alive and non-reprod	0.394	$0.210^{\dagger}$
Mother*month	-0.038	0.016*
Mother*month^2	0.001	0.0003*
Father alive	0.079	0.077
Husband's mother alive	0.208	0.076**
Husband's father alive	-0.798	0.106*
Husband's father*month	0.103	0.035**
Husband's father*month^2	-0.002	0.0008**
Elder brothers	-0.222	0.088*
Elder sisters	0.065	0.091
Living sons at least 10 yrs older than index child	0.677	0.186**
Sons*month	-0.034	0.006**
Living daughters at least 10 yrs older than index child	-0.490	0.132**
Daughters*sex of child	0.445	0.156**
Polygynous	0.012	0.070
Biodemographic variables		
Month	0.420	0.017**
Month^2	-0.006	0.0003**
Child death	5.525	0.252**
Child death*month	-0.300	0.019**
Child death*month^2	0.004	0.0003**
Male index child	0.018	0.059
Age at birth	-0.076	0.009**
Age at birth^2	-0.005	0.0005**
Parity	0.136	0.024**
Between woman variance	0.272	0.038**

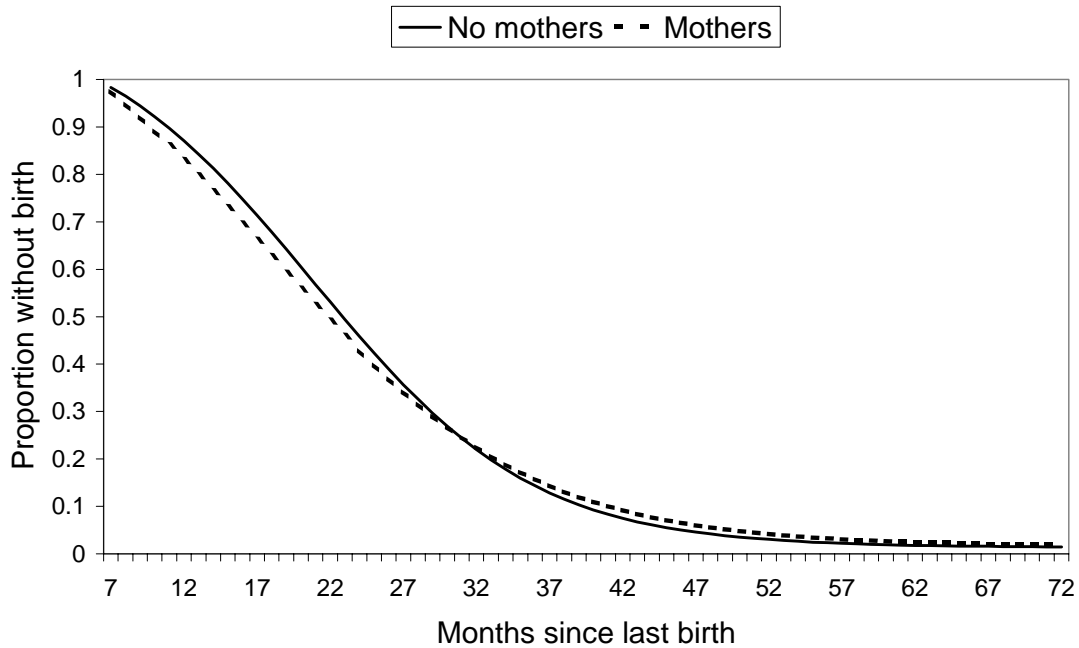** $p < 0.01$, * $p < 0.05$, † $p < 0.1$

Figure 1: survival plot using model predictions of the effects of the husband's mother on probability of birth for cases where the index child was alive (a) and cases where the index child was dead (b). Model was fitted using reference categories for all variables but child death, husband's mother, maternal age and parity (model was fitted at mean maternal age of 27 years and mean parity of 4)
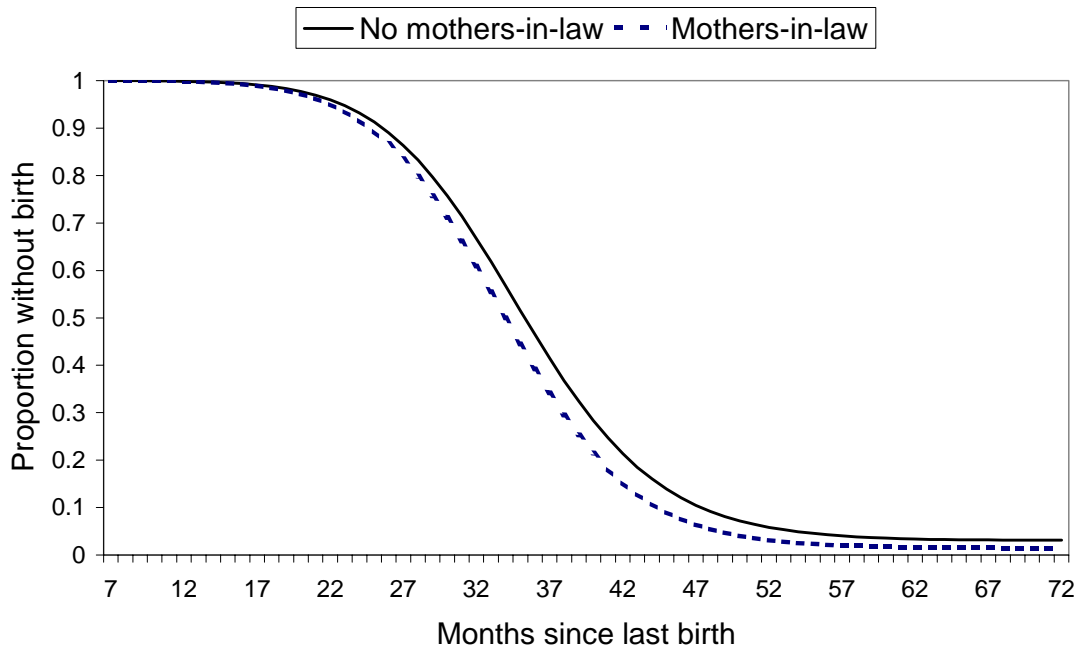
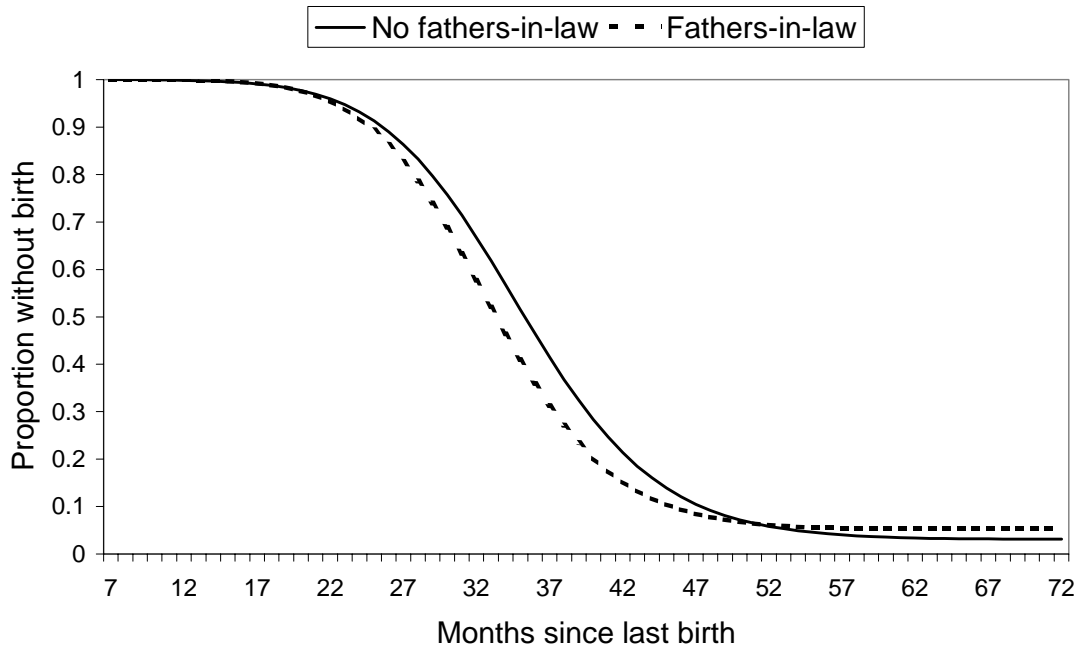**(a) index child alive**
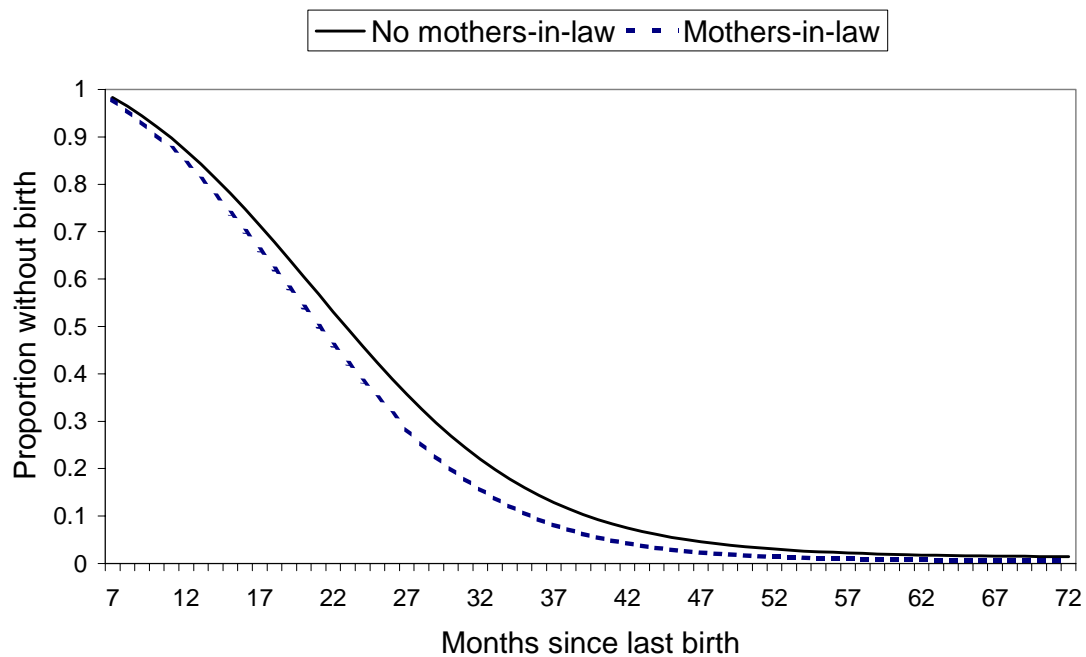
(b) index child dead

Figure 2: survival plot using model predictions of the effect of the woman's mother on probability of birth for cases where the index child was alive (a) and cases where the index child was dead (b). Model was fitted using reference categories for all variables but child death, woman's mother, maternal age and parity (model was fitted at mean maternal age of 27 years and mean parity of 4)
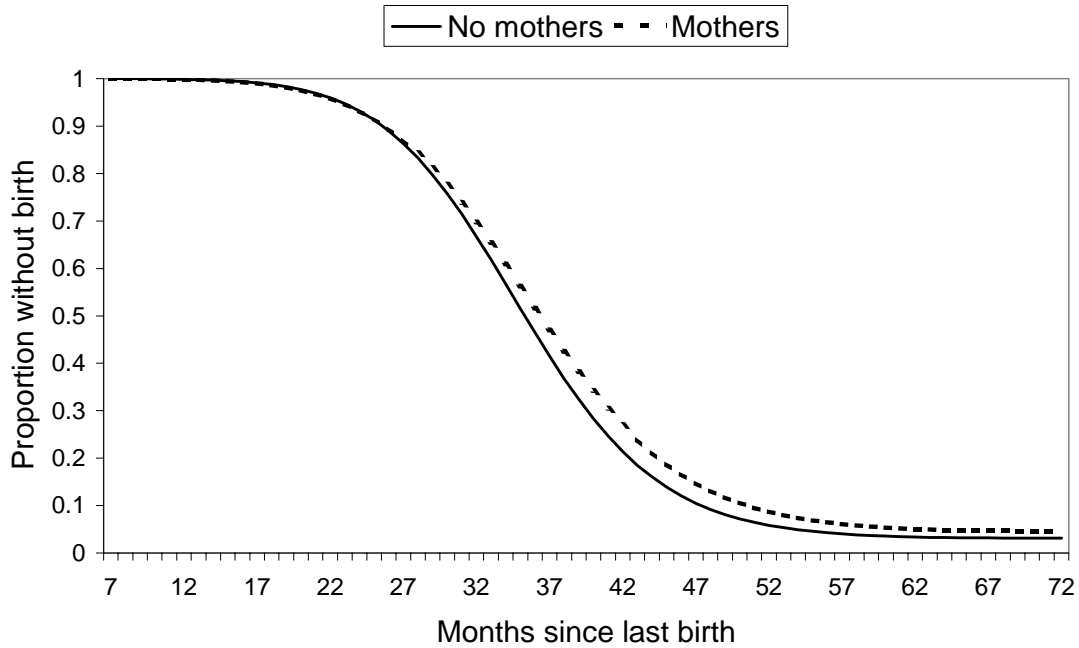
(a) index child alive

(b) index child dead

Figure 3: survival plot using model predictions of the effect of the husband's father on probability of birth for cases where the index child was alive (a) and cases where the index child was dead (b). Model was fitted using reference categories for all variables but child death, husband's father, maternal age and parity (model was fitted at mean maternal age of 27 years and mean parity of 4)

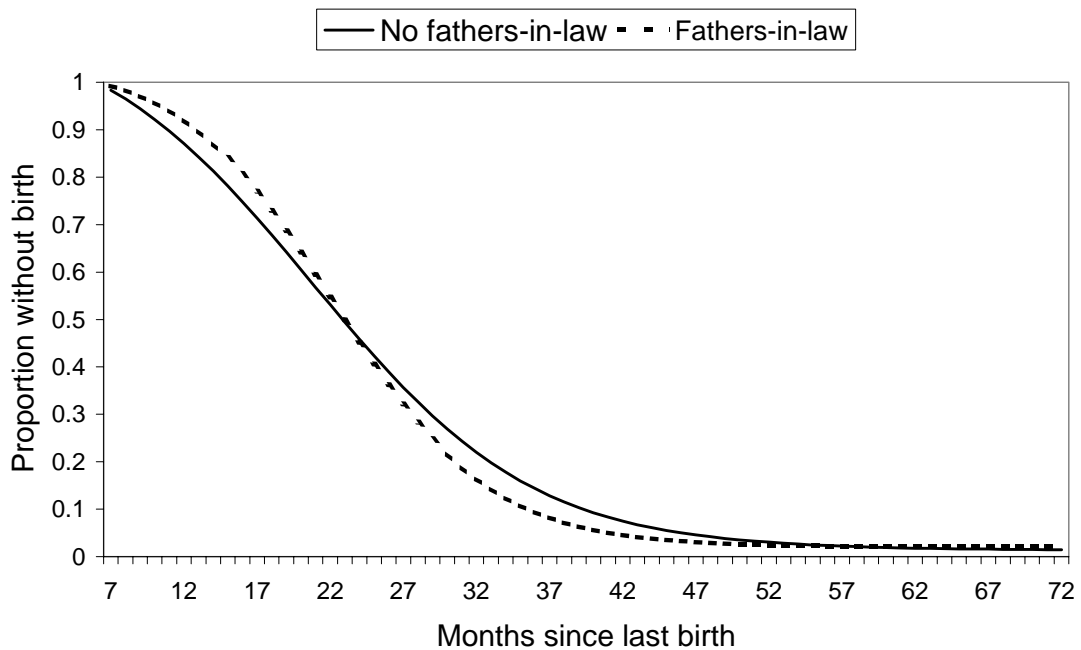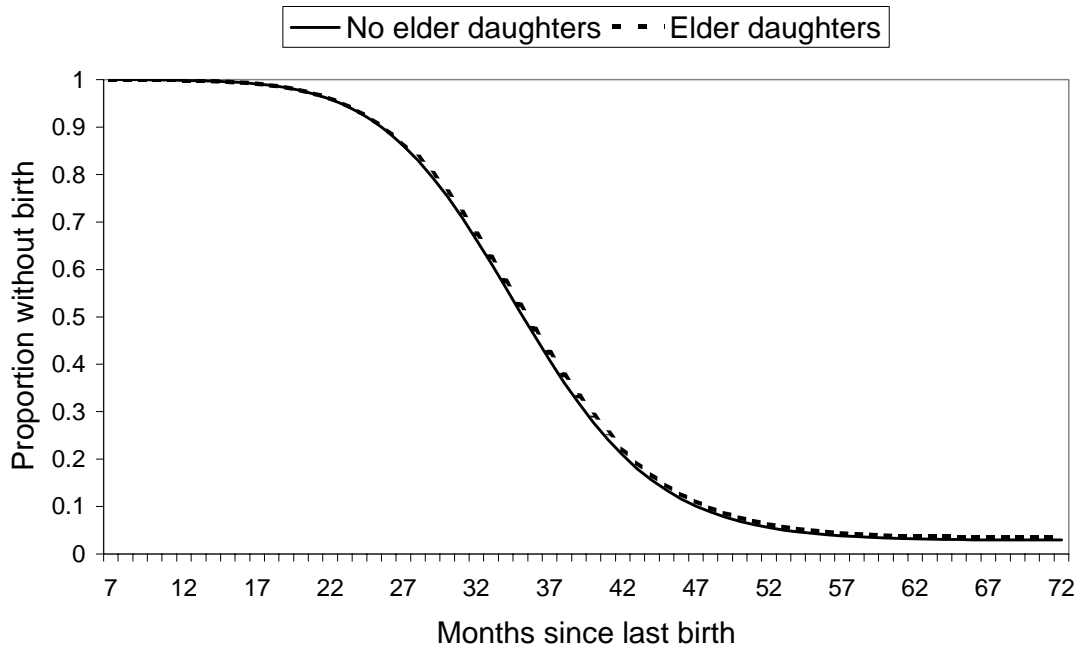**(a) index child alive**

(b) index child dead

Figure 4: survival plot using model predictions of the effect of the elder daughters on probability of birth for male (a) and female (b) index births. Model was fitted using reference categories for all variables but child death, elder daughters, maternal age and parity (model was fitted for cases where the index child survived, at mean maternal age of 27 years and mean parity of 4)
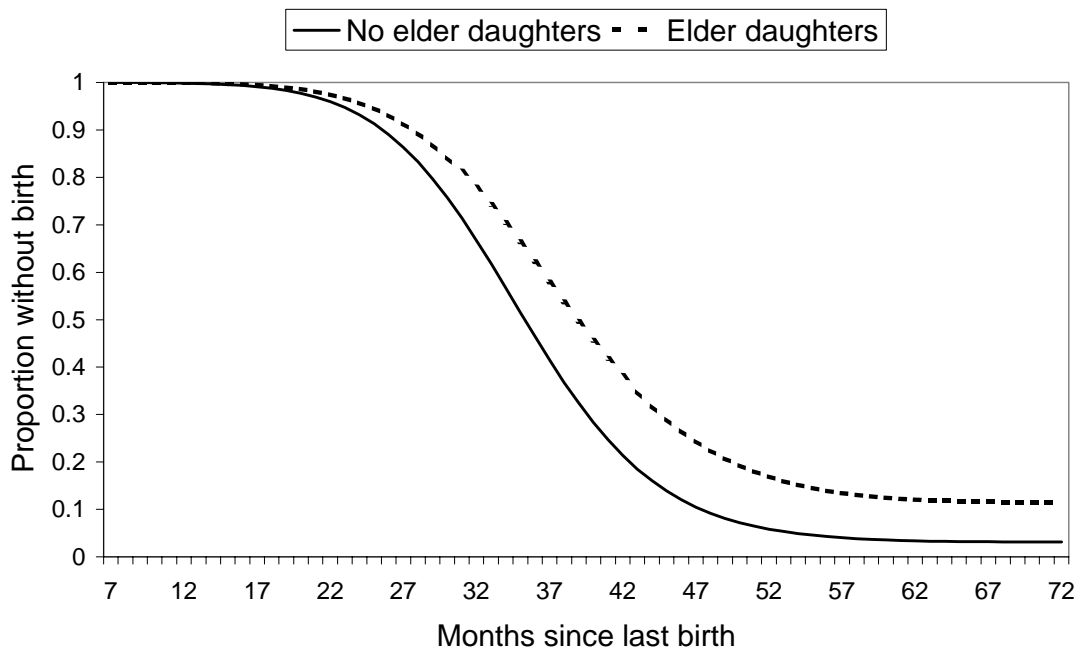
(a) males

(a) females

Figure 5: survival plot using model predictions of the effect of elder sons on probability of birth for male (a) and female (b) index births. Model was fitted using reference categories for all variables but child death, elder sons, maternal age and parity (model was fitted for cases where the index child survived, at mean maternal age of 27 years and mean parity of 4)

(a) males

(b) females