To be published in Bentley, G.R. & Mace, R. (eds) Substitute Parents: Alloparenting in Human Societies. Berghahn Books.

Family matters: kin, demography and child health in a rural Gambian population

by

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Abstract

The idea that humans are co-operative breeders has been around for several decades, but has only recently been subjected to empirical testing across disparate cultures. We have investigated this issue in a farming community in the Gambia, by analysing whether there is any evidence that a woman's relatives affect her reproductive patterns. We have analysed the effects on kin on child mortality and anthropometric status, female age at first birth and female fertility rates. We find that relatives matter for all the life history traits we have investigated. There is evidence that mothers receive help from their mothers and elder daughters in raising children: the presence of maternal grandmothers and elder sisters improves both the survival and anthropometric status of children. Male and paternal kin appear less important to child outcomes, but do affect female fertility. Having a living father or elder brothers lowers a woman's age at first birth, and her fertility rate is increased in the presence of both her mother-in-law and father-in-law. These analyses demonstrate the importance of kin to components of reproductive success, but also show that different relatives have different roles to play in a woman's life history. Maternal grandmothers and elder sisters provide direct care to young children, which is important enough to show up as improved survival rates. Male and paternal kin have no role to play in direct childcare, but do affect women's reproductive lives through their social roles: fathers are involved in arranging women's marriages; and a woman's parents-in-law may apply social pressures on her to have many children to increase the reproductive success of their own son.

Introduction

Alloparental care is a rare phenomenon (Solomon and Hayes this volume). The costs of investing in another individual's offspring usually outweigh any potential benefits gained through inclusive fitness (increasing one's reproductive success by helping genetically related individuals survive and reproduce) or reciprocation (where the benefits derive from the recipient of the helping behaviour returning the favour in the future). But the human species appears to be one of the few mammalian examples where alloparenting is common. In traditional societies, mothers often receive help from their relatives in raising children. In post-industrial societies, help is often bought in or provided by the state. In this study, we focus on a traditional society, and assume inclusive fitness arguments largely provide an explanation for allocare. Hamilton's rule states that help will be provided to recipients by their relatives, provided that the costs of helping are less than the benefits to the recipient, discounted by the degree of relatedness between recipient and donor:

$$rb>c$$

where r represents the coefficient of relatedness (the probability that any gene will be shared by recipient and donor), b the benefits of helping and c the costs (Hamilton 1964). For allocare to become common between a given set of relatives, the benefits of allocare (b) must be relatively high, the costs (c) relatively low, or both.

The particular features of human life history mean that the benefits of helping are likely to be relatively high, while the costs are relatively low. Human infants are altricial compared to other primates, and require many years of investment before they become self-sufficient in food production. Any help provided by relatives to the mother may therefore yield large benefits both in terms of the survival and well-being of the child, and in enabling the mother to speed up her reproductive rate. The unusual human female life history may also make the costs of helping relatively low. The long pre-reproductive and, in particular, the long post-reproductive period of women's lives means that there is a large pool of potential helpers who are available to help.

These non-reproductive helpers will face no conflicts of interest in helping raise another woman's offspring since they are unable to have children of their own.

Note that in the last paragraph we have discussed the help that human *mothers* receive from kin in raising offspring, rather than human parents. Strictly speaking, paternal care is not considered alloparenting since fathers are also parents of the child. But paternal care is unusual, particularly among mammals, and requires explanation (Clutton-Brock 1991). In the majority of primate species mothers receive little or no help from males in raising their young (though there are exceptions, such as siamang and callitrichids: Chivers 1974; Goldizen 1987). The human species is often cited as an example where paternal investment is high (e.g. Geary 2000). But given the cross-cultural variation in paternal involvement (Draper and Harpending 1982; Hewlett 1992), we do not take paternal care for granted, and for the remainder of the chapter will discuss allomaternal, rather than alloparental, care.

We have suggested that allomaternal care has large benefits and low costs in the human species because of the peculiarities of the human life history. But an idea of long-standing influence is that the causal arrow may point in the opposite direction: rather than allomaternal care arising because of the features of human life history, it is the human life history that has been shaped by the benefits of allomaternal care. The large brain of the human baby, necessitating an altricial birth and long period of dependence, has required human mothers to rely on other relatives in order to raise children successfully to adulthood. This help then allowed to women to have relatively short inter-birth intervals, compared to the other great apes (Galdikas and Wood 1990), since they could delegate the care of weaned children to other individuals. For many years the dominant hypothesis was that paternal provisioning with high calorie meat has shaped human life histories, by relieving women of the burden of feeding so many dependent children simultaneously (Washburn and Lancaster 1968; Lovejoy 1981). More recent research has suggested that behaviours such as hunting, which were initially interpreted as paternal investment, may be mating effort instead and that men contribute relatively little to raising children (Hawkes 1990). Direct childcare by fathers is certainly rare, though there is some cross-cultural variation, and frequently dwarfed by the amount of childcare done by the mother's female relatives (Waynforth 2002). Which leads us to the alternative hypothesis that has been proposed to explain the unusual features of human female life history: that it can be explained by help from the mother’s relatives, particularly their own mothers and elder daughters. The ‘grandmother hypothesis’ suggests that the long post-reproductive lifespan of women evolved so that older women could invest in their grandchildren (e.g. Alvarez 2000; Hawkes 2003). This hypothesis simultaneously explains both the short inter-birth intervals of human females, and the most unusual feature of human female life history – menopause. Pre-reproductive offspring may also act as ‘helpers-at-the-nest’ enabling women to raise more children than they would be able to support alone (Lee and Kramer 2002; Kramer this volume).

Though these ideas about the importance of kin to the evolution of human life history have been around for several decades (Williams 1957; Hamilton 1966), only relatively recently has empirical investigation of the impact of kin on demographic outcomes begun in earnest. If kin do contribute significantly to childcare or child provisioning, then this leads to the testable predictions that child survival and growth rates and/or female fertility rates should be higher in the presence of fathers, grandmothers or other helpers. During the late 1980s and 90s this prediction began to be tested in contemporary populations by evolutionary ecologists (see Turke 1988 for an early example). Among the pioneers of this research, Hawkes and colleagues, working with Hadza hunter-gatherers in Tanzania, have been influential in promoting the ideas that grandmothers have important roles to play in provisioning children (Hawkes, O'Connell and Blurton Jones 1989; Hawkes, O'Connell and Blurton Jones 1997; Hawkes, O'Connell and Jones 2001). Hill and Hurtado, working on Ache hunter-gatherers in South America, broadly represent the ‘men matter’ point of view, having found little evidence that grandmothers make a difference to demographic patterns (Hill and Hurtado 1991; Hill and Hurtado 1996). Investment from the father does not necessarily preclude investment from female relatives, or vice versa. Both fathers and female kin may help mothers out, though the roles they play may differ. Marlowe, for example, has suggested that men may enable forager women to increase their fertility rates, though they may have no impact on child survival (Marlowe 2001). These hunter-gatherer studies have led to a recent explosion of interest investigating the effects of kin on various demographic outcomes across a variety of ecological niches (Bereczkei 1998; Sear, Mace and McGregor 2000; Crognier, Baali and Hilali 2001; Quinlan 2001; Sear et al. 2002; Sorenson Jamison et al. 2002; Voland and Beise 2002; Waynforth 2002; Reher and González-Quiñones 2003; Sear, Mace and McGregor 2003; Lahdenpera et al. 2004; Leonetti and Nath 2004; Tymicki 2004; Beise 2005; Leonetti et al. 2005).

Here we draw together research we have conducted over the last few years to investigate the effects of relatives on demographic outcomes, using an unusually rich database from a farming community in rural Gambia. This database, which includes a combination of demographic, anthropometric and genealogical data, has allowed us to analyse the effects of kin on a number of life history characteristics, including both child outcomes and fertility patterns. We demonstrate that kin is important to all the components of reproductive success that we have looked at, but that different relatives have different roles in play in a woman's reproductive life.

Data

The data were collected by Ian McGregor under the auspices of the UK Medical Research Council (McGregor and Smith 1952; McGregor 1991). The main focus of this research program was to study tropical disease, but McGregor's holistic approach to research resulted in the collection of an impressive array of data from the inhabitants of four villages in rural Gambia. The longitudinal nature of this project makes it a particularly useful data source. Demographic data have been continuously collected since 1950, and McGregor conducted anthropometric surveys at least annually between 1950 and 1980. He also collected genealogical information, which allows us to match individuals with their parents, grandparents, siblings, children and other relatives.

Between 1950 and 1974 this was a natural fertility population which had little access to medical care or contraception, though McGregor (a medical doctor) did treat individuals as necessary during the annual surveys. Both fertility and mortality were high during this period. Women gave birth to around 7 children on average, but almost 50% of these children died before the age of 5 years (Billewicz and McGregor 1981). In 1975, a permanent research station was set up by the MRC Dunn Nutrition Unit, who began to conduct research in this area in that year. Though data collection continues at this research station today, we have restricted our analysis to the earlier, natural fertility period between 1950 and 1974 (with a single exception, noted below). The permanent research station, which provides free medical services to all villagers, has had significant effects on both the demography and economy of these villages (Lamb et al. 1984; Weaver and Beckerleg 1993; Beckerleg, Austin and Weaver 1994; Sear 2001).

The villagers were patrilineal, patrilocal, Muslim and predominantly of the Mandinka ethnic group. Polygyny was widespread, and divorce and remarriage were also common, so that women as well as men may have had a number of marital partners during their reproductive lives (Thompson 1965). Though women did eventually move to their husbands' compounds after marriage, they often remained in their natal homes until after the birth of a child or two. Most women married within their village of birth (80%), or one of the neighbouring villages (11%), so that both their own parents, as well as their spouse's parents, would have been readily available during the marriage. Ethnographic evidence suggests that mothers do receive help in raising children in this society (Thompson and Rahman 1967). Older women and pre-adolescent children help women out with direct childcare. Fathers do no childcare, but can potentially contribute to child well-being through productive work.

This was primarily a subsistence agriculture community. Women were responsible for a substantial proportion of subsistence farming. Men did some subsistence farming and a little cash-cropping of groundnuts. The environment was highly seasonal. Villagers suffered considerably from outbreaks of infectious and parasitic disease during the rainy season, which was also the season of low food availability and hard subsistence labour. These Gambian individuals were relatively short and light compared to Western standards. Women were 158cm tall and weighed 51 kg on average; men averaged 168cm and 58kg. The growth (and growth faltering) of the children in these villages has been well documented both by McGregor and by the MRC Dunn Nutrition Unit (e.g. McGregor et al. 1968; Billewicz and McGregor 1982; Poskitt, Cole and Whitehead 1999).

Methods

We have conducted statistical analysis comparing child growth and survival rates in the presence and absence of various categories of kin in order to infer patterns of helping behaviour in this population. We also want to know whether kin have effects on other reproductive outcomes. So we have examined the effects of kin on female reproduction in this community: comparing age at first birth and female fertility rates in the presence and absence of kin.

Child survival

We used event history analysis (EHA) to analyse the effects of kin on child survival over the first 5 years of the child's life (see Sear *et al.* 2000; Sear *et al.* 2002 for further details). Relatively few children died after the age of 5 years, so we were unable to identify any effects of kin after this age. EHA models the probability of an event happening over time, and is particularly useful for this analysis as it allows the inclusion of time-dependent covariates, such as the presence or absence of kin (Allison 1984). Multi-level discrete-time EHA was performed using MLwiN (Rasbash et al. 2000). Most mothers had several children entered into the analysis, and the survival probabilities of siblings are known to be correlated (e.g. Curtis and Steele 1996). Multi-level models were necessary to control for this non-independence of datapoints. The models controlled for sex of child, maternal age, parity, length of preceding and succeeding birth intervals, village of birth and whether the child was lastborn.

The determinants of child mortality change over the first 5 years of the child's life: endogenous causes predominate in the first year of lie, exogenous causes after infancy. Relatives are also likely to be important at different ages: mothers being of paramount importance while children are still dependent on breast-milk, but other relatives having opportunities to take over the care of older children. To control for these potential confounds, we divided the first 5 years into three periods: infancy (under 12 months), toddlerhood (12-23 months) and older childhood (24-59 months) and ran the analysis separately on each age group. Sample sizes for the infant, toddler and childhood analyses were 2,294, 1,664 and 1,341 children respectively.

We analysed the effects of the following relatives on child mortality: mothers, fathers, maternal grandmothers and grandfathers, paternal grandmothers and grandfathers, elder sisters and elder brothers of the child. For parents and grandparents, we entered the survival status of each category of kin into each model as a time dependent categorical variable: kin were coded as alive until the point that they died, and were coded as dead after that point. We also included a dummy variable for missing data for each category of kin. Though we are describing these variables as the ‘survival status’ of kin, we are effectively constructing variables for the presence or absence of kin in the child’s village or one of the neighbouring three villages. We only have information on those individuals who lived in these four villages at some time between 1950 and 1974. ‘Missing’ relatives are therefore likely to be either those who died before 1950 or who are living in a village some distance from the child’s village. Those relatives coded as ‘alive’ are thus only those who were alive and living in the same or nearby village as the child.

The elder sisters and elder brothers variables were included as time-dependent dichotomous variables, coded for whether or not the child had any sisters or brothers who were at least 10 years older than the child. We restricted this variable to siblings at least 10 years older as these siblings are likely to be the most useful carers of the child, and are less likely to be in competition with the child for parental resources than siblings closer in age.

We also tested whether the mother’s remarriage to a new husband increased a child’s mortality risk, as step-parents have been shown to be a risk factor for child death in other studies (Daly and Wilson 1988; but see Temrin, Nordlund and Sterner 2004). This variable was only included in the later childhood model as few remarriages occurred when women had very young children.

Child anthropometric status

The death of a child is an extreme outcome and may be a relatively crude measure of allomaternal investment. Analysing other child outcomes, such as anthropometric status, may allow a more sensitive investigation of the effects of alloparents on child health. Analysing this measure of child health also allows us to investigate the effects of kin beyond the first 5 years of life. We used multi-level linear regression to determine the effects of relatives on three measures of child anthropometric status: height, weight and haemoglobin level. All three measures should indicate the child's level of health: children who are poorly nourished and suffer frequent infections will be shorter, lighter and should have lower haemoglobin levels than those in better health (McGregor et al. 1966; Rowland, Cole and Whitehead 1977). All three models controlled for: age, sex, whether the child was a twin, village, season and cohort of birth, maternal age and parity. The height model controlled for both maternal and paternal height, the weight model for maternal and paternal weight and the haemoglobin model for maternal and paternal haemoglobin.

Because of the longitudinal nature of the dataset, most individuals have a number of measurements taken at different ages. We included all measurements in our models, and performed multi-level models to control for these repeated measurements, as measurements from the same individual will be highly correlated. We tested whether mothers, fathers, maternal grandmothers and grandfathers, and paternal grandmothers and grandfathers had any impact on child anthropometric status. We also included variables for the number of living elder sisters and brothers, and whether the mother had remarried a new husband. In each analysis, approximately 28,000 measurements were included from 3,960 children.

Age at first birth

EHA was used to model the probability of a woman having a first birth between the ages of 13 and 25 years (no woman had a first birth earlier than 13, and first births after the age of 25 were considered unlikely given that women were married at menarche in this population. See Allal et al. 2004 for further details). For all the EHA analyses we have measured time in months, rather than years, in order to increase the sensitivity of the analysis. This means that for the first birth analysis, we needed to know both the woman's date of birth and her age at first birth by month and year. We only have this information on month of birth for women born in 1950 or later, so for this analysis only we included all data collected by the MRC to 2001 in order to obtain a reasonable sample size. Age at first birth has not been as dramatically affected as child mortality by the presence of the permanent research station, but has started to decline in recent years. We have included a variable for birth cohort in the model to control for this effect. This model also controls for the woman’s anthropometric status, which is strongly related to age at first birth, as well as village and season of birth. 437 women were included in the analysis. For this analysis, we tested for any effects of the woman’s mother, father and elder brothers and sisters on her age at first birth.

Reproductive rate

Finally, we investigated the effects of kin on female reproductive rates. Again, we used discrete-time EHA. In this case we modelled the probability of a birth over time since a previous birth, effectively investigating the impact of kin on the length of birth intervals (Sear *et al.* 2003). Multi-level models were again used as most women had several different birth intervals included in the analysis, and women are known to differ in their fecundability. This model controlled for the following factors known to affect fertility: survival status of the index child (born at the start of the interval), maternal age and parity. We tested for the effects of the woman’s mother and father, her husband’s mother and father, whether the women herself had elder living brothers and sisters, and whether she had living daughters and sons at least 10 years older than the index child. 2,532 birth intervals from 765 women were included in the analysis.

Results

Child survival

Relatives are clearly important to child survival over the first 5 years of the child’s life, but different relatives are important at different ages. Table 1 shows the results of the multi-level models of infant, toddler and child mortality. For the parent and grandparent ‘dead’ category, the odds ratios illustrate the risk of death for a child whose relative has died, compared to the risks for children with a living relative. In infancy, mothers are the only relative to exert any impact on child survival rates. Mothers are vitally important at this age: of the 13 children who lost their mothers before reaching the age of 1 year, 12 died (the only survivor was 11 months old when she lost her mother – all the others lost their mothers at an earlier age). This is reflected in the highly statistically significant relationship between mother's death and infant death. During the first year of life, children who have lost their mothers have risks of dying which are more than 6 times greater than those with living mothers.

Mothers are also important during the second year of the child's life, though the odds ratio is slightly lower (5.2). But at this age, maternal grandmothers also have a significant impact on child survival (Figure 1). Children without maternal grandmothers are 1.7 times more likely to die than children with maternal grandmothers. Neither the loss of the mother nor maternal grandmother appears to affect child survival after the age of 2 years, but elder sisters are able to improve child survival rates between 2-5 years. Children with living elder sisters at least 10 years older have risks of dying which are only 0.6 times as great as those without sisters. This effect is independent of the sex of the child (an interaction term between elder sisters and sex of child is not significant - results not shown). Fathers, paternal grandmothers, elder brothers and grandfathers do not have any impact on child survival at any age. However, remarriage of the mother to a new husband did increase the risk of mortality for children between 2-5 years.

Child anthropometric status

Table 2 shows the results of the analysis of child height, weight and haemoglobin level. Here a negative parameter estimate indicates the anthropometric status is lower in the absence of a particular relative. These analyses provide further evidence that mothers, maternal grandmothers and elder sisters are important for improving child outcomes. The absence of a mother or maternal grandmother results in lower anthropometric status for children in all three models, though for both categories of kin this is only significant in the case of height. There is a consistently positive effect of the number of elder sisters on child height, weight and haemoglobin. This is significant for height at the 5% level, and marginally significant ($p<0.1$) for haemoglobin level. Height is a measure indicating long-term anthropometric status, less susceptible to fluctuations due to temporary food shortage or illness than either weight or haemoglobin. Kin effects on weight and haemoglobin may be washed out by other fluctuations in these measurements, at least when the whole 15 year period of childhood is considered in a single model.

There is little evidence that male and paternal kin are beneficial for child health. Fathers, paternal grandmothers and grandfathers have inconsistent effects on child growth across the three measures of anthropometric status. Fathers and paternal grandmothers have no significant effects on anthropometric status in any model. The lack of a paternal grandfather has a significant positive effect on height (i.e. children without paternal grandfathers are significantly taller than those with paternal grandfathers), but non-significant and negative effects on weight and haemoglobin level. The lack of the maternal grandfather also has a significant positive effect on height but a significant negative effect on weight, and a negative but non-significant effect on haemoglobin level. There appear to be no detrimental effects of remarriage to a new husband on child anthropometric status, when all 15 years of childhood are considered.

The number of elder brothers has a consistent negative effect on child growth, significantly so in the case of both height and weight. The effects of both elder brothers and elder sisters were independent of the sex of the child. Interactions between the elder sibling variables and child sex were included in initial models, but dropped because they were not significant. Note that the elder sibling variables are coded as number of elder siblings rather than as a dichotomous variable, as with the other categories of kin (so that a positive estimate means a positive relationship between the number of elder siblings and anthropometric status).

Age at first birth

In contrast to the analysis of child outcomes, female kin don’t appear to make any difference to the age at which a woman has her first birth. Table 3 shows the results of the EHA of women’s first births. In this table, the odds ratios for parents indicate the likelihood of having a first birth per unit time if the parent is living compared to cases where the parent is dead. Higher odds ratios therefore mean a younger age at first birth, lower odds ratios an older age at first birth. There is no significant effect of mothers, but there is a marginally significant (p=0.062) effect of fathers: women with living fathers have earlier first births than those without. Elder brothers also matter for women’s age at first birth. Women with more elder brothers than sisters have relatively early first births compared to women with no elder siblings.

Fertility rate

Once again, kin matters for this reproductive outcome. Table 4 shows the results of the fertility EHA. Parameter estimates and standard errors only, and not odds ratios, are presented in Table 4. When performing EHA it is important to test for significant interactions between each variable of interest and time (in this case, time since last birth) to ensure that the assumption these models make of proportional hazards is not violated. These interactions were not significant in previous analyses so were dropped from the final models. A number of interactions with time were significant in this fertility model, so were retained in the final model. These interactions make the odds ratios hard to interpret, so they have not been presented here. Time in this analysis was modelled as a quadratic function, so interactions with both time (which is indicated by the ‘month’ variable) and time squared were included.

There are no significant effects of having either a living mother or father on the probability of birth. There is a significant interaction between having a living mother and time, suggesting the effects of the mother vary over time since last birth, but no main effect of having a living mother. Having a mother-in-law speeds up a woman’s fertility rate (in Table 4 a positive parameter estimate indicates a higher probability of birth per unit time, and therefore shorter birth intervals). This effect is independent of time since last birth. There is a significant effect of having a living father-in-law, and also a significant interaction between this variable and time. The main effect of fathers-in-law is negative, but the interaction with time alters the interpretation of the estimate. Figure 2 plots out model predictions of the probability of birth over time for women with and without living fathers-in-law, both for cases when the child at the start of the birth interval, or index child, was alive and when the index child was dead (the strongest determinant of the length of birth intervals). These plots indicate that in most cases, the presence of the father-in-law increased, rather than decreased, fertility. The effects of both parents-in-law are small but highly statistically significant. This analysis demonstrates the effects of kin over a single birth interval. The cumulative effect of the presence of parents-in-law on overall fertility is likely to be larger.

Having elder sisters makes no difference to a woman's fertility rate, but having elder brothers decreases her fertility rate. Both elder daughters and sons have significant effects on fertility rate but these relationships are more likely to be explained by parental investment strategies rather than any helping behaviour from older children. Having elder sons and elder daughters slows down, rather than speeds up, a woman's birth rate (though the effect of elder daughters is seen only if the index child is a girl). This suggests women may be slowing down their reproductive rate once a desired family size and composition is achieved.

Discussion

We have shown that relatives matter for all the outcomes we have investigated for this project, but that different relatives matter for different reproductive outcomes. Children without mothers clearly suffer a penalty of poorer growth and higher mortality rates, and have little chance of survival if they lose their mothers during infancy. Perhaps surprisingly, mothers do not have an impact on child survival after the second year of life, but this may be because other relatives are picking up some of the burden of childcare. Maternal grandmothers and elder sisters become important for child survival in toddlerhood and later childhood. The results of the analysis of anthropometric status confirm that maternal grandmothers and elder sisters are beneficial for children, at least in terms of child height (which is perhaps the best long-term measure of child growth).

Both the mortality and anthropometric status analysis suggest that male and patrilineal kin matter little to children, with the exception of elder brothers. Fathers and paternal grandmothers are irrelevant to child growth and survival, as they have no significant impact on any indicator of anthropometric status nor any impact on mortality rates at any age. Grandfathers also make no difference to child mortality. The results of the anthropometric models for grandfathers are hard to interpret given their inconsistency across different measures, but we certainly don't see the consistently positive effect we observe for female, matrilineal kin. Elder brothers even seem to be detrimental to child growth (for both sexes), though this does not show up in increased mortality rates. We may be observing competition between siblings for parental resources here. This is a patrilineal society, and early born sons will have the highest status amongst a family's children, which is likely to result in preferential treatment in terms of food and healthcare allocation.

The importance of female kin

The mortality analysis suggests maternal grandmothers are most important around the time of weaning (which occurs between 18 and 24 months in this population). In this community, maternal grandmothers are known to have an important role around this time in a child's life. Women usually send their toddlers away to another relative to 'forget the breast' when they want to wean a child, and the preferred relative for this task is the woman's own mother (Thompson 1965). Maternal grandmothers are traditionally supposed to prepare high energy foods, such as peanut mashes, for weanlings at this stage, and children without maternal grandmothers may suffer more from the stress of weaning than those whose maternal grandmothers are available to provide such good quality care.

An alternative explanation is that the mortality of children and their grandmothers could be positively associated because of genetic or environmental correlations. Some families could be healthier than others, because of fortunate genetic or environmental endowments, which would lead to a correlation between the survival of different family members. We do not think this is an adequate explanation in this case for the following reasons. Firstly, the effect is specific to the maternal grandmother. If genetic or environmental factors were important, we would expect to see this relationship with other grandparents (particularly as the child is more likely to live with his paternal than his maternal relatives). Secondly, the mortality effect is specific to the period around weaning, and is not seen in early or later childhood. If the correlation were due to genetic or environmental effects, then we would expect to see it at all ages. Finally, we have a plausible mechanism: we know that maternal grandmothers have a role to play in childcare that is particularly important around the time of weaning.

We find that elder sisters are also important for child anthropometric status and survival, regardless of the child's sex. Elder sisters have a role to play in childcare in the Gambia, as is common in other traditional societies (Weisner and Gallimore 1977; Borgerhoff Mulder and Milton 1985; Bove, Valeggia and Ellison 2002). Weaned children are allocated a nursemaid, preferably an elder sister of the child (though other young female relatives or occasionally brothers may be co-opted into this duty). Nursemaids are responsible for looking after small children while their mothers are busy in the fields, or with other chores (Thompson and Rahman 1967). Again, our analysis suggests that the quality of care provided by elder sisters is sufficient to show up as improved child anthropometric status, and improved mortality rates for children between the ages of 2 and 5 years. The effects on mortality and growth are independent of sex, and should not be confounded by birth order since this is controlled for in the model. The effect therefore seems unlikely to be due to parental investment strategies. It also seems unlikely that phenotypic correlations are causing the relationship, since we have controlled for differences in mortality experience between women, and because we do not see the same positive correlation between elder brothers and mortality or growth. In fact, for anthropometric status the relationship with elder brothers is negative.

Implications for the evolution of menopause

In the Introduction, we described the grandmother hypothesis for the evolution of menopause. This hypothesis states that, as the costs of giving birth to one's own children increase with age, it becomes adaptive for women to switch to investing in their existing children and grandchildren rather than continuing to risk giving birth themselves (Hawkes et al. 1998). More recently the hypothesis has been re-phrased to emphasise that it is long post-reproductive survival that is the derived trait that needs to be explained, rather than menopause itself (Hawkes 2003). Whichever way this hypothesis is framed, it predicts that children will have higher survival rates in the presence of grandmothers, exactly the pattern we see in this Gambian society. However, despite recent claims to the contrary (Hawkes 2004; Lahdenpera *et al.* 2004), finding positive effects of grandmothers on child survival or other components of reproductive success in a single society does not allow us to come to any conclusions about the evolution of menopause. Menopause may have evolved so that grandmothers could switch to investing in their grandchildren, or grandmothers could be investing in their grandchildren because menopause makes them unable to continue having children of their own (and investing in grandchildren is better than investing in nothing at all).

One way to try to understand the evolution of menopause is to build mathematical models which can be used to investigate theoretically the costs and benefits of menopause or long post-reproductive life (Rogers 1993; Shanley and Kirkwood 2001; Lee 2003). Our collaborators at the University of Newcastle, Daryl Shanley and Tom Kirkwood, have built a model based on parameters estimated from this Gambian population to do just this (Shanley et al. in prep). Their model finds important support for the contribution of the grandmother effect to the evolution of menopause, although the optimal age at last birth is predicted to be a little later than the average age at menopause. The loss of the mother has a much stronger detrimental effect on child survival than the loss of the grandmother, but the loss of the mother is a rare event. The loss of the grandmother, therefore, has a more important effect on the costs and benefits of menopause than the loss of the mother, and may help explain the evolution of this phenomenon.

Do men matter?

Contrary to the hypothesis that it is male provisioning and care which is a distinguishing feature of human life history, fathers make absolutely no difference to child anthropometric status and survival in this society. There is marked division of labour by sex in this community: fathers are not involved in direct childcare, and mothers produce a substantial proportion of the food consumed by children. This is a highly polygynous society, and men may direct their labour towards acquiring resources which can be used to marry other wives, rather than invest in their existing children. However, we do find a negative effect of divorce and remarriage on child survival rates. The mother’s divorce and remarriage means that the child will either move to a new (and unrelated or distantly related) man’s compound, or be left behind in the father’s compound without the mother. Either event is likely to increase stress and disruption (see Flinn and England 1995; also Flinn this volume for increased stress in children with step-parents), apparently increasing mortality rates (we have never come across any suggestion in the ethnographic literature that step-fathers may be involved in deliberate infanticide of children in the Gambia). The mother’s widowhood, on the other hand, may frequently involve minimal disruption to the life of a child. This society practises the levirate (widows being inherited by their husband's brother), and patrilineally related men tend to live together in the same compounds in the Gambia. The death of a father may then mean little change to the child's life, as well a step-father who is closely genetically related.

Male and patrilineal kin do seem to be more important for a woman's fertility than her female, matrilineal kin, however. There is some suggestion that fathers do matter for a woman's age at first birth, though this is not a particularly strong effect: women without fathers have later first births than those with fathers. Fathers are responsible for arranging women's marriages, and women without fathers may have slightly delayed marriages if they have to rely on other relatives to perform this task. This contrasts with studies in other ecologies which have found the presence of fathers inhibits their daughters' sexual and reproductive behaviour (Flinn 1988; Ellis et al. 2003), (but see Waynforth 2002 for a similarly positive effect of fathers on their daughters' first births). Having elder brothers also speeds up a woman's first birth. Girls are useful to their mothers in terms of childcare and other domestic tasks, and mothers may be reluctant to let a daughter marry and leave home until her brothers have brought in wives to replace her. Additionally, families with elder brothers may be keen to see their daughters married off quickly, as the brideprice a daughter brings in can be used to buy wives for her brothers.

Conflicts of interest between women and their husband's kin

While the lack of a father effect on child growth or survival can be explained away by the division of labour in this society, that paternal grandmothers also do not provide care for their grandchildren perhaps needs more explaining, especially as children are more likely to live with their paternal than their maternal grandmothers in this patrilocal society. Grandmothers may invest their limited time and energy in their daughters' children rather than their sons' children, because investing in the matrilineal line is a safer genetic bet. Their daughter's children will certainly be related to them; their sons' (putative) children might not be. We have no quantitative estimates of paternity uncertainty in this population, but a few cases of children being fathered by men other than the mother's husband were documented by McGregor.

The large age differences between spouses in this society, and the late age at which men marry might suggest some opportunity for uncertain paternity.

A simpler explanation may be that the large age differences between husbands and wives in this community mean that grandmothers are younger and healthier when their daughters' children need care than by the time their sons have children. However, controlling for grandparents' age in both the child mortality and anthropometric status models made no difference to the results. And other studies have shown that the presence of paternal grandmothers is either less beneficial to their grandchildren than that of maternal grandmothers, or may even increase the mortality rates of their grandchildren (Sorenson Jamison *et al.* 2002; Voland and Beise 2002). This has been attributed to conflict between women and their mothers-in-law, which results in higher mortality rates of young children, and may increase the risk of dying of the women herself (Skinner 1997).

There are clearly conflicts of interest between men and women in their reproductive strategies, particularly so in a highly polygynous society such as this, where men's reproductive strategies are very different from women's. Men in the Gambia desire much larger family sizes than do women (Ratcliffe, Hill and Walraven 2000). These conflicts of interest may spill over onto the relationships between a woman and her husband's kin, as a woman's in-laws will be attempting to maximise the reproductive success of their own kin rather than that of his wife. Our study found that the presence of a mother- or father-in-law speeds up a woman's fertility rate, while her own relatives have no impact on her reproductive rate. As both the husband's father and mother have this effect, it seems unlikely that it can be explained by any helping effect of parents-in-law reducing the energetic burden on women (by taking over some childcare or subsistence duties) and thus allowing them to conceive earlier. Instead, we suggest husband's parents may put social pressures on women to give birth to many children, to maximise their son's reproductive success. Such social pressures may be less likely to come from a woman's own family, as giving birth to many closely-spaced children can be detrimental to women's health (Jelliffe and Maddocks 1964; Tracer 1991). Women are not genetically related to their husbands' parents, so that in-laws may emphasise a woman's reproductive duties even at the expense of her own health, as daughters-in-law are to some extent expendable.

Elsewhere, mothers-in-law have been found to have stronger desires for their daughters-in-law to continue reproducing than did the women themselves, and these views tended to coincide with their sons’ opinions on family size (Kadir et al. 2003). Such conflicts of interest may, in some cases, result in the increased mortality rates of women and children described above (see the paper entitled "The husband's mother is in the devil in the house" for a more detailed discussion of this topic: Voland and Beise 2005).

Conclusion

We have conducted a detailed investigation of the effects of relatives on various components of reproductive success in a single society, and found significant effects of kin on all the life history characteristics that we have investigated. But can these results be generalised to draw useful conclusions? Given the wide variety of social and ecological environments the human species inhabits, it is dangerous to extrapolate from the study of a single society to the human species as a whole. As evolutionary ecologists, we believe research such as this is most useful when it can be considered alongside similar studies which have been conducted in different socio-ecological environments. Generalisable conclusions can then be drawn from a comparison of the similarities and differences in the helping behaviour of kin across a variety of populations. The growing body of research investigating the effects on kin on aspects of reproductive success has been carried out across a variety of environments and subsistence strategies including: South American hunter-gatherers (Hill and Hurtado 1991; Hurtado and Hill 1992; Waynforth 2002); farmers in historical Europe, Canada and Japan (Sorenson Jamison *et al.* 2002; Voland and Beise 2002; Lahdenpera *et al.* 2004; Beise 2005); contemporary populations in Eastern Europe, North Africa and Asia (Bereczkei 1998; Crognier *et al.* 2001; Griffiths, Hinde and Matthews 2001; Leonetti and Nath 2004; Leonetti et al. 2005).

In a recent review of this research, we found a number of common themes, but concluded that ecological context is also important in determining the importance of kin to demographic outcomes (Mace and Sear 2005). Of most importance to this symposium was the finding that in all populations there were beneficial effects of at least one relative (apart from the mother) on child survival. This suggests that alloparenting is an adaptive strategy, and that mothers are disadvantaged if they cannot co-opt other individuals into helping them raise their children. But we find some variation between societies in which relatives are beneficial. A common theme is that maternal grandmothers are good for child survival, whereas paternal grandmothers are less important or even detrimental (though there are exceptions: see Sear 2003 for an example of paternal grandmothers who are more beneficial than maternal, and; Beise 2005 for an example where both paternal and maternal grandmothers improve child survival). The effects of fathers are mixed, suggesting that paternal investment is contingent on environmental conditions (see chapters in Hewlett 1992 for cross-cultural perspectives on paternal investment strategies). These results suggest that the Western emphasis on the nuclear family as the most important unit for child well-being may be misguided, and that there is a variety of family structures in which children can thrive.

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Table 1: results of multi-level EHA showing effects of kin on child mortality (separate models shown for infant, toddler and later childhood mortality).

	Infant			Toddler			Later childhood		
Variable	Estimate	(SE)	**Odds ratio**	Estimate	(SE)	**Odds ratio**	Estimate	(SE)	**Odds ratio**
Constant	-3.35	(0.35)**		-5.02	(0.58)**		-3.52	(0.47)**	
Mother:									
Dead	1.82	(0.51)**	**6.2**	1.66	(0.61)**	**5.2**	0.35	(0.56)	**1.4**
Alive	0		**1.0**	0		**1.0**	0		**1.0**
Father:									
Dead	0.13	(0.61)	**1.1**	-0.73	(0.73)	**0.5**	-0.33	(0.39)	**0.7**
Alive	0		**1.0**	0		**1.0**	0		**1.0**
Maternal grandmother:									
Dead	0.13	(0.19)	**1.1**	0.55	(0.27)*	**1.7**	-0.09	(0.26)	**0.9**
Alive	0		**1.0**	0		**1.0**	0		**1.0**
Paternal grandmother:									
Dead	-0.25	(0.19)	**0.8**	-0.17	(0.24)	**0.8**	-0.05	(0.23)	**0.9**
Alive	0		**1.0**	0		**1.0**	0		**1.0**
Maternal grandfather:									
Dead	0.07	(0.18)	**1.1**	0.28	(0.26)	**1.3**	0.01	(0.24)	**1.0**
Alive	0		**1.0**	0		**1.0**	0		**1.0**
Paternal grandfather:									
Dead	0.28	(0.16)	**1.3**	-0.05	(0.38)	**0.9**	-0.29	(0.21)	**0.7**
Alive	0		**1.0**	0		**1.0**	0		**1.0**
Living sisters 10+ years older:									
Yes	-0.03	(0.18)	**1.0**	-0.07	(0.25)	**0.9**	-0.48	(0.24)*	**0.6**
No	0		**1.0**	0		**1.0**	0		**1.0**
Living brothers 10+ years older									
Yes	0.06	(0.19)	**1.1**	-0.22	(0.26)	**0.8**	-0.30	(0.24)	**0.7**
No	0		**1.0**	0		**1.0**	0		**1.0**
Mother remarried:									
Yes	-	-		-	-		0.65	(0.27)*	**1.9**
No									**1.0**
Mother level variance	0.39*	0.16		0.36	0.28		0.44*	0.12	

* p < 0.05, ** p < 0.01. All models control for sex of child, maternal age, parity, length of preceding and succeeding birth intervals, village of birth and whether the child was lastborn

Table 2: results of multi-level regression models showing effects of kin on child anthropometric status (separate models shown for child height, weight and haemoglobin level)

	Height		Weight		Haemoglobin	
Variable	**Estimate**	**(SE)**	**Estimate**	**(SE)**	**Estimate**	**(SE)**
Constant	7.05	(3.33)**	-8.49	(0.42)**	6.85	(0.31)**
Mother dead	-0.63	(0.29)*	-0.11	(0.10)	-0.09	(0.09)
Father dead	-0.25	(0.19)	-0.04	(0.06)	0.09	(0.06)
Maternal grandmother dead	-0.55	(0.19)*	-0.02	(0.06)	-0.05	(0.05)
Paternal grandmother dead	0.18	(0.18)	-0.02	(0.06)	-0.03	(0.05)
Maternal grandfather dead	0.39	(0.17)*	-0.27	(0.06)*	-0.03	(0.05)
Paternal grandfather dead	0.65	(0.22)*	-0.08	(0.07)	-0.18	(0.06)
Living sisters	0.19	(0.09)*	0.02	(0.03)	0.04	(0.02) †
Living brothers	-0.20	(0.09)*	-0.07	(0.03)*	-0.01	(0.02)
Mother remarried	0.18	(0.34)	0.02	(0.11)	-0.09	(0.08)
Child level variance	17.91	0.52**	1.87	(0.06)**	0.75	(0.03)**

† p<0.1, * p<0.05, **p<0.01. All models control for age, sex, whether the child was a twin, village, season and cohort of birth, maternal age and parity, and parental anthropometric status

Table 3: results of EHA showing effects of kin on female age at first birth

Variable	**Odds ratio**
Mother:	
Dead	1
Alive	0.95
Father:	
Dead	1
Alive	1.27†
Elder siblings:	
None	1
More sisters than brothers	0.95
More brothers than sisters	1.48*
Same number brothers and sisters	0.90
Missing data on birth order	0.96
Missing data on sibling sex	0.60*

† p <0.1, * p < 0.05. Model controls for birth cohort, anthropometric status, village and season of birth

Table 4: results of multi-level EHA showing the effects of kin on female fertility

Variable	**Estimate**	**SE**
Constant	-9.86	(0.27)**
Mother alive	-0.01	(0.15)
Mother*month	-0.04	(0.02)*
Mother*month^2	0.001	(0.0003)*
Father alive	0.08	(0.08)
Husband's mother alive	0.21	(0.08)**
Husband's father alive	-0.80	(0.11)*
Husband's father*month	0.10	(0.03)**
Husband's father*month^2	-0.002	(0.0008)**
Elder brothers	-0.22	(0.09)*
Elder sisters	0.06	(0.09)
Living sons at least 10 yrs older than index child	0.68	(0.19)**
Sons*month	-0.03	0.006)**
Living daughters at least 10 yrs older than index child	-0.49	(0.13)**
Daughters*sex of child	0.44	(0.16)**
Woman level variance	0.27	(0.04)*

* $p < 0.05$, ** $p < 0.01$. Model controls for survival status of the index child (born at the start of the interval), maternal age and parity

Figure 1: Kaplan-Meier plot showing the effect of maternal grandmothers on child mortality. Solid line shows children with living maternal grandmothers, dotted line children without maternal grandmothers

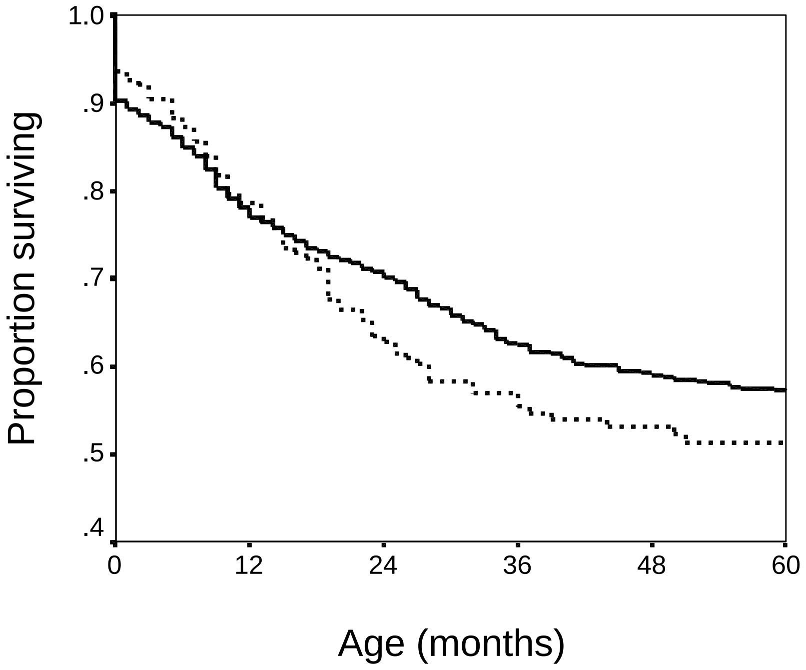
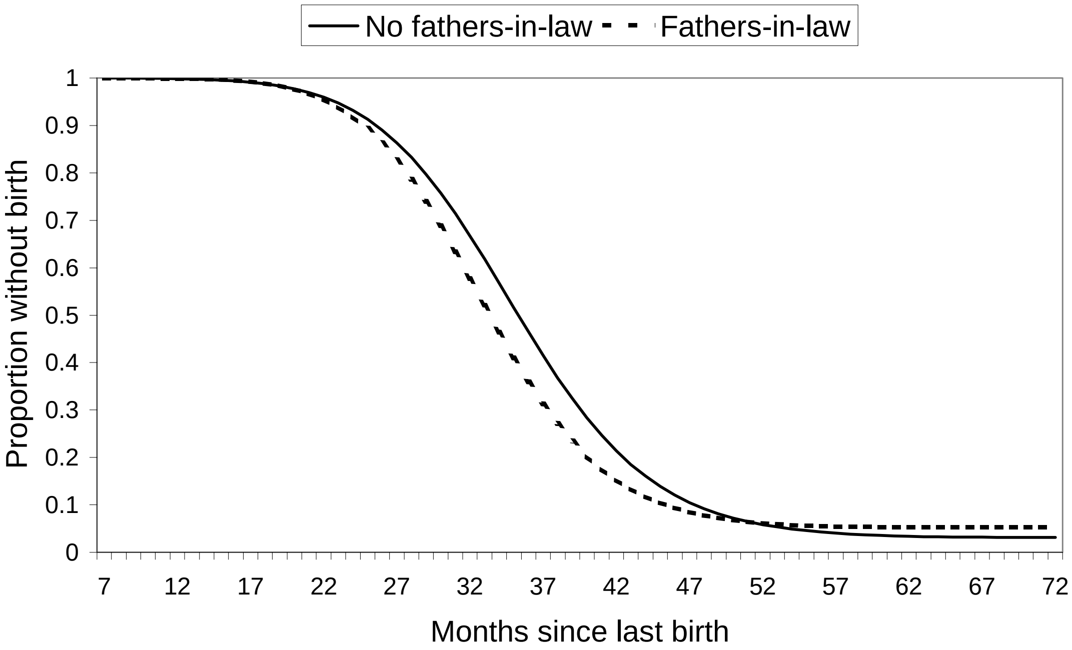


Figure 2: survival plot using model predictions of the effect of the husband's father on probability of birth for cases where the index child was alive (a) and cases where the index child was dead (b). Model was fitted using reference categories for all other variables but maternal age and parity (model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

(a) index child alive



(b) index child dead