

Are humans cooperative breeders?

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Summary

There is evidence to suggest that human female reproduction is assisted by other members of her family. In particular studies show that fathers and grandmothers are important in supporting her reproductive success. In this paper, we examine the effects of specific kin on specific components of fitness, and show that the contributions of matrilineal and patrilineal kin are very different. Fathers contributions to child survival are mixed, possibly being more significant in monogamous societies. Maternal grandmothers and other matrilineal kin tend to improve child survival but not female fertility, whereas patrilineal grandparents and male kin tend not to help child survival but do enhance the mothers rate of birth. We argue that these different strategies emerge as a response to different relatedness to the mother, because the costs of maternal mortality differ between the two lineages: patrilineal kin are less concerned about women paying the high costs of reproduction associated with high fertility.

Models of the grandmother hypothesis for the evolution of menopause generally find that the magnitude of grandmother effects is not large enough to compensate for the loss of later life fertility. However recent developments in modelling approaches do highlight the importance of transfers (be it of care or resources) in the evolution of human longevity and fertility schedules. These remain the most plausible explanation for the unusual features of the human female life history, including high birth rates and menopause.

Introduction.

The human life history suggests that human females do not raise their children without help. The human interbirth interval of about 3 years, in natural fertility populations, is out of line with that of other great apes of similar body size. For example, the orangutan has an interbirth interval of about 8 years, and chimpanzee 4-5 (Galdikas and Wood 1990). Only the gibbon (less than 25% of the weight of human) has an interbirth interval of 3 years. The ape mothers rear their offspring without help. If human females are capable of such rapid reproduction (albeit possibly with a higher rate of infant mortality too), most anthropologists agree that this is due to the support they receive from other family members. The 'traditional view' has been that this help comes from the father – hence the human pair-bond is based on mutual interdependence of husband and wife to raise their children. In hunter-gatherer societies, the division of labour is nearly always such that men bring back meat to the band, whereas women gather. However, the importance of the male contribution to the subsistence of the women and children has been questioned (Hawkes 1990). The observation that calories brought back from gathered foods tends to exceed that from hunting, combined with the fact that meat is nearly always shared widely throughout the band rather than strictly within the nuclear family, have led to the suspicion that women are not as dependent on men to raise their family as once thought (Hawkes, O'Connell et al. 1997). It is possible that older women, grandmothers in particular, fill that gap. If grandmothers were helping to support their daughter's children, then two unusual features of human female life history – menopause and high birthrates - can potentially be explained in one go. Both arise because menopause is an adaptation to enable grandmaternal support, which in turn enables a high human birth rate.

Who supports the family in hunter-gatherer societies?

How might empirical studies help us to distinguish between these two views of the human family? Empirical studies on hunter-gatherer communities are data-limited, due to both the very small number of such societies that survive, and the very small number of individuals living in something approaching a hunter-gatherer lifestyle within those societies. This may have contributed to the fact that a consensus view on the relative importance of fathers as compared to grandmothers has not emerged.

The main line of evidence in this debate came from nutritional studies. Hawkes et al (1997) point out that in the Hadza of Tanzania, children with older female relatives in their band are better nourished, and their data suggest that the hunting season is not actually a particularly good time of year for children. Studies on foraging strategies in the Ache of Paraguay and in the Hadza highlight the fact that total calories and energy return rates from gathering often equal or even exceed that from hunting (Hill, Kaplan et

al. 1987; Blurton Jones, Marlowe et al. 2000; Marlowe 2003). Isotope studies on pre-historical Californians suggest that male and female diets were so different that they appeared to be almost on different trophic levels (Walker and Deniro 1986); the males appeared to have been living almost entirely off marine resources whereas the females must have been eating food almost exclusively terrestrial in origin. This suggests that food sharing between the sexes was minimal. But Hill (1993) and others have argued that the nature of the food brought back by males is superior and very important, leading them to conclude that the contribution of males to family nutrition is very significant, at least in the Ache. And Marlow (2003) shows that male provisioning occurs at very important times in the Hadza, such as when women's foraging is handicapped because she recently gave birth. Arctic hunters, like the Inuit, are almost entirely dependent on hunted food brought in by men. In the coldest areas, babies and young children could barely survive outside for much of the year, and thus females are almost by definition dependent on their spouse for almost everything.

A second line of evidence comes from attempts to measure the impact of kin on components of fitness directly; specifically on fertility and mortality. In this sphere, hunter-gatherer studies are even further handicapped by the lack of data. Demographers prefer sample sizes in the thousands rather than the hundreds to estimate age-specific fertility and mortality rates (and estimates that are not adjusted for age are rarely meaningful). To date, really only one study of a hunter-gatherer group – the Ache – have had sufficient demographic data collected to measure kin effects on fitness (Hill and Hurtado 1996). Using life history data from several hundred Ache children, Hill and Hurtado find that fathers are very important to child survival, probably largely through their roles as protectors from infanticide. There were very few surviving grandmothers in the Ache population at the time of Hill and Hurtado's study, and so, although anecdotal evidence suggested that grandmothers could play an important role, there was little statistical evidence that grandmothers had much impact on the fitness of their descendants.

All these findings raise the possibility that the ecology of the system influences the relative importance of fathers, grandmothers, and potentially other kin such as siblings or older offspring, in the rearing of human children. This should come as no surprise to behavioural ecologists. The variability in hunter-gatherer ecology further highlights the fact that data from just one type of population cannot answer our initial question – are humans communal breeders? We will argue here that it is not necessary or sufficient to restrict our studies to hunting and gathering communities, none of which are necessarily cases of special importance in human history. Furthermore, very few hunter-gatherer studies can generate large enough sample sizes to estimate important determinants of rare events like mortality, or low variance measures like fertility. There are a small number natural fertility and natural mortality populations for which large sets of demographic data are available, some of which are historical populations. These are now being analyzed to enhance our understanding of which kin have an influence on the fitness of their descendants. Most of these populations are of farmers, but still farmers with high workloads, high disease burdens and high reproductive rates. Whilst most of these populations are/were growing rather than stable, the same can be said of contemporary

hunter-gatherers populations too. We need to use as much data as is available to us to unpack the full story of the evolutionary ecology of human family life.

Kin effects on components of fitness in a range of natural fertility/natural mortality populations.

When measuring the interdependence of family members, it is studies of how the presence or absence of kin is related to the survival of children or the fertility of women that have provided measures most closely related to biological fitness. There are many studies on the contributions of different kin to childcare, to nutrition and to other aspects of development (Hurtado and Hill 1992; Hewlett, Lamb et al. 2000; Ivey 2000) that contribute greatly to our understanding of social networks and child-rearing, and can help us interpret findings from demographic data. However it is not always easy to determine the extent to which such help enhances the fitness of the beneficiary. So in this review we shall concentrate in particular on studies that have examined specific components of fitness.

Table 1 lists some of the studies published to date that have investigated how the loss of either a parent or a grandparent has influenced child mortality, in a natural fertility/natural mortality population. Rates of child mortality are usually one of the strongest determinants of a woman's lifetime reproductive success (and are clearly the strongest determinant for the child concerned!). Therefore the results found in these studies are likely to be a good reflection of how family members influence each other's fitness. However the results of such analyses still have to be interpreted with caution. Correlational studies are helpful, but do of course suffer from the usual problem of attributing causation. Given that kin can share not only genes but frequently much of the same environment, there is a high possibility that confounding variables, not included in the analysis, are of great significance. Thus, if the absence of certain kin is associated with high child mortality, this is not necessarily evidence of their importance as carers. Event history analysis with logistic regression, in which the death of a key relative can be entered as a time varying co-variate, can go some way towards alleviating this problem; this is because the change in child mortality risk before and after the death of the relevant kin is estimated, whilst many of the potentially confounding variables will remain constant over time. Many studies are now employing this technique (taking their lead from Hill and Hurtado 1996), when the quality of the demographic data allow, and we have restricted Table 1 to those studies that have used this approach or something similar. Multilevel event history analysis can be used to estimate family level variance in mortality, and attempt to remove it. This allows the use of the maximum amount of data, because several children from the same family can be included in the same statistical analysis. Sear et al (2000, 2002) use this technique to show that mothers, maternal grandmothers and older sisters all had a positive impact on the survival of children under 5 in rural Gambia, whereas fathers did not have any measurable effect.

Nonetheless, spurious correlations between the mortality of kin could still emerge. For example, if epidemics or other waves of mortality were to hit family members at the same time they would cause correlated mortality that was actually independent of the effect of

parental care. In a study of early Quebec, Pavard et al (in press) use carefully selected data that excluded peaks of mortality and compared the rates of death in families before and after the death of the mother, to estimate the effect of maternal care. They show that the effect of the death of the mother on her children, especially her daughters, is harmful to their survival prospects for over a decade after her death, and throughout the child's teenage years.

Interpreting the absence of an effect is also difficult. It could be lack of data, or it could be simply that a large number of relatives are important, so no single relative emerges as having a significant impact. Thus, a string of non-significant results should not necessarily be taken to mean that mothers are capable of rearing children without help. Relationships based on reciprocal altruism (such as with co-wives) may come into play when kin relationships are absent. Different relatives may be substitutable to at least some extent. It is possible that the death of one relative, such as a grandmother, could cause another relative, such as a father, to greatly increase their level of support; Leonetti et al (in press) give examples of how husbands workloads are reduced by the presence of maternal grandmothers. In this way one helper would be sharing some of the burden of the loss of the other kin helper with the mother. If such facultative helping is occurring, then many of the kin effects that we describe that are estimated by the impact of bereavement could be underestimates of the actual contribution of the relative concerned.

Who keeps children alive?

Whilst taking the appropriate caution, it is nonetheless possible to examine the results in Table 1 to enhance our understanding of human families. There are clearly differences between groups and/or between studies in which kin are important. Many studies only address one kin relationship, and different sample sizes mean that effects may not be detected in some studies simply because data quantity or quality does not allow. However, despite this, several clear patterns emerge.

All studies that have sought it, have found mothers have an exceedingly important influence on child survival, especially in the first two years of life. This is not surprising, not least due to the requirement of breast-feeding, but some authors have been surprised at the magnitude of the effect when compared to the effect of fathers, especially in societies where fathers generate more of the household income (Reher and Gonzalez-Quinones 2003). What is of particular interest to our study here, is the fact that the effect usually declines rapidly with the child's age. Older children are disadvantaged by their mother's death, but children as young as two, who are still hopelessly incapable of independent life, often have a very good chance of survival. In our Gambian study the survival of children who had lost their mother after their second birthday was not significantly lower than that of children with mothers (Sear et al 2002). Whilst a significant effect may well have become apparent had there been more data, it nonetheless emphasizes how other kin are capable of playing a key role in child-rearing.

The role of fathers is inconsistent. Most studies have not found much effect of fathers on their children's survival. The Ache are an exception in this regard, possibly due to their

role in reducing the risk of infanticide (Hill and Hurtado 1996). Where effects are found, authors generally attribute the father's contribution to socioeconomic status as the key intervening variable. It is possible that the care and domestic labour that is generally provided by mothers is even more important to a child's welfare than the additional material resources often provided by fathers. In polygynous societies, men have the option of spending their resources on attracting additional wives. This could account for some of the variation, for example the absence of a father effect in polygynous Gambians (Sear et al 2002), but a significant positive effect of fathers in monogamous, historical Quebec (Beise, this volume). In some patrilineal societies like the Mandinka in the Gambia, it is common practice for women to marry her husband's brother in the advent of her husband's death – thus children and property and the women herself remain within the patriline, from which they should be supported. This could explain why divorce appeared to me more damaging to children's survival prospects than father death in the Gambia (Sear et al 2002).

It is clear that divorce almost always leads to poor outcomes for child survival. But it is not clear how much of this is due to father absence or to step-father presence or to mother absence (divorcing women may be unwilling or unable to take children with them) or indeed to the stress and violence of the divorce itself (Bhuiya and Chowdhury 1997).

The role of maternal grandmothers is clearly positive. Whilst renewed interest in the grandmother hypothesis for the evolution of menopause, combined with the difficulty of publishing non-significant results, may have influenced the published literature on this topic, it nonetheless appears unambiguous that maternal grandmothers are beneficial to the survival of their grandchildren. The magnitude of the maternal grandmother effect is not as large as the effect of mothers (Table 2); but the data do seem to suggest that their importance to child survival generally equals or exceeds that of fathers.

The role of paternal grandmothers is less clear. In most studies their impact is not significant or mixed. This may be in part due to their greater age than maternal grandmothers (due to females reproducing earlier than males) and also to their lower level of genetic relatedness to their patrilineal descendants (due to paternity uncertainty). But there are repeated suggestions not just of no effect but of negative effects, non-significant in the case of the Gambia (Sear et al 2002) but more significant in historical Germany (Volland & Beise 2002) and historical Japan (Jamison, Cornell et al. 2002). The fact that paternal and maternal grandmothers often have opposing effects may also explain why studies that do not distinguish between the two do not find any effect of grandmothers (such as the Ache study, Hill and Hurtado 1996). Jamison et al (2002) highlight the possibility that paternal grandmothers in Japan are influenced by concerns of lineage, which means that certain children (such as later born boys who may be unwelcome competitors for favoured male heirs) are particularly disadvantaged, whereas other grandchildren may be supported. Such sex-specific and birth order biases, which are found in a number of wealth-inheriting societies, would confound attempts to label individual kin relationships as always positive or negative for child survival. Such

grandmothers would, nonetheless, be attempting to promote their lineage, albeit at the expense of certain unfortunate grandchildren.

Finally, there are indications in at least one study (Sear et al 2002) that sisters old enough to be helpful carers (aged 10+) are enhancing the survival prospects of their younger siblings. Correlational evidence from Bolivian Aymara (Crognier et al 2002) and Moroccan Berbers (Crognier et al 2001) also suggest older siblings reduce infant mortality, probably in these cases through economic contributions as well as direct care. But it is hard to generalize about sibling effects, as young siblings are usually in competition with each other for food and parental care, and are frequently detrimental to each others survival (LeGrand and Phillips 1996). So support from offspring helpers at the nest (which is so significant in communally breeding birds) are unlikely to be the underlying cause of the high human birth rate (in the way that support from fathers or grandmothers may be). Nonetheless, for a small window in middle age, older daughters who are not yet reproductive may transfer significant assistance to their mother's children lower down the birth order. This window coincides with a time period when grandmothers are more likely to be dead, so older children could be taking their grandmother's place as alloparents.

In Table 2 we show relative size of the effect of loss of a relative for each category of kin, from our Gambian study (Sear et al 2002). This is one of the few studies that has looked at all these kin relationships and thus allows relative effect sizes to be compared. Clearly one study does not speak for all, but it is notable that so many of the main effects in other studies are similar in outcome.

Which kin influence female fertility?

Interpreting kin effects on fertility is even more problematic than interpreting effects on mortality. Reproductive success is a combination of fertility (birth rates and reproductive span) and child mortality. Correlates of reproductive success frequently tell us more about infant mortality than they do about birth rates. Furthermore, infant mortality and birth rate are usually highly correlated for the simple reason that the death of an infant speeds the onset of the next pregnancy. Therefore high fertility is a double-edged sword – it may tell you as much about wasted parental investment as it does about reproductive success. Furthermore, fertility is very heavily dependent on age, so any statistical analyses that do not control for age effects run the risk of becoming severely confounded. Fertility also has many components (age at first birth, several birth intervals, age at last birth). So if, for example, effects on birth interval are small, it should be remembered a woman will have many birth intervals so lifetime effects may be cumulative.

In Table 3 we present studies that have examined kin effects on specific components of fertility, such as birth interval and age at first reproduction, in natural fertility populations. We only include studies that have attempted to control for both age and prior mortality of infant (if relevant) and have used data based on time-series when effects can be precisely associated with the absence of a certain relative. We have not

included husbands in this table, as clearly the death of a husband is likely to reduce the birth interval in almost any society (albeit only by 9 months in the case of the Gambia (Sear et al 2003)).

Data are limited, but it is nonetheless striking that the kin who influence fertility tend to be completely different from those influencing child survival. Whereas maternal grandparents and matrilineal kin in general reduce child mortality, they do not appear to have any significant effect on women's rate of giving birth. Although (Berezkei 1998) use correlational evidence to argue that elder female siblings do enhance mothers fertility and Crognier et al (2002) argues that they correlate with later age at last birth, there are as yet no studies using event history analysis that confirm such findings. Several studies using event history analysis seem to suggest adult siblings can even have a negative effect (Hill and Hurtado 1996, Sear et al 2003). However patrilineal kin (husband's parents), who tended to have no effect or a negative influence on child survival, tend to be positively associated with female fertility. Studies report patrilineal kin shortening birth intervals and bringing forward age at first birth. Two studies which examine it show father presence correlated with earlier age at first birth in their daughters, which is actually an effect in the opposite direction of that generally seen in Western society (Ellis, Bates et al. 2003). The effect in the natural fertility populations could be through nutrition or political influence on marriage and fertility decisions: in the case of the Gambia we suspect the latter, as children with fathers were no better nourished than those without (Sear et al 2000). When brideprice is an issue, early marriage of daughters might assist with paying for the marriage of their brothers or remarriage of their fathers, so the extent to which early marriage is beneficial to daughters is actually not clear. A study of Pakistani families found that fathers and mothers-in-law wanted women to have more children (irrespective of gender) than did the mothers themselves (Kadir et al 2003). The data we review here suggests that such preferences from the patriline do have an influence on women's fertility. Whilst these kin effects on fertility are small, what is striking is that they are so diametrically opposite to those found for child mortality.

In cases where residence is patrilocal, the husband's parents do have more opportunity to help directly with domestic chores and income generation; but if this were the root of the effect, it is surprising that it does not equally influence child survival. We suspect the explanation lies in the relative importance of female survival to matrilineal and patrilineal kin. In natural fertility populations, women's optimal reproductive rates are likely to be the result of a trade-off between the benefits of high fertility and the costs in terms of both higher child and maternal mortality. Clearly the death of either mother or child would have a strong negative effect on the inclusive fitness of all kin, but the magnitude of the effect nonetheless differs between matrilineal and patrilineal kin. Children are more closely related to matrilineal than equivalent patrilineal kin by $1/p$ where p is the probability of paternity. Thus in all circumstances except that where $p=1$, grandparents are more closely related to their daughters' children than to their sons' children. Mothers are not related to their children's patrilineal kin at all. Thus the death of either a child or a mother is weighted differently in the currency of inclusive fitness. In the case of the mother's death, whilst her children do suffer fitness costs, the husband can continue to reproduce through remarriage; whereas to the matriline she is irreplaceable. Costs of

reproduction in women are hard to demonstrate in natural populations, due to phenotypic correlations. But life history theory (Kirkwood and Rose 1991) and experiments on animals (Gustafsson and Part 1990) and careful statistical analyses of human life histories (Doblhammer and Oeppen 2003) show us that they are likely to be real. High birth rates are a gamble that hardy mothers may pull off but weaker mothers and their children will suffer from. It is possible that the negative effects of patrilineal grandparents on grandchild survival are a direct consequence of the effect they exert through pressure on women, or on the women's husbands, to achieve higher fertility. It is notable in our Gambia data that, whilst those women who had the highest birth rates of all had the highest rates of infant mortality, they did nonetheless have the largest families of surviving children. Whether this was at some cost to their own longevity remains to be seen.

What are the implications for the grandmother hypothesis for the evolution of menopause?

The grandmother hypothesis has several forms, all basically asserting that menopause is a kin selected adaptation allowing older mothers to assist with the rearing of either their children or grandchildren (Williams 1957; Hamilton 1966; Peccei 2001). Packer et al (1998) argue that a period of reproductive senescence is inevitable for a period at the end of the lifespan over which offspring are totally dependant on their mothers for survival; but the data reviewed here suggest that period is only a few years in humans – not enough to explain the twenty years of post-reproductive survival that is seen even in hunter-gatherer societies. The other models all weigh the costs of maternal mortality risk at later births against the benefits of parental and grandparental care for existing descendants. Most attempts to build quantitative models in which women can compensate for lost fertility in later life through enhancing the fitness of children and grandchildren have failed to find fitness benefits sufficiently large to favour menopause at 50 (Hill and Hurtado 1991; Rogers 1993). Shanley and Kirkwood (2001) argue that menopause at a slightly older age could be favoured if a range of selective forces are combined: in particular the impact of mothers on their daughters fertility and grandchild survival both need to be large. When parameterising this model with data from the Gambia (Shanley et al in prep), we find that parental contributions to daughters fertility are less important, and that maternal and grandmaternal effects on child survival are important, but again realistic parameter values still suggest a late menopause is adaptive suggesting that some important effect may still be missing from the model. However what this approach highlights is an important point about the relative contributions to fitness of grandmothers and mothers. The loss of its mother clearly has a larger impact on a child's survival chances than the loss of its grandmother, especially in early years; but because adult mortality is so low in humans, the chance of a child losing its mother in early childhood is actually very low. The loss of a grandmother may have a smaller effect on child survival, but the chances of losing a grandmother in early childhood are quite high. Therefore the impact of grandmaternal deaths on population levels of infant mortality is greater than that of mothers, and thus the relative fitness benefits of grandmaternal care are actually more significant than those of maternal care (Shanley, Kirkwood et al. in prep) – grandmothers give children that competitive edge.

That these quantitative analyses suggest marginal, if any, benefits of menopause at 50, has contributed to a belief that grandparental and parental care are a significant selective force on human longevity, but not necessarily on the timing of menopause (Hawkes, O'Connell et al. 1998). Some have argued that the human reproductive span is constrained to something similar to that of a chimpanzee, therefore selection for longevity simply 'left reproductive span behind' due to life history invariants (Hawkes, O'Connell et al. 2000). However explanations that rely on constraints are somewhat unsatisfactory. If age at menopause is resistant to selection, then we need to be specific about what the constraint might be – and it will need to be a good explanation given that life history traits are generally very plastic across species. The adaptive logic of models such as Shanley and Kirkwood's (2001) still applies even if lifespan rather than menopause is the derived trait – we would still expect reproductive span to expand with lifespan unless specific selective forces were favouring early reproductive senescence. The mathematical framework needed to address these problems continues to develop. A full explanation needs to include both the selective forces on dying as well as the selective forces on reproductive senescence and a reason for the two to differ. Mace (1998) models optimal human fertility schedules in an environment that includes competition between children for parental resources and predicts optimal family sizes well below the theoretical maximum; thus reproduction right up to the end of life may not be favoured in cases where transfers of this kind are important. Lee (2003) develops such ideas, building on the models of Hawkes et al (1998) and Kaplan and Robson (2002), to formulate a bio-economic framework which he uses to argue that transfers (be it of care, resources, or status) from older generations to descendant can select for both longer lifespans and unusual schedules of fertility in any social species. Whether elaborations of this model using realistic human parameters can explain menopause more fully than existing models awaits further analysis.

Conclusions.

We have presented evidence that human children benefit from an extended family and that kin support can enhance female reproductive success. Whilst nuclear families can survive and reproduce, they are likely to lose out in competition with those families that can draw on a more extensive network of kin. There are several studies on reproductive success that further support this view, but we narrowed our discussions here mainly to those that could identify a kin effect on a particular component of fitness so that we could unpick differing influences within the family. This unpicking reveals that different kin help in different ways. Grandmothers are important, but maternal grandmothers seem to concentrate on offspring survival, whereas paternal grandmothers are more interested in increasing birth rates. Both theoretical and empirical evidence is building that caring roles in later life are key to long human lifespans. The human life history presents many puzzles that have not yet been fully resolved. But our long lives and early reproductive senescence are still best explained by the benefits that older generations pass down to their descendants. We are not obligate communal breeders, but the most convincing explanation for a range of theoretical and empirical analyses of our life history suggest that we are evolved to raise children as an extended family enterprise.

Table 1. Studies of the effects of parents and grandmothers (gms) on child survival.

Population and study	Effect of mothers	Effect of fathers	Effect of maternal gms	Effect of paternal gms	Other effects and notes
Ache (Hill and Hurtado 1996)	+	+	n.s.	n.s.	Maternal and paternal gms not distinguished
Gambia (Sear, Mace et al. 2000; Sear, Steele et al. 2002)	+	n.s	+	n.s	Teenage sisters + Divorce –
Germany (historical) (Volland & Beise 2002)	Not tested	Not tested	+	Mostly -	Paternal GM –ve in infants, +ve in older children
India (Khasi) (Leonetti et al in press & this volume)	Not tested	n.s.	+	Not tested	
India (Bengali) (Leonetti et al this volume)	Not tested	Not tested	Not tested	n.s.	
Japan (historical) (Jamison et al 2002)	+	n.s.	+	Mostly -	Paternal grandfathers - (All effects borderline)
Spain (historical) (Reher & Gonzalez 2003)	+	n.s.	Not tested	Not tested	Fathers important for nutrition
Bangladesh (Bhuiya & Chowdury 1997)	Not tested	Not tested	Not tested	Not tested	Divorce –
Quebec (historical) (Pavard et al. In press)	+	Not tested	Not tested	Not tested	
(Beise this volume)	+	+	+	Mostly n.s. but see note	Paternal GM+ in 1 st month of life. Siblings -

Table 2. The effect of the death or absence of a relative on childhood mortality (adapted from Sear et al 2002) measured by logistic regression using event history analysis. Effect sizes are Odd Ratios, compared to that relative being alive/present (so OR less than 1 mean the death of the kin is associated with lower mortality). Effects controlled for include age, sibling mortality and village. Effects reaching statistical significance ($p < 0.05$) are shown in bold.

Kin relationship	Effect during infancy (under 1 year old)	Effect during toddlerhood (1-2 years old)	Effect in childhood (2-5 years old)
Mother dead	6.2	5.2	1.4
Father dead	1.1	0.5	0.7
Maternal gm dead	1.1	1.7	0.9
Maternal gf dead	1.1	1.3	1.0
Paternal gm dead	0.8	0.8	0.9
Paternal gf dead	1.3	0.9	0.7
No teenage sister	1.0	1.1	1.7
No teenage brother	0.9	1.2	1.4
Mother reproduces with new husband			1.9

Table 3. The effects of parents* and siblings on female fertility in natural fertility populations. (+ and – are with respect to reproductive success, so + means shorter birth intervals and earlier age at first birth)

Population and study	Life history variable	Effect of mothers	Effect of fathers	Effect of husbands mothers	Effect of husbands Fathers	Other effects and notes
Ache (Hill and Hurtado 1996) (Waynforth 2002)	Birth interval Age at first birth	n.s. Not tested	n.s. +.	n.s. Not tested	n.s. Not tested	Adult brothers and sisters -
Gambia (Sear, Mace et al. 2003) (Allal et al in press)	Birth interval Age at first birth	n.s. n.s.	n.s. +	+ n.s.	+ n.s.	Brothers – Brothers +
Germany (historical) (Volland & Beise 2002)	Birth interval	n.s.	n.s.	n.s.	n.s.	Mothers and mothers-in-law + on parity progression
Caribbean (Quinlan 2001)	Age at first birth	Not tested	n.s.	Not tested	Not tested	Co-resident sisters –
India (Khasi) (Leonetti et al this volume)	Birth interval	n.s.	Not tested	Not tested	Not tested	
India (Bengali) (Leonetti et al this volume)	Birth interval	Not tested	Not tested	+	Not tested	Mothers-in-law + via parity progression

*Note that parents in this table are the same as maternal grandparents in Table 1 and husbands mothers and fathers are the same as paternal grandparents in Table 1

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