

Who keeps children alive? A review of the effects of kin on child survival

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Abstract

Children pose a problem. The extended period of childhood dependency and short interbirth intervals mean that human mothers have to care for several dependent children simultaneously. Most evolutionary anthropologists now agree that this is too much of an energetic burden for mothers to manage alone and that they must enlist help from other relatives to share the costs of raising children. Which kin help is the subject of much debate. Here, we review the evidence for whether the presence of kin affects child survival rates, in order to infer whether mothers do receive help in raising offspring and who provides this help. These 45 studies come from a variety of (mostly) natural fertility populations, both historical and contemporary, across a wide geographical range. We find that in almost all studies, at least one relative (apart from the mother) does improve the survival rates of children but that relatives differ in whether they are consistently beneficial to children or not. Maternal grandmothers tend to improve child survival rates as do potential sibling helpers at the nest (though the latter observation is based on rather few studies). Paternal grandmothers show somewhat more variation in their effects on child survival. Fathers have surprisingly little effect on child survival, with only a third of studies showing any beneficial effects. Overall, this review suggests that whilst help from kin may be a universal feature of human child-rearing, who helps is dependent on ecological conditions.

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1. Introduction

Human life history poses a problem for women: that of raising several dependent children simultaneously. The human birth interval, of about 3 years in natural fertility populations, is out of line with that of other great apes of similar body size. The orangutan, for example, has an interbirth interval of about 8 years, and the chimpanzee 4–5 years (see [Galdikas & Wood, 1990](#), for a review). If human females are capable of such rapid reproduction, most anthropologists now agree that this is due to the support they receive from other family members. Whilst demographers used to argue that children were an economic asset rather than a cost ([Cain, 1977](#); [Caldwell, 1978](#)), [Kaplan \(1994\)](#) showed that wealth in families tends to flow down the generations, not up, helping to establish the view that children

are especially costly in humans requiring much more parental investment than, for example, do chimpanzees ([Kaplan & Lancaster, 2003](#)). The ‘traditional view’ of the family has been that help for the mother comes from the father—hence, the human pair-bond is based on mutual interdependence of husband and wife to raise their children (e.g., [Lovejoy, 1981](#)). 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 observation that the number of calories brought back from gathered foods often exceeds that from hunting, combined with the fact that meat is often shared widely throughout the band rather than strictly within the nuclear family ([Hawkes, 1990](#); [Hawkes, O’Connell, & Jones, 2001](#); [Kaplan & Hill, 1985](#)), has led to the suggestion that women are not as dependent on men to raise their family as once thought ([Hawkes, O’Connell, & Blurton Jones, 1997](#)).

If human life history poses a problem for women, then it may also provide the solution. Unusually, human females spend a relatively high proportion of their lives in a nonreproductive state. Both pre- and postreproductive

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individuals may be available to help mothers in raising offspring as they can do so at relatively little cost to their own reproduction. Grandmothers, in particular, are often proposed as an alternative to male care. If grandmothers are helping to support their daughters' children, then two unusual features of human female life history—menopause and high birthrates—can potentially be explained at once. Both may arise because menopause is an adaptation to enable grandmaternal support, which in turn enables a high human birth rate (Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998). Mothers may also use the labour of their older children, particularly daughters, to spread the costs of raising offspring. The extended juvenile period of human young is another unusual characteristic of our species, and the economic contributions of older children may also help to ameliorate the costs of large family size, although this effect has only been shown in agricultural societies (Kramer, 2005; Lee & Kramer, 2002).

1.1. *Who supports the family in hunter–gatherer societies?*

How might empirical studies help us to distinguish between the two views of the human family: that the pair-bond with the father is key or that other kin, especially grandmothers, are more important as allocarers? 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 (see also Hadley, 2004). Some 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 those from hunting (Blurton Jones, Marlowe, Hawkes, & O'Connell, 2000; Hill, Kaplan, Hawkes, & Hurtado, 1987; Marlowe, 2003). Isotope studies on prehistorical Californians suggest that male and female diets may have been very different (Walker & Deniro, 1986), with males having been living predominantly off marine resources, whereas the females must have been eating food mostly terrestrial in origin—though small sample sizes have not enabled this to be properly tested. But Hill, Kaplan, and others (see, e.g., Gurven & Hill, 1997; Gurven & Kaplan, 2006; Hill, 1993; Kaplan & Lancaster, 2003) 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 group nutrition is very significant, perhaps around 80% of the calories (though note that an important contribution by

males to the diet does not necessarily imply that fathers are directly provisioning their families). As an extreme example, 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, women are dependent on men for almost everything. Marlowe (2003) shows that male provisioning occurs at very important times in the Hadza, such as when a woman's foraging is handicapped because she recently gave birth.

These findings suggest 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 evolutionary ecologists. The variability in hunter–gatherer ecology further highlights the fact that data from just one type of population cannot answer the question of whether humans are cooperative breeders. We will argue here that it is not necessary or sufficient to restrict our studies to extant 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 of 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 analysed to enhance our understanding of which kin have an influence on the fitness of their descendants. Most of these populations are farmers but 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 untangle the full story of the evolutionary ecology of human family life.

2. Kin effects on child survival in a range of natural fertility/natural mortality populations

There are many studies on the contributions of various relatives to child care, nutrition, and other aspects of development (Hewlett, Lamb, Leyendecker, & Schölmerich, 2000; Hurtado & Hill, 1992; Ivey, 2000) that contribute greatly to our understanding of social networks and child-rearing, but it is not always easy to determine from these studies the extent to which such help enhances the fitness of the beneficiary. In this review, we shall concentrate solely on studies that have examined the effects of kin on one specific component of fitness: child mortality. For women, at least, child survival may be the most important determinant of reproductive success (Jones, 2005; Strassmann & Gillespie, 2002) since women (compared to men) have relatively low variance in fertility. Improving the survival chances of a woman's children may be the most important thing relatives can do to increase her reproductive success.

This review includes 45 populations in which the impact of at least one category of kin on child mortality has been investigated. This data set includes, to the best of our knowledge, all studies published in the English language that have investigated the effects of at least one relative on child survival (with a couple of exceptions where the results were too ambiguous to be included). Many of these studies have been conducted by evolutionary scientists interested explicitly in the issues discussed in this review, which have followed on from Hill and Hurtado's (Hill & Hurtado, 1991) pioneering investigation of the effects of grandmothers on child survival (see also Hurtado & Hill, 1992, and Hill & Hurtado, 1996). The rest have been largely conducted by

demographers, who have slightly different reasons for performing such analyses but who have still provided data suitable for inclusion.

Most populations had little or no access to modern medical care, including contraception. A few studies do include data from populations that are moving through the demographic transition, so cannot strictly be described as natural fertility, natural mortality populations, but are nevertheless from societies in which child mortality is sufficiently high to demonstrate variation according to the presence or absence of kin. Such studies correlating the presence (often approximated by the survival status) of relatives with the survival of children do, of course, need to

Table 1A
Studies of the effect of the mother on child survival

Population	Authors	Effect of mothers	Age of children studied	Timing of mother effect	% Surviving mother's death	Notes
Nepal (Sarlahi) 1994–97	Katz et al. (2003)	+	0–24 weeks	0–24 weeks ^a		Maternal deaths ^b only considered. Effect size increased with age of infant.
Caribbean (St. Barthélemy) 1878–1976	Brittain (1992)	+	0–1 yr		35%	% survival to 1 yr after mother's death in 1st yr.
Gambia (four villages) 1950–74	Sear et al. (2000, 2002)	+	0–5 yrs	<2 yrs only		Nutritional status also lower without mothers.
Kenya (Kipsigis) 1945–90	Borgerhoff Mulder, (2007)	+	0–5 yrs			
Burkina Faso (Nouna) 1992–99	Becher et al. (2004)	+	0–5 yrs	0–5 yrs	50%	% survival in follow-up period (0–5 yrs) after mother's death in 1st yr. Effect weakens with child's age.
Sub-Saharan Africa ^c 1980s–2000	Zaba et al. (2005)	+	0–5 yrs	<2 yrs only		Effect limited to 1st yr after mother's death. Relationship holds for HIV-negative children.
Canada (Quebec) 1680–1750	Beise (2005)	+	0–5 yrs	0–5 yrs		Effect weakens with child's age.
Poland (Bejsce) 1737–1968	Tymicki (2006)	+	0–5 yrs	0–5 yrs		
Guinea-Bissau 1990–98	Masmas et al. (2004)	+	0–8 yrs	<2 yrs only		Low HIV prevalence, so effect not due to mother-to-child transmission of HIV.
Paraguay (Ache) 1890–1971	Hill and Hurtado (1996)	+	0–9 yrs	0–9 yrs		Weak evidence that effect declines with child's age (interaction between mother and child's age significant at $p=.09$).
Netherlands (Woerden) 1850–1930	Beekink et al. (1999, 2002)	+	0–12 yrs	<6 mths/ 0–12 yrs		1999 paper suggests effect only seen <6 mths; 2002 paper effect seen up to age 12, though weakens with child's age.
Italy (Tuscany) 1819–59	Breschi and Manfredini (2002)	+	0–12 yrs			
Canada (Quebec) 1625–1759	Pavard et al. (2005)	+	0–15 yrs	0–15 yrs		Effect weakens with child's age. Neonates excluded. Effect stronger on girls after age 3 yrs.
Sweden (Sundsvall) 1800–1895	Andersson et al. (1996)	+	0–15 yrs	<1 yr only	40%	% survival to 15 yrs after mother's death in 1st yr.
Japan (Central) 1671–1871	Sorenson Jamison et al. (2002)	+	1–16 yrs			Effect stronger for boys (but seen in all children).
China (North East) 1774–1873	Campbell and Lee (1996, 2002)	+	~1–15 yrs	Strongest ~6–10 yrs		Timing of effect only tested for boys.

yr, year; mth, month.

^a Excluded from discussion of timing effects since only very young children were included in the study.

^b Definition of maternal death may differ between studies but broadly refers to death due to childbirth.

^c Pooled data from 3 cohort studies in Tanzania, Malawi, and Uganda.

be interpreted with caution. Correlational studies are helpful but 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. Appropriate statistical analysis needs to be employed to minimise the chance that confounding factors will obscure genuine kin effects or result in false-positives (Allison, 1984; Singer & Willett, 2003). Ideally, longitudinal data sets should be analysed using event history analysis (which allows a sensitive analysis of the effects of time-dependent variables, such as the presence of relatives, on the probability of dying over time) and including control variables for potentially confounding factors. As not all studies that have investigated this topic have used such adequately controlled statistical analysis, we have divided the sample into two groups. The statistically valid sample ($n=31$) includes only those studies in which at least some attempt was made to statistically control for confounding factors. Not all of these studies are longitudinal, nor do they all use event history analysis, but all have recognised the importance of confounding factors and tried to control for them in some way. The supplementary studies ($n=13$) present data on the impact of relatives but either do not attempt statistical analysis to demonstrate associations or have not adequately controlled for possible confounding

variables (i.e., only univariate analysis was used). The statistically valid and supplementary studies do not sum to 45 because one study (Derosas, 2002) presented an appropriately controlled event history analysis investigating the effects of grandparents but only descriptive data (and no statistical analysis) on the effects of parents.

We have presented the data in three sets of tables. Tables 1A and 1B give details of the effect of the presence of the mother on child survival (Table 1A shows the statistically valid sample, Table 1B supplementary data). Tables 2A and 2B demonstrate the effects of other kin on child survival (Table 2A the statistically valid sample, Table 2B supplementary data). In these tables, ‘+’ indicates that the presence of a particular relative improves child survival, ‘-’ that the relative lowers survival, and ‘none’ that the relative has no effect. Brackets indicate that the relationship was of borderline significance ($.05 > p > .1$), only applied to certain children (e.g., boys or girls), or was otherwise qualified. In several cases, the kin effects only applied to children of certain ages. These age-specific effects are mentioned in the ‘Other effects and notes’ columns. Blank cells indicate that category of relative was not included in the study. Table 3 provides a numerical summary of the previous tables and shows the number of studies that have found positive, negative, or no effects of each relative on child survival.

Table 1B
Supplementary data on the effect of mothers on child survival (not statistically controlled for confounding factors)

Population	Authors	Effect of mothers	Age of children studied	Timing of effect	% Surviving mother's death	Notes
US (New York State) 1936–38	Yerushalmy et al. (1940)	+	0–1 mth			Maternal deaths only considered.
Bangladesh (Matlab) 1967–70	Chen et al. (1974)	+	0–1 yr		5%	% survival to 1 yr after maternal death.
Bangladesh (Matlab) 1976–85	Koenig et al. (1988)	+	0–1 yr		25.9%	% survival to 1 yr after maternal death. Deaths among older siblings <3 yrs not affected by maternal death.
US (eight cities) 1920s	Woodbury (1926)	+	0–1 yr		40%	% survival to 1 yr after mother's death in 1st mth.
Tanzania (Hadza) 1980s–90s	Blurton Jones et al. (1996)	+	0–5 yrs			
Uganda (Rakai) 1994–2000	Bishai et al. (2003)	+	0–6 yrs			Effect holds for HIV-negative children.
Bangladesh (Matlab) 1983–85	Over et al. (1992)	+	0–9 yrs			Effect substantially stronger for girls.
Spain (Aranjuez) 1870–1950	Reher and González-Quiñones (2003)	+	0–9 yrs	<2 yrs only		Effect strongest for boys in neonatal period; girls at older ages. Effect increases over calendar time. Nutritional status also lower without mothers.
Italy (Venice) 1850–69	Derosas (2002)	+	0–10 yrs			
Germany (Ostfriesland) 1668–1879	Voland (1988)	+	0–15 yrs		48.5%	% survival to 15 yrs after loss of mother in 1st yr.
Sweden (seven parishes) 19th century	Högberg and Broström (1985)	+	0–15 yrs	<5 yrs only	1.6%, 3%, 13%	% survival to age 5 if child lost mother at birth, during 1st yr, and between 1 and 5 yrs, respectively.
UK (Cambridgeshire) 1770–1861	Ragsdale (2004)	+	0–15 yrs			Loss of mother within 2 yrs of birth of child.

Even when statistics strongly support the hypothesis that the death of kin accelerates the death of a child, it can be argued that a lack of effect does not mean that that kin is not a contributor, but only that their role can be replaced by others facultatively if they die. Thus, by extension, using impact on mortality as an indicator of kin help does not tell us about kin effects in the full sense. Whilst we are aware that kin can be substituted for, and often are, we feel that this analysis is still among the most important tools that we have. Whilst kin can be substituted, on average, such substitution should involve some cost to the child if that kin is truly important. One area that is exceptionally hard to control for is wealth effects—wealth inheritance patterns might mean that certain family structures are associated with lower wealth often due to competition between siblings or other means by which family resources are lost or redistributed on death, causing increased mortality or reduced reproductive success (Borgerhoff Mulder, 2007; Lahdenpera, Lummaa, Helle, Tremblay, & Russell, 2005; Mace, 1996), but such kin effects cannot necessarily be attributed to factors more normally implied by the notion of parental care. For example, in some societies, where patrilocal postmarital residence is the norm, living in close proximity to matrilineal kin could be a strategy only adopted by the poor (as in Gibson & Mace, 2005), making careful unpicking of effects necessary. Where data permit, a careful analysis of the timing of an effect (for example, Sear, Steele, & McGregor, & Mace, 2002, has shown that grandmothers are only important around weaning time); supplementation with time-budget data (for example, Gibson & Mace, 2005, show that grandmothers help out with their daughters' workload); or very careful attempts to eliminate confounding effects (for example, Pavard, Gagnon, Desjardins, & Heyer, 2005, show the long-term impact of maternal loss controlling for possible shared confounds) can strengthen the analysis and help to identify the true effects of care.

3. Who keeps children alive?

3.1. The importance of mothers

It comes as no surprise that in all 28 populations in which the association between mother's death and child death has been investigated, the death of the mother is clearly associated with higher child mortality (Tables 1A and 1B). That this effect exists is expected. What we wanted to determine from this analysis was, firstly, how long this association lasted (i.e., is it seen throughout the whole period of childhood, or do mothers only matter to young children?), and secondly, can even young children survive the loss of their mothers? If this association is confined to young children, and if children are able to survive the loss of their mother, this would indicate that other relatives are stepping in to help children out, if their mothers die.

Tables 1A and 1B indicate that the mother effect is strongly dependent on the age of the child. The conse-

quences of losing a mother in very early life are catastrophic, as evidenced by the tiny proportion of children who survive if their mothers die giving birth to them: only 1.6% of Swedish children survived such a maternal death in the 19th century and 5% of Bangladeshi children in the late 1960s (although by the 1980s, 26% of children survived maternal deaths in the same Bangladeshi population). A child's survival chances appear to improve rapidly with age. Much higher proportions of children manage to survive the death of their mothers if it occurs during their first year of life in some populations: 35% in the 19th century in the Caribbean and 40% in the 1920s in the US (though these studies only investigated survival to age 1 year), 50% in Burkina Faso, 40% in historical Sweden, and 48% in historical Germany (all looked at survival of the child to at least age 6 years). Studies that have statistically investigated the timing of the mother effect confirm that the effect of mother's death on child survival weakens or even disappears entirely after children are weaned. Almost all of the 13 studies that have tested whether the mother effect varies with the age of the child found evidence that the effect declines substantially as the child ages (11 found a decline with age; of the remaining 2, one only investigated child mortality up to the age of 5 years, and the other tested the timing of the effect for boys only). Five studies found that the mother effect disappeared entirely after the child reached 2 years of age.

Clearly, 2-year-old children are not self-sufficient, so the good survival prospects of children who lose their mothers in later childhood must be due to other individuals taking over child care and provisioning. Tables 2A and 2B suggest who those individuals might be. These tables demonstrate clear evidence that the presence of kin is important in improving child survival. In every single study that has examined the impact of *multiple* family members on child survival (apart from the mother), at least one relative has a significant impact on child survival. This widespread importance of kin apart from the mother supports the hypothesis that women are cooperative breeders, sharing child-rearing with other family members. However, which relatives help is less consistent than the fact of help itself.

3.2. How much do fathers matter?

Every study that has compared the effects of the loss of mother and father on child survival found that the loss of the father has substantially less impact than the mother's death. Indeed, Tables 2A and 2B demonstrate that fathers frequently make no difference to child survival. Table 3 shows that in 8 (53%) of the 15 populations studied using appropriate statistical techniques, there is no association between the death of the father and the death of the child. If supplementary studies are included, this proportion rises to 68% (15 of 22 studies). Even where associations between the loss of the father and increased child mortality are found, it is not clear that this is a direct result of the loss of paternal care. In at least one case where an association was found, the

Table 2A
Studies of the effects of fathers, grandparents, and older siblings on child survival

Population	Authors	Age of child (yrs)	Effect of fathers	Effect of mgms	Effect of pgms	Effect of mgfs	Effect of pgfs	Effect of older sibs	Other effects and notes
Gambia (four villages) 1950–74	Sear et al. (2000, 2002)	0–5	None	+	None	None	None	+	Elder sisters only increase survival (not brothers) and only at 24–59 mths; divorce, –
Canada (Quebec) 1680–1750	Beise (2005)	0–5	+	+	+	+	(+)	+	Fathers improve survival 1–23 mths; pgms in 1st mth; mgms 12–35 mths; mgfs 36–59 mths; pgfs 36–59 mths but only for girls
Malawi (Chewa) 1992–1997	Sear (2007)	0–5	None	(–)	(+)	None	None	+	Mgms borderline but significant at $p < .05$ for girls only; mat aunts – in families where women own resources, + where men do; divorce –
Kenya (Kipsigis) 1945–90	Borgerhoff Mulder (2007)	0–5	None	None	+	None	None	None	Mat and pat uncles +; pgm and mat uncle effects stronger in poor households; pat uncle effect stronger in rich households
Poland (Bejsce) 1737–1968	Tymicki (2006)	0–5	+	+	+	+	+	+	All grandparental effects seen only in 1st yr; father effect seen at all ages
Japan (central) 1671–1871	Sorenson Jamison et al. (2002)	1–16	None	(+)	(–)	None	(–)	None	Mgm effect borderline; pgm effect only seen for boys; pgfs only for girls
Ethiopia (Oromo) 1993–2003	Gibson (in preparation); Gibson and Mace (2005)	0–5	+/-	(+)	(+)	None	None	None	Father effect only investigated 0–1 yr: no overall effect but + for boys and – for girls; mgm effect borderline; pgm effect only seen for girls
Germany (Ludwigshafen) 1700–1899	Kemkes–Grottenthaler (2005)	0–2	None	None	+	None	–	None	Pgm effect only in 1st yr
Germany (Krummhörn) 1720–1874	Beise (2002); Volland and Beise (2002)	0–5	None	+	–	None	None	None	Pgm effect seen in 1st mth; mgm effect especially pronounced 6–12 mths
Italy (Venice) 1850–69	Derosas (2002)	0–10	None	None	(+)	None	(–)	None	Pgm effect only seen in orphaned children; pgf effect only <1 yr; both effects borderline; no effect aunts/uncles
India (Khasi) 1980–2000	Leonetti et al. (2004, 2005)	0–10	None	+	None	None	None	None	Mgm effect seen in 1st yr only

Bolivia (Tsimane) 1930s–2000s	Winking et al. (2006)	0–10	None				Child's risk of murder was increased if father was dead, but not overall mortality
Italy (Tuscany) 1819–59	Breschi and Manfredini (2002)	0–12	None				Death of father increased risk of emigration
Sweden (Sundsvall) 1800–95	Andersson et al. (1996)	0–15	None				Stepmother +
Japan (North East) 1716–1870	Tsuya and Kurosu (2002)	2–14	+				
Netherlands (Woerden) 1850–1930	Beekink et al. (1999, 2002)	0–12	(+)				Fathers only had effect within 1 mth of their deaths
India (Bengali) 1980–2000	Leonetti et al. (2005)	0–10		+			Pgm effect only seen in children 1–9 yrs
India (Uttar Pradesh) 1990–3	Griffiths et al. (2001)	0–2		+			Pgm effect only in 1st mth
India (Tamil Nadu) 1990–3	Griffiths et al. (2001)	0–2		None			
India (Maharashtra) 1990–3	Griffiths et al. (2001)	0–2		None			
North East India (8 states) 1994–9	Ladusingh and Singh (2006)	0–5		None			
Bolivia (Aymara) 1960s–90s	Crognier et al. (2002)	0–15			+		Elder brothers and sisters improve survival
Morocco (Berber) 1930–80	Crognier et al. (2001)	0–15			+		Elder brothers and sisters improve survival
Finland (5 communities) 18th and 19th centuries	Lahdenpera et al. (2004)	0–15		(+)			Pgms and mgms not distinguished; effect only seen 2–15 yrs and only for gms <60 yrs old
Paraguay (Ache) 1890–1971	Hill and Hurtado (1996)	0–9	+	None	None	None	Mat and pat grandparents not distinguished; elder sibs only include adult sibs; no effect aunts or uncles
China (North East) 1774–1873	Campbell and Lee (1996, 2002)	~1–15	(+)	None	–		Father effect only in girls; pat and mat grandparents not distinguished; presence of “adult women” increases mortality for boys if no mother or stepmother present; stepmother +

mgm, maternal grandmother; pgm, paternal grandmother; mgf, maternal grandfather; pgf, paternal grandfather; sib, sibling; mat, maternal; pat, paternal; gm, grandmother.

(+) and (–) indicate borderline significance or that the effect only applies to certain children.

Table 2B

Supplementary data on the effects of fathers, grandparents and older siblings on child survival (not statistically controlled for confounding factors)

Population	Authors	Age of child (yrs)	Effect of fathers	Effect of mgms	Effect of pgms	Effect of mgfs	Effect of pgfs	Effect of older sibs	Other effects and notes
UK (Cambridgeshire) 1770–1861	Ragsdale (2004)	0–15	None	+	None	None	None		
Utah (Mormons) 19th century	Heath (2003)	0–1		+	None	None	(+)		Pgf effect borderline; mat aunts, mat uncles, and pat aunts +
Tanzania (Hadza) 1980s–90s	Blurton Jones et al. (2000)	0–5	None						Father absence tested (including death and desertion)
Venezuela (Hiwi) ~1980s	Hurtado and Hill (1992)	0–5	None						Father absence tested (including death and divorce)
Uganda (Rakai) 1994–2000	Bishai et al. (2003)	0–6	None						
Bangladesh (Matlab) 1983–85	Over et al. (1992)	0–9	None						
Spain (Aranjuez) 1870–1950	Reher and González–Quiñones (2003)	0–9	None						Fathers improve nutritional status
Italy (Venice) 1850–69	Derosas (2002)	0–10	None						

relationship was more likely to have been caused by mortality crises that killed family members simultaneously (such as infectious disease) rather than any causal effect of the loss of the father: Beekink, van Poppel, and Liefbroer (2002) found that child mortality was only increased for one month after the death of the father (whereas the effect of the mother's death lasted considerably longer). In another case, that of rural Ethiopia, father absence increased the mortality of male infants only (Gibson, in preparation). This was interpreted as a Trivers–Willard effect, with father absence acting as a proxy for household resources (father absence actually increased the survival of female infants in this population).

We interpret this variation in the impact of fathers as an indication that paternal investment in young children is facultative and dependent on ecological conditions. Even where fathers are important for child survival, it is not clear that the benefits they bring to children are the traditionally assumed benefits of provisioning and economic support. Hurtado and Hill (1992) compared the effects of fathers on child survival in two South America hunter–gatherer groups. The loss of the father had a significant impact on Ache children, where marriages are unstable, meat widely shared among the group, and fathers little involved in child care, but no effect on Hiwi children, who are raised in nuclear families, with considerable input from the father in terms of

Table 3

Summary of kin effects on child survival

	Statistically valid				Supplementary				Total			
	No. of studies	Positive effect	Negative effect	No effect	No. of studies	Positive effect	Negative effect	No effect	No. of studies	Positive effect	Negative effect	No effect
Mothers	16	16 (100)	0	0	12	12 (100)	0	0	28	28 (100)	0	0
Fathers ^a	15	7 (47)	1 (7)	8 (53)	7	0	0	7 (100)	22	7 (32)	1 (4)	15 (68)
Mgms	11	7 (64)	1 (9)	3 (27)	2	2 (100)	0	0	13	9 (69)	1 (8)	3 (23)
Pgms	15	9 (60)	2 (13)	4 (27)	2	0	0	2 (100)	17	9 (53)	2 (12)	6 (35)
Nonspecific gms	3	1 (33)	0	2 (67)	0	0	0	0	3	1 (33)	0	2 (67)
Mgfs	10	2 (20)	0	8 (80)	2	0	0	2 (100)	12	2 (17)	0	10 (83)
Pgfs	10	2 (20)	3 (30)	5 (50)	2	1 (50)	0	1 (50)	12	3 (25)	3 (25)	6 (50)
Nonspecific gfs	2	0	1 (50)	1 (50)	0	0	0	0	2	0	1 (50)	1 (50)
Older sibs	6	5 (83)	0	1 (17)	0	0	0	0	6	5 (83)	0	1 (17)

Figures in brackets represent percentages. gf indicates grandfather.

Figures in italic indicate percentages.

^a Percentages do not sum to 100 in this row because one study found a positive effect of fathers on the survival of sons and a negative effect on the survival of daughters.

both provisioning with meat and direct child care. The importance of Ache fathers may instead lie in protecting their children from other males rather than direct provisioning (infanticide of orphans was not uncommon in this group). Indirect evidence that the importance of fathers lies at least partly in protecting children from other males comes from studies of the impact of the mother's divorce and remarriage. Divorce and remarriage have been shown to increase a child's risk of dying (Alam, Saha, Razzaque, & Van Ginneken, 2001; Bhuiya & Chowdhury, 1997; Sear et al., 2002). It is often not clear how much of this is due to father absence, to stepfather 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. However, stepchildren have been found to be at greater risk of homicide than children living with natural parents (Daly & Wilson, 1988) and have higher stress levels than children living with both biological parents (Flinn & England, 1995).

Though these studies suggest that the importance of fathers in provisioning their young children has previously been overestimated, it does not mean that men do not invest in their offspring. Many of these analyses focus on relatively young children: 10 of the 22 father studies looked only at children under the age of 5 years. Such analyses may well underestimate the importance of fathers. The mortality risks of young children are likely to be highly dependent on the quality of care received (including lactation). Fathers can take no part in lactation and in most populations take relatively little part in direct child care (though there are exceptions: Hewlett, 1992; Huber & Breedlove, 2007) so may have little opportunity to affect the survival chances of young children, with the exception of protecting them from other males. Fathers may play more important roles in the lives of older children, teaching them subsistence skills and perhaps enhancing their marriage and fertility prospects. There is some evidence that women in traditional societies who lack fathers have later first births than those with fathers, suggesting that fathers may be instrumental in arranging marriages for women (Allal, Sear Prentice, & Mace, 2004; Waynforth, 2002).

Secondly, the lack of a father effect may be because what fathers do for children can be more easily substituted than the services mothers provide to children. The care given to young children by reproductive-aged women is usually directed exclusively towards the women's own children (i.e., lactation). There are rare cases of a lactating woman adopting and feeding an infant after the mother's death, but lactation is energetically costly and also inhibits conception, so that reproductive-aged women can usually gain more from investing in their own offspring than looking after less closely related children. In contrast, the productive work or protection that men provide for children can more easily be directed towards children other than their own. Though evidence does suggest that men are disinclined to invest in

the progeny of other men (hence the role fathers play in some societies as protectors against other men), there are strategies that can be used to spread the 'fathering' role among other men. Hrdy (2000), in a review of the ethnographic literature on mating behaviour, suggests that women are more polyandrous than has been traditionally supposed. This polyandry functions in part to improve child survival by confusing or spreading paternity in order to protect children from potentially infanticidal males and/or encourage several males to invest in mothers and children. For example, in some South American hunter-gatherer communities, paternity is considered to be 'partible', i.e., any man who has sex with the mother around the time of conception and pregnancy is regarded as a father of the child. In both the Ache and among Bari hunter-gatherers of Venezuela, children with multiple fathers do better than those with only one (Beckerman et al., 2002; Hill & Hurtado, 1996)—though Ache children with many fathers did less well than those with one primary and one secondary father. An alternative strategy for spreading the fathering role may be patriliney, where patrilineally related men and their wives may live and work in close proximity. In such societies, patrilineally related males may take over the father's responsibilities if a child's father dies, especially where the levirate is practiced (women marrying their husband's brother after widowhood). In the Gambian population we have studied, patrilineal live in extended family compounds, and the levirate is common (around 40% of widows married their dead husbands' brothers). Children may therefore suffer little after the death of their fathers, as any services provided by the father can be taken over by other related males in the compound.

Additionally, the loss of the father may affect the investment decisions of other relatives, such as grandmothers and grandfathers, who may increase their investment to compensate for the lack of the father (Winking, *in press*). For example, though illegitimate children tended to have higher mortality rates than legitimate children in historical Europe (providing indirect evidence for the importance of male support: van Poppel, 2000), there is some suggestion that kin support from maternal grandparents could alleviate the disadvantages of illegitimacy, indicating interactions between the presence of the father and extended kin (Blaikie, 1998).

The facultative and time-varying nature of paternal investment makes adaptive sense if child mortality is not the most important determinant of male reproductive success, such as when significantly greater gains in fitness can be made by directing their efforts towards gaining additional mates rather than investing in existing children. 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 or Kipsigis (Borgerhoff Mulder, 2007; Sear et al., 2002) but a significant positive effect of fathers in monogamous, historical Quebec

(Beise, 2005). Even if polygynous men were inclined to provide for children, they would find it rather difficult to provision all of their offspring; men with multiple wives can father considerable numbers of children (the most reproductively successful man in our Gambian population had 36 children). We conclude that a full investigation of how much fathers matter requires analysing the effects of fathers on all components of reproductive success; investigating how such investment may vary over the life cycle of both fathers and children; and how such investment varies according to specific environmental conditions.

3.3. Grandmothers and child mortality

If the impact of fathers on the survival of children is variable, is there any evidence that the impact of grandmothers is more consistently beneficial? The results presented in Tables 2A and 2B suggest that grandmothers may be more reliable sources of help than fathers, though they do not have universally positive effects on child survival. There are also some differences between maternal and paternal grandmothers, with maternal grandmothers appearing to be somewhat more reliable helpers than paternal grandmothers. In total, maternal grandmothers improved child survival in 69% of cases (9 of 13 studies); the proportion is similar if only statistically valid studies are taken into account (7 of 11: 64%). Paternal grandmothers seem to be somewhat less consistent helpers if all studies are considered: they improve child survival in 53% of cases (9 of 17), though the proportion rises to 60% of statistically valid studies. Tables 2A, 2B, and 3 also highlight that kin are not necessarily always beneficial to children: in two studies, there was a detrimental effect of paternal grandmothers on child survival, and in one case, the maternal grandmother had a detrimental effect (though this latter data set did not include grandmaternal effects for children whose mothers had died, and in such cases, anecdotal evidence suggested that maternal grandmothers play a crucial role: Sear, 2007). This greater variability in the effects of paternal grandmothers may be in part explained by the greater age of paternal than maternal grandmothers due to females reproducing earlier than males (though maternal age, and sometimes age of grandparents, is controlled for in those studies in Table 2A). It may also reflect their lower level of genetic relatedness to their patrilineal descendants (due to paternity uncertainty). Separating out the effects of maternal and paternal relatives on female fitness is clearly important as maternal and paternal kin may therefore differ in both their ability and inclination to invest in children. This may explain why two of the three studies that have not separated out the effects of maternal from paternal grandmothers have found no effect.

A closer inspection of the timing of these grandmaternal effects suggests evidence that maternal and paternal relatives have different roles to play in the lives of mothers and children. In some populations, maternal grandmothers appear

to have the strongest effect around the age of weaning (Beise, 2002, 2005; Sear et al., 2002). Weaning is a dangerous time for children. It increases their exposure to pathogens in food and is often associated with the arrival of a younger sibling, when mothers divert their attention away from weaned children and to their new babies. Maternal grandmothers may be stepping in to protect children from the dangers associated with this stage of childhood (see Thompson & Rahman, 1967, for an example of this in the Gambia). Paternal grandmothers, in contrast, often appear to have the strongest effect (whether beneficial or detrimental) during the first month or year of a child's life (Beise, 2002, 2005; Kemkes–Grotenthaler, 2005). Mortality in this period is less dependent on exogenous causes (such as quality of care received) and more dependent on endogenous causes (such as low birth weight: Mosley & Chen, 1984). Birth weight is correlated with the condition of the mother during pregnancy (Andersson & Bergstrom, 1997; Kirchengast & Hartmann, 1998). Paternal grandmothers may therefore affect child mortality by affecting the condition of the mother during pregnancy. This effect may be beneficial (perhaps by helping out with domestic or productive tasks) or detrimental (stress and harassment may lead to worse maternal condition and higher neonatal mortality rates). The pathways through which maternal and paternal grandmothers affect child survival may therefore be somewhat different: the former help out with direct child care; the latter affect the condition of the mother, and thereby the child, by helpful (or occasionally harmful) behaviour during pregnancy.

Most of the studies in this review have only used correlational evidence to infer helping behaviour from kin, but Gibson and Mace (2005) also collected time-budget data to establish what relatives were actually doing for one another. Maternal grandmothers were found to help women out with heavy domestic tasks, thus freeing mothers for child care. Paternal grandmothers, on the other hand, were more likely to help women with agricultural work, an activity from which they may gain a direct benefit (i.e., a share in the harvest).

3.4. What about grandfathers and other adult kin?

Grandfathers are much less important to children. In 10 (83%) of 12 cases, maternal grandfathers had no effect on child survival, though they had a positive effect in the remaining two cases. Paternal grandfathers had no effect in 6 (50%) of 12 cases; a negative effect in 3 (25%), and a positive effect in 3 (25%) cases. However, even where associations are found between grandfathers and child survival, they tend to be of borderline statistical significance. In four of the six cases where paternal grandfathers had an impact on child survival, for example, the effect was borderline or applied only to female children.

Data on the effects of related reproductive-aged adults on child survival (apart from parents, such as aunts and uncles) is relatively scarce. The little evidence available suggests that

the effects of such relatives are very mixed (see the ‘Other effects and notes’ columns in [Tables 2A and 2B](#) for details). The children of Kipsigis agropastoralists in Kenya do better if they have either paternal or maternal uncles, although these effects are largely attributable to how family structure interacts with wealth inheritance rather than providing any evidence of care ([Borgerhoff Mulder, 2007](#)). Chewa children in Malawi have lower survival in the presence of maternal aunts but only in households in which women own resources. In the minority of households in which men own resources, maternal aunts protect against child mortality ([Sear, 2007](#)). Venetian children apparently neither gain nor suffer from aunts or uncles (but neither maternal and paternal nor aunts and uncles were distinguished: [Derosas, 2002](#)). Similarly, aunts and uncles have no impact on Ache children (though maternal and paternal relatives were not distinguished: [Hill & Hurtado, 1996](#)). In historical China, the presence of reproductive-aged females (usually paternal aunts) increased mortality for motherless children ([Campbell & Lee, 2002](#)). Nineteenth-century Mormon children benefited from maternal uncles and either kind of aunt ([Heath, 2003](#)). Reproductive-aged adults may be in a position to help one another with child care, domestic tasks, or productive activities but also may either be too concerned with the well-being of their own small children or actively in competition with each other for resources to be consistently beneficial. In a study of child care arrangements in Efe hunter–gatherers, [Ivey \(2000\)](#) found that children were frequently looked after by individuals other than their mothers, but these allocarers were rarely other women who had nursing infants of their own. Data from historical studies do, however, suggest that one category of reproductive-aged women may be beneficial for child survival: stepmothers. Despite numerous folktales warning of the dangers of the wicked stepmother, both [Andersson, Högberg, and Åkerman \(1996\)](#) and [Campbell and Lee \(2002\)](#) found that children with stepmothers had similar risks of dying to those children who still had their own mothers, which were considerably lower than the mortality risks of children without either mothers or stepmothers. Such analyses need to be interpreted with care as children with stepmothers will be older and have experienced the death of their mothers further in the past than most motherless children. But if this is not a statistical artifact, such philanthropic behaviour on the part of stepmothers may be a form of mating effort, as has been suggested for stepparental behaviour in nonhuman animals ([Rohwer, Herron, & Daly, 1999](#)).

3.5. *Helpers at the nest*

Rather few studies have investigated the effect of potential sibling ‘helpers at the nest’ on child survival, despite the widespread observation that the labour of older children is used by parents both for domestic work (including child care) and productive activities ([Borgerhoff Mulder & Milton, 1985](#); [Cain, 1977](#); [Kramer, 2002, 2005](#); [Weisner & Gallimore, 1977](#)). The effects of older siblings,

however, are complicated by competitive relationships. Several studies have found that older siblings increase, rather than decrease, the risk of death for children (e.g., [Das Gupta, 1987](#); [Kemkes, 2006](#); [Muhuri & Preston, 1991](#)). These effects are usually interpreted as parental manipulation of the size and sex composition of their families for optimal allocation of limited family resources. Here, we present studies that have investigated the effect of older siblings who are potential helpers, rather than competitors for their mothers’ attention, by restricting the analysis to those children several years older than the focal child (at least 3 years older, and often more, depending on the study). Restricting the analysis in this way is not a perfect method of identifying the effect of helpers at the nest and will bias the sample in other ways, e.g., it will include a disproportionate number of later-born children and exclude firstborns. Only six studies analysed helping at the nest, but five of these studies find that potential helpers have a positive effect on child survival. The sixth study only investigated the effects of adult siblings, who may have been occupied with children of their own. In some cases, this positive effect is specific to older sisters, suggesting that the domestic responsibilities of juvenile girls (including child care) are important, but in other cases, the sex of helpers does not matter, suggesting that all activities contributed by prereproductives are beneficial (or that there are confounding effects with family size).

3.6. *Confounding effects*

Some of the studies in the sample found that kin effects are not straightforward. In a few populations, the effect of a particular category of kin was only seen for children of one sex. Mothers themselves are known to invest differentially in children according to sex and birth order. Other kin may mirror the investment decisions of mothers by investing in similarly favoured children. The reproductive interests of kin are not necessarily identical to those of the mother, however. [Sorenson Jamison, Cornell, Jamison, and Nakazato \(2002\)](#) 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. Similarly, female maternal kin (grandmothers and aunts) appear to be detrimental to child survival in a matrilineal Malawian society ([Sear, 2007](#)). These harmful effects are most noticeable in female children and in households in which women own household resources, suggesting that they may result from competition between female, matrilineal kin for family resources. 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.

Availability of resources may also alter kin effects (with the caveat expressed earlier that there are potential problems separating wealth effects from care—in some cases, one may directly effect the other; in other cases this confounding may just generate statistical artifacts). Both [Borgerhoff Mulder \(2007\)](#) and [Leonetti, Nath, Hemam, and Neill \(2004\)](#) found interactions between kin effects and wealth. In the Kipsigis, paternal uncles are most important for buffering rich children against mortality, but maternal uncles are more important in poor families ([Borgerhoff Mulder, 2007](#)). In India, husbands were more likely to be beneficial in poorer households ([Leonetti et al., 2004](#)). In the latter study, the condition of the mother also mattered. There was a tendency for men to be more useful to women with fewer resources, both economic and physiological: shorter women were more likely to be helped by husbands. There were also interactions between help given by husbands and grandmothers (more help from grandmothers correlated with less help from husbands). These complications to the story of kin help suggest that help from any category of kin may be facultative to some extent, depending on other factors such as the available resources, the mother's ability to rear children, and the presence of other kin.

Finally, a common criticism of studies that find a correlation between the survival of a particular relative and child survival is that these effects might simply be due to shared genes or environment, i.e., certain children come from 'healthy' families where both they and their relatives have good survival prospects, and others come from 'unhealthy' families where their own survival chances are low, as is the probability that their relatives have survived long enough to help care for them. Whilst such explanations cannot entirely be ruled out, the results presented in [Tables 1A, 1B, 2A, and 2B](#) suggest that shared genes or environment is unlikely to be the full explanation in all cases. For example, if such confounding effects were important, we would expect to see positive relationships between children and all categories of kin. Instead we see considerable variation between relatives and between populations in which kin are important for child survival. The effects of kin are also often dependent on the age of the child and occasionally the sex of the child. Again, if shared genes or environment were responsible for these results, then the survival of kin should be correlated with child survival throughout the child's life and for both sexes. Thirdly, several studies have attempted to control for shared environment between relatives by including statistical controls for economic factors (e.g., [Borgerhoff Mulder, 2007](#); [Gibson & Mace, 2005](#); [Leonetti, Nath, Hemam, & Neil, 2005](#)) or by using hierarchical models that control for family-level effects (e.g., [Beise, 2002](#); [Borgerhoff Mulder, 2007](#); [Sear et al., 2002](#); [Tymicki, 2006](#)). Significant kin effects are still seen even using such controls. Finally, the authors of these studies are frequently aware of this potential

confound and have often used additional analysis or ethnographic evidence to interpret the results of their correlational analysis, to provide assurances that these results are unlikely to be entirely due to shared genes or environment (see, e.g., [Sear & Mace, in press](#)).

4. Discussion

4.1. *Evolution and the human family*

What does this review tell us about the evolution of the human family? Whilst there clearly is a problem using data on current populations to infer anything about evolutionary history, it is all we have. Certainly the study of a single society tells us little about evolution of a particular trait. In the Gambia, we found positive effects of maternal grandmothers and no effect of fathers on child survival, but this does not constitute strong evidence in favour of the importance of older women and the unimportance of men in the human family. These results could have arisen due to some peculiarities of Gambian ecology. Cross-cultural analysis is essential to determine which traits are common across societies and which vary according to environmental conditions (see, e.g., [Walker et al., 2006](#) for an example on growth). This review offers hints about which features of the human family may have been common throughout our evolutionary history and which are adaptations to local environments. We conclude from this review that kin support in rearing offspring does appear to be a human universal. Support from maternal kin (especially grandmothers) may perhaps be more reliable than that from paternal kin, though no category of kin is universally beneficial. Support from fathers for young children also appears to be facultative and dependent on ecological conditions.

However, does even this cross-cultural review tell us anything about the *evolution* of the human family? This data set has relatively few hunter–gatherers and is biased towards those who made at least some of their living from farming. Is it possible that throughout most of our history, we have lived in relatively stable (perhaps nuclear) families where fathers assume more importance in provisioning children, or even where mothers were better able to provision their children alone? The variation we see among extant populations may be, at least in part, a response to a shift in subsistence and demographic patterns to a set of conditions which make helping by extended kin more favourable. For example, if agricultural populations have higher fertility and lower adult mortality than hunter–gatherers, this might make kin (such as grandmothers and older children) both available and necessary as helpers. [Draper and Harpending \(1987\)](#) have suggested that paternal involvement and sibling care may differ systematically between foraging and farming communities, with father involvement much more common among foragers and sibling care more frequent among farmers (see also [Hewlett, 1991](#)). [Kaplan and Lancaster \(2003\)](#) have also argued that shifts in subsistence strategy during human

history have been accompanied by shifts in optimal family structure. In particular, they assert that the move from foraging to horticulture and agriculture was accompanied by a significant reduction in the importance of male provisioning to children.

It seems unlikely to us that one particular family structure has been of paramount importance throughout human history. Existing hunter–gatherer populations are hardly uniform in either their subsistence strategies or demographic patterns. Hunter–gatherer populations have, after all, been used to illustrate both the importance of fathers (Ache) and the importance of grandmothers (Hadza). This particular debate might reflect differences between Old World and New World foragers since foragers in the Old World tend to rely relatively more on gathering and have lower male contributions to the diet than New World foragers (Marlowe, 2005). There are also problems in using extant hunter–gatherer populations as models for past hunter–gatherers as many of the remaining hunter–gatherers occupy marginal environments unsuitable for farming activities (though this view has recently been questioned: Marlowe, 2005). This variability shown by hunter–gatherer populations is unlikely to have been of recent origin, given that recent estimates suggest that hominins have had a wide geographical distribution (i.e., outside of Africa) for nearly 2 million years (Dennell & Roebroeks, 2005). If early hominins had a wide geographical distribution, then they probably occupied a variety of different environments, with associated plasticity in behavioural characteristics.

It seems more parsimonious to us to assume that human family systems have always been somewhat flexible and responsive to ecological conditions, as are those of many other primates. After all, as Hrdy (2005) points out, relying exclusively on a single category of kin (such as fathers) seems a rather risky strategy, given the improbability that one particular relative will survive and be able to help throughout a woman's reproductive career.

4.2. *Evolution of human life history*

We introduced this paper by describing the unusual features of human female life history—late puberty, short birth spacing, and menopause. Does this review tell us anything important about the evolution of human female life history characteristics? We have found unmistakable support for the hypothesis that women receive help from kin in raising children in extant populations, but can we infer from this that characteristics of human life history can be explained by the cooperative nature of human reproduction? Grandmothers (of one kind or another) do appear to be almost universally beneficial across societies in improving the fitness of their relatives: in all 12 studies that investigated the impact of both maternal and paternal grandmothers, as least one kind of grandmother was beneficial for child survival. This provides some support for the grandmother hypothesis for menopause, but we still cannot be entirely

certain that menopause evolved because of its fitness benefits. It may be that grandmothers invest in their grandchildren because they are unable to continue having children of their own, and investing in grandchildren is better than investing in nothing at all.

Rather than relying solely on statistical investigations of patterns of behaviour, mathematical modelling is necessary to test whether a particular trait is likely to have evolved given a set of life history parameters; we do not have real women without menopause whose fitness we can examine empirically. 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 (Grainger & Beise, 2004; Hill & Hurtado, 1991; Rogers, 1993), which has contributed to a belief (in our view, erroneous) that grandparental and parental care are a significant selective force on human longevity but not necessarily on the timing of menopause (Hawkes et al., 1998). This argument also relies on the notion that the fertile span is somehow constrained, for which there is no particular evidence. However, Shanley and Kirkwood (2001) argue that menopause at a slightly older age could be favoured if a range of selective forces are combined, including an increase in maternal mortality with age as well as grandmaternal effects both on grandchild survival and on their daughters' fertility (and these latter effects need to be large). When parameterizing this model with data from a natural mortality/fertility population in the Gambia (Shanley, Sear, Mace, & Kirkwood, 2007), we find that grandmaternal effects on child survival are particularly important. The reasons for this lie in the fact that selection is derived from the size of the effect of a loss of kin, combined with how likely that loss is to occur. In the Gambian case, whilst maternal deaths posed much more serious risks for a child, they were rare (due to low mortality in reproductive age adults), whereas grandmaternal deaths were very common; hence, the total number of child deaths caused by grandmaternal deaths per year actually exceeded those caused by maternal deaths. The model, which is one of the only ones to incorporate the full life history (necessary because changing one aspect of life history necessarily alters selective forces on other areas of the life course), shows that the grandmother effect is therefore a far more potent selective force on menopause than maternal or other effects, and if demographic patterns found in the Gambia applied in ancestral populations, then this effect can explain the evolution of menopause (Shanley et al., 2007).

Mathematical modelling can also help us understand the evolution of other features of human life history. A shift towards modelling the mortality schedules and aging patterns of our species, rather than a specific component of human life history such as menopause, has suggested that many of the peculiarities of human life history, including a long juvenile period, long life span, and postreproductive life, may hinge on intergenerational transfers in general (not

specifically those from grandmothers, but all transfers from older to younger individuals: Kaplan & Robson, 2002; Lee, 2003; Pavard, Sibert, & Heyer, 2007). The mathematical framework needed to address these problems continues to develop. Such models would also benefit from more information on the parameters needed to inform these models: effect sizes for kin help across a number of different populations would illustrate the relative importance of mothers, fathers, and grandmothers.

4.3. Next steps

This review has of necessity been a fairly crude analysis of the effects of kin on child mortality: we have simply presented numerical data on the number of populations that have found, or failed to find, an effect of various relatives on child survival. We have attempted no meta-analysis of the data presented here because of the considerable variation in statistical methodology (or lack of it) used in these studies. Even in those studies that do calculate effect sizes, the magnitude of the effects cannot be compared directly for a number of reasons, including differences in the age of children being studied, in which confounding factors were controlled, and whether interactions between the effect and child's age were included in the models. Additionally, not all studies in this sample can be considered independent data points since a few come from similar populations. Nevertheless, we believe that this is a useful exercise as a first step in systematically determining which kin are helpful to mothers in raising children and under which circumstances these kin help. This review has found some commonalities but also substantial variation between populations in which kin help women raise children. The next step is to explain this variation within an evolutionary ecological framework. This could involve a meta-analysis of those studies that have investigated this issue, testing hypotheses about the circumstances under which particular kin help, preferably using appropriately phylogenetically controlled methods (Mace & Pagel, 1994), though this is unlikely to be practical until more studies can be collated on the effects of kin on child survival. We suggest that the following, by no means exhaustive, list of potential factors may affect the level of help offered by particular relatives. (1) Subsistence strategy: this may affect (a) the degree to which certain kin may help (e.g., children may be economically productive in some agricultural societies, but less so in hunter–gatherer communities) and (b) the division of labour between sexes, which affects what kind of help kin can provide and the extent to which help is necessary. (2) Demography: the probability of having a particular relative around to help depends on a number of demographic factors such as sex-specific mortality rates, age-specific fertility rates, and age difference between spouses. (3) Marriage and mating systems (which will also be linked to demography through the operational sex ratio): polygynous men are likely to find it difficult to invest in children from several mothers and will also have alternative mating

opportunities, which make mating effort more productive than parental effort. (4) Resource availability: this may affect the demography and marriage patterns of a population. (5) Inheritance patterns: this may result in selective helping of certain children. (6) Residence patterns: this will affect which kin are most available for help.

This study has only examined statistical correlations between the survival of kin and survival of children. Whilst we have attempted to separate out studies which are likely to have demonstrated genuine correlations from those that have not adequately controlled for potentially confounding factors, even those studies which have used appropriate statistical analysis have not demonstrated a *causal* relationship between the presence of kin and the survival of children. A better understanding of the pathways by which kin help would improve our understanding of why these associations are found (and provide reassurance these effects are not merely statistical artifacts). The studies that are presented here suggest that the pathways through which kin influence reproductive success may well differ between relatives. Men and women appear to help in different ways, because of sexual division of labour within societies (e.g., help in direct child care is much more likely to come from female kin than male kin). There also appear to be differences in the kinds of help offered by maternal and paternal kin (and not only in the frequency with which they offer help: Beise, 2005; Gibson & Mace, 2005). Pathways may also be more variable for fathers than for other kin. Fathers can potentially provide a variety of services to children including provisioning with food, providing protection from other males, child care, and other social benefits. Female kin tend to confine their roles to lifting energetic burdens from women by helping out with child care, domestic, and subsistence activities. This review has also highlighted that not all kin are beneficial. Suggestions to explain the detrimental effects of relatives on child survival have included competition for resources (Campbell & Lee, 1996; Sear, 2007) and conflicting interests between women and their husband's kin (Beise, 2002; Volland & Beise, 2005). These results suggest that any models that attempt to investigate the evolution of certain life history traits need to take into account differences between maternal and paternal kin as well as potential conflicts between relatives.

4.4. Relevance to current family policy debates

Finally, we conclude with a brief discussion of the relevance of such evolutionary analysis to family policy. There is a tendency for policy makers in Western countries to believe that the nuclear family model is most beneficial for individuals, children, and society and that the decline in marriage and increase in divorce and single motherhood in recent years marks an unprecedented decline in the family in human history (McDonald, 2000). This nuclear family model also usually includes a rather rigid view of the division of labour within families, with mothers primarily

concerned with child care and the domestic sphere and fathers responsible for economic provisioning. Policy theorists have claimed that all welfare states were initially predicated on the nuclear family model, and most still subscribe to some degree to this model (Lewis, 1992; Sommestad, 1997). There is an enormous literature arguing that father absence has detrimental consequences for children (see Sigle-Rushton & McLanahan, 2004, for a review), reinforcing the view that marriage is good for children, divorce is bad, and that children should grow up in a home with both biological parents. However, this review shows that the human family is clearly a diverse entity and that the nuclear family system may not be the normative solution to the problem of raising children in all circumstances (though it may be in others).

What is clear from this review is that this nuclear model is a rather unusual family system in extant populations, which gives us little reason to assume that it has been common throughout our evolutionary history. The three features that make this nuclear family model somewhat unusual are that women are expected to care for children alone; that women are not expected to contribute any productive labour; and the vital role that fathers play in the economic support of the family. The studies cited here demonstrate that mothers do not raise their children alone in many societies but receive substantial help from others, so that it is not at all unusual for children to receive care from other kin and group members. It is also extremely unusual for women to take no part in productive activities. Hewlett (2000), in a table titled ‘The Myth of the Male Breadwinner,’ tabulates the contribution of women to the family diet from 90 societies worldwide and observes that in half the societies, the breadwinner role was shared roughly equally between men and women and that the number of societies in which men were the main breadwinners was equalled by the number of societies in which females contributed the majority of the family diet. Not dissimilar results are seen if only hunter–gatherers are considered (Hewlett, 1991; Marlowe, 2005). This questions both the lack of female involvement in production and also the role that fathers play within the family. Whilst fathers may well be important to their offspring, exactly what they do to support their children, and how this investment is patterned across the life cycle, is likely to vary substantially both between and within societies, according to the level of available resources, degree of paternity certainty, and other factors. Additionally, if the lack of a substantial father effect on child mortality in many societies suggests that when fathers are absent, other relatives or group members may be able to compensate for the loss of the father, these observations of considerable variation in optimal family structure suggest that it might be useful for policymakers to take a slightly less rigid approach when considering what is the best environment to raise a child.

This does raise the question of exactly how such evolutionary analyses can be used to inform family policy, if at all. For example, knowledge that the best kind of family

to raise a child can take several forms may not be necessarily useful to policymakers trying to formulate policies at a national level. A recent attempt to use evolutionary psychology to inform family policy appeared to conclude that evolutionary approaches are useful because they allow us to understand better the preferences of individuals, so that social policy can be directed towards fulfilling these preferences (Browne, 2002). However, an evolutionary perspective also tells us that the preferences of individuals may be well in conflict: the preferences of men may not coincide with the preferences of women; the preferences of children may not coincide with those of parents; and the preferences of the family may very well be in conflict with those of institutions such as employers, governments, etc. Evolutionary analyses can be used to gain a better understanding of human behaviour but cannot be used to provide easy policy solutions.

5. Conclusion

We have presented evidence that human children benefit from an extended family and that kin support can enhance female reproductive success. There are several studies focussing on components of reproductive success that further support this view, but we narrowed our discussion here to those that could identify a kin effect on child survival, an unambiguous determinant of reproductive success, so that we could unpick differing influences within the family. This analysis reveals some commonalities and some differences in kin help. A consistency across studies is that at least one relative is beneficial in almost all populations, suggesting that we are evolved to raise children as an extended family enterprise. Maternal grandmothers tend to improve child survival, as do elder sibling helpers at the nest. Paternal grandmothers are frequently beneficial but show rather more variation than maternal grandmothers in their effects on child survival. Fathers’ contributions to child survival appear to be surprising small. This review has also highlighted that kin interactions are not always beneficial and that the presence of certain kin may occasionally be harmful for child survival. A systematic analysis of what causes this variation in kin support should be the next step in furthering our understanding of the human family.

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References

- Alam, N., Saha, S. K., Razzaque, A., & Van Ginneken, J. K. (2001). The effect of divorce on infant mortality in a remote area of Bangladesh. *Journal of Biosocial Science*, 33, 271–278.

- Allal, N., Sear, R., Prentice, A. M., & Mace, R. (2004). An evolutionary model of stature, age at first birth and reproductive success in Gambian women. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 271, 465–470.
- Allison, P. D. (1984). *Event history analysis: Regression for longitudinal event data*. Newbury Park: Sage Publications.
- Andersson, R., & Bergstrom, S. (1997). Maternal nutrition and socio-economic status as determinants of birthweight in chronically malnourished African women. *Tropical Medicine & International Health*, 2, 1080–1087.
- Andersson, T., Högberg, U., & Åkerman, S. (1996). Survival of orphans in 19th century Sweden: The importance of remarriages. *Acta Paediatrica*, 85, 981–985.
- Becher, H., Muller, O., Jahn, A., Gbangou, A., Kynast-Wolf, G., & Kouyate, B. (2004). Risk factors of infant and child mortality in rural Burkina Faso. *Bulletin of the World Health Organization*, 82, 265–273.
- Beckerman, S., Lizarralde, R., Lizarralde, M., Bai, J., Ballew, C., Schroeder, S., et al. (2002). The Bari partible paternity project, phase one. In S. Beckerman, & P. Valentine. (Eds.), *Cultures of multiple fathers: The theory and practice of partible paternity in lowland South America* (pp. 27–41). Gainesville: University Press of Florida.
- Beekink, E., van Poppel, F., & Liefbroer, A. C. (1999). Surviving the loss of the parent in a nineteenth-century Dutch provincial town. *Journal of Social History*, 32, 641–670.
- Beekink, E., van Poppel, F., & Liefbroer, A. C. (2002). Parental death and death of the child: Common causes or direct effects? In R. Derosas, & M. Oris. (Eds.), *When dad died: Individuals and families coping with distress in past societies* (pp. 234–260). Bern: Peter Lang.
- Beise, J. (2002). A multilevel event history analysis of the effects of grandmothers on child mortality in a historical German population, Krummhörn, Ostfriesland, 1720–1874. *Demographic Research*, 7, 13.
- Beise, J. (2005). The helping grandmother and the helpful grandmother: The role of maternal and paternal grandmothers in child mortality in the 17th and 18th century population of French settlers in Quebec, Canada. In E. Voland, A. Chasiotis, & W. Schiefelhoevel. (Eds.), *Grandmotherhood: The evolutionary significance of the second half of the female life* (pp. 215–238). New Brunswick: Rutgers University Press.
- Bhuiya, A., & Chowdhury, M. (1997). The effect of divorce on child survival in a rural area of Bangladesh. *Population Studies*, 51, 57–62.
- Bishai, D., Brahmabhatt, H., Gray, R., Kigozi, G., Serwadda, D., Sewankambo, N., et al. (2003). Does biological relatedness affect child survival? *Demographic*, 8–9.
- Blaikie, A. (1998). Survival chances, unmarried motherhood and domestic arrangements in rural Scotland, 1845–1945. *Local Population Studies*, 60, 34–46.
- Blurton Jones, N., Hawkes, K., & O'Connell, J. F. (1996). The global process and local ecology: How should we explain the differences between the Hadza and the !Kung? In S. Kent. (Ed.), *Cultural diversity among twentieth-century foragers* (pp. 159–187). Cambridge: Cambridge University Press.
- Blurton Jones, N. G., Marlowe, F., Hawkes, K., & O'Connell, J. F. (2000). Paternal investment and hunter-gatherer divorce rates. In L. Cronk, N. Chagnon, & W. Irons. (Eds.), *Adaptation and human behaviour: An anthropological perspective* (pp. 69–89). New York: Aldine de Gruyter.
- Borgerhoff Mulder, M. (2007). Hamilton's rule and kin competition: The Kipsigis case. *Evolution and Human Behavior*, 28, 299–312.
- Borgerhoff Mulder, M., & Milton, M. (1985). Factors affecting infant care in the Kipsigis. *Journal of Anthropological Research*, 41, 231–262.
- Breschi, M., & Manfredini, M. (2002). Parental loss and kin networks: Demographic repercussions in a rural Italian village. In R. Derosas, & M. Oris. (Eds.), *When dad died: Individuals and families coping with distress in past societies* (pp. 369–387). Bern: Peter Lang.
- Brittain, A. W. (1992). Birth spacing and child mortality in a Caribbean population. *Human Biology*, 64, 223–241.
- Browne, K. R. (2002). *Biology at work: Rethinking sexual equality*. New Brunswick: Rutgers University Press.
- Cain, M. (1977). The economic activities of children in a village in Bangladesh. *Population and Development Review*, 3, 201–227.
- Caldwell, J. C. (1978). A theory of fertility: From high plateau to destabilisation. *Population and Development Review*, 4, 553–577.
- Campbell, C., & Lee, J. Z. (1996). A death in the family: Household structure and mortality in rural Liaoning: Life-event and time-series analysis, 1792–1867. *History of the Family*, 1, 297–328.
- Campbell, C., & Lee, J. Z. (2002). When husbands and parents die: Widowhood and orphanhood in late Imperial Liaoning, 1789–1909. In R. Derosas, & M. Oris. (Eds.), *When dad died: Individuals and families coping with distress in past societies* (pp. 301–322). Bern: Peter Lang.
- Chen, L. C., Gesche, M. C., Ahmed, S., Chowdhury, A. I., & Mosley, W. H. (1974). Maternal mortality in rural Bangladesh. *Studies in Family Planning*, 5, 334–341.
- Crognier, E., Baali, A., & Hilali, M. K. (2001). Do “helpers at the nest” increase their parents’ reproductive success? *American Journal of Human Biology*, 13, 365–373.
- Crognier, E., Villena, M., & Vargas, E. (2002). Helping patterns and reproductive success in Aymara communities. *American Journal of Human Biology*, 14, 372–379.
- Daly, M., & Wilson, M. (1988). *Homicide*. New York: Aldine de Gruyter.
- Das Gupta, M. (1987). Selective discrimination against female children in India. *Population and Development Review*, 13, 77–101.
- Dennell, R., & Roebroeks, W. (2005). An Asian perspective on early human dispersal from Africa. *Nature*, 438, 1099–1104.
- Derosas, R. (2002). Fatherless families in 19th century Venice. In R. Derosas, & M. Oris. (Eds.), *When dad died: Individuals and families coping with distress in past societies* (pp. 421–452). Bern: Peter Lang.
- Draper, P., & Harpending, H. (1987). Parent investment and the child's environment. In J. B. Lancaster, J. Altmann, A. S. Rossi, & L. R. Sherrod. (Eds.), *Parenting across the lifespan: Biosocial dimensions* (pp. 207–235). New York: Aldine de Gruyter.
- Flinn, M. V., & England, B. G. (1995). Childhood stress and family environment. *Current Anthropology*, 36, 854–866.
- Galdikas, B. M. F., & Wood, J. W. (1990). Birth spacing patterns in humans and apes. *American Journal of Physical Anthropology*, 83, 185–191.
- Gibson, M. A., & Mace, R. (2005). Helpful grandmothers in rural Ethiopia: A study of the effect of kin on child survival and growth. *Evolution and Human Behavior*, 26, 469–482.
- Gibson, M. A. (in preparation). Does investment in the sexes differ when fathers are absent? Sex-biased infant survival and child growth in rural Ethiopia.
- Grainger, S., & Beise, J. (2004). Menopause and post-generative longevity: Testing the “stopping early” and “grandmother” hypotheses. *Max Planck Institute for Demographic Research Working Paper 2004-003*.
- Griffiths, P., Hinde, A., & Matthews, Z. (2001). Infant and child mortality in three culturally contrasting states of India. *Journal of Biosocial Science*, 33, 603–622.
- Gurven, M., & Hill, K. (1997). Comment on ‘Hadza women's time allocation, offspring provisioning and the evolution of long postmenopausal life spans’ by Hawkes et al. *Current Anthropology*, 38, 566–567.
- Gurven, M., & Kaplan, H. (2006). Determinants of time allocation across the lifespan: A theoretical model and an application to the Machiguenga and Piro of Peru. *Human Nature*, 17, 1–49.
- Hadley, C. (2004). The costs and benefits of kin: Kin networks and children's health among the Pimbwe of Tanzania. *Human Nature*, 15, 377–395.
- Hawkes, K. (1990). Why do men hunt? Benefits for risky choices. In E. Cashdan. (Ed.), *Risk and uncertainty in tribal and peasant economies* (pp. 145–166). Boulder, CO: Westview Press.
- Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. (1997). Hadza women's time allocation, offspring provisioning and the evolution of long postmenopausal life spans. *Current Anthropology*, 38, 551–578.
- Hawkes, K., O'Connell, J. F., & Jones, N. G. B. (2001). Hunting and nuclear families: Some lessons from the Hadza about men's work. *Current Anthropology*, 42, 681–709.

- Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., Alvarez, H., & Charnov, E. (1998). Grandmothering, menopause and the evolution of human life histories. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 1336–1339.
- Heath, K. M. (2003). The effects of kin propinquity on infant mortality. *Social Biology*, 50, 270–280.
- Hewlett, B. S. (1991). Demography and childcare in preindustrial societies. *Journal of Anthropological Research*, 47, 1–37.
- Hewlett, B. S. (1992). Husband–wife reciprocity and the father–infant relationship among Aka pygmies. In B. S. Hewlett. (Ed.), *Father–child relations* (pp. 153–176). New York: Aldine de Gruyter.
- Hewlett, B. S. (2000). Culture, history and sex: Anthropological contributions to conceptualizing father involvement. *Marriage and Family Review*, 29, 59–73.
- Hewlett, B. S., Lamb, M. E., Leyendecker, B., & Schölmerich, A. (2000). Parental investment strategies among Aka foragers, Ngandu farmers and Euro–American urban–industrialists. In L. Cronk, N. Chagnon, & W. Irons. (Eds.), *Adaptation and human behaviour: An anthropological perspective* (pp. 155–177). New York: Aldine de Gruyter.
- Hill, K. (1993). Life history theory and evolutionary anthropology. *Evolutionary Anthropology*, 2, 78–88.
- Hill, K., & Hurtado, A. M. (1991). The evolution of premature reproductive senescence and menopause in human females: An evaluation of the “grandmother hypothesis”. *Human Nature*, 2, 313–350.
- Hill, K., & Hurtado, A. M. (1996). *Ache life history: The ecology and demography of a foraging people*. New York: Aldine de Gruyter.
- Hill, K., Kaplan, H., Hawkes, K., & Hurtado, A. M. (1987). Foraging decisions among Ache hunter–gatherers: New data and implications for optimal foraging models. *Ethology and Sociobiology*, 8, 1–36.
- Högberg, U., & Broström, G. (1985). The demography of maternal mortality: 7 Swedish parishes in the 19th century. *International Journal of Gynecology & Obstetrics*, 23, 489–497.
- Hrdy, S. B. (2000). The optimal number of fathers: Evolution, demography, and history in the shaping of female mate preferences. *Annals of the New York Academy of Sciences*, 907, 75–96.
- Hrdy, S. B. (2005). Cooperative breeders with an ace in the hole. In E. Voland, A. Chasiotis, & W. Schiefelhoevel. (Eds.), *Grandmotherhood: The evolutionary significance of the second half of female life* (pp. 295–317). New Brunswick: Rutgers University Press.
- Huber, B. R., & Breedlove, W. L. (2007). Evolutionary theory, kinship, and childbirth in cross-cultural perspective. *Cross-Cultural Research*, 41, 196–219.
- Hurtado, A. M., & Hill, K. R. (1992). Paternal effect on offspring survivorship among Ache and Hiwi hunter–gatherers: Implications for modeling pair-bond stability. In B. S. Hewlett. (Ed.), *Father–child relations: Cultural and biosocial contexts* (pp. 31–55). New York: Aldine de Gruyter.
- Ivey, P. K. (2000). Cooperative reproduction in Ituri Forest hunter–gatherers: Who cares for Efe infants. *Current Anthropology*, 41, 856–866.
- Jones, J. H. (2005). Fetal programming: Adaptive life-history tactics or making the best of a bad start? *American Journal of Human Biology*, 17, 22–33.
- Kaplan, H. (1994). Evolutionary and wealth flows theories of fertility: Empirical tests and new models. *Population and Development Review*, 20, 753–791.
- Kaplan, H., & Hill, K. (1985). Food sharing among Ache foragers: Tests of explanatory hypotheses. *Current Anthropology*, 26, 223–246.
- Kaplan, H., & Lancaster, J. (2003). An evolutionary and ecological analysis of human fertility, mating patterns and parental investment. In K. W. Wachter, & R. A. Bulatao. (Eds.), *Offspring: Human fertility in biodemographic perspective* (pp. 170–223). Washington: National Academies Press.
- Kaplan, H. S., & Robson, A. J. (2002). The emergence of humans: The coevolution of intelligence and longevity with intergenerational transfers. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 10221–10226.
- Katz, J., West, K. P., Khatry, S. K., Christian, P., LeClerq, S. C., Pradhan, E. K., et al. (2003). Risk factors for early infant mortality in Sarlahi district Nepal. *Bulletin of the World Health Organization*, 81, 717–725.
- Kemkes, A. (2006). Does the sex of firstborn children influence subsequent fertility behavior? Evidence from family reconstitution. *Journal of Family History*, 31, 144–162.
- Kemkes-Grottenthaler, A. (2005). Of grandmothers, grandfathers and wicked step-grandparents: Differential impact of paternal grandparents on grandoffspring survival. *Historical Social Research*, 30, 219–239.
- Kirchengast, S., & Hartmann, S. (1998). Maternal prepregnancy weight status and pregnancy weight gain as major determinants for newborn weight and size. *Annals of Human Biology*, 25, 17–28.
- Koenig, M. A., Fauveau, V., Chowdhury, A. I., Chakraborty, J., & Khan, M. A. (1988). Maternal mortality in Matlab Bangladesh: 1976–85. *Studies in Family Planning*, 19, 69–80.
- Kramer, K. L. (2002). Variation in juvenile dependence: Helping behavior among Maya children. *Human Nature*, 13, 299–325.
- Kramer, K. L. (2005). Children's help and the pace of reproduction: Cooperative breeding in humans. *Evolutionary Anthropology*, 14, 224–237.
- Ladusingh, L., & Singh, C. H. (2006). Place, community education, gender and child mortality in North–East India. *Population, Space and Place*, 12, 65–76.
- Lahdenpera, M., Lummaa, V., Helle, S., Tremblay, M., & Russell, A. F. (2004). Fitness benefits of prolonged post-reproductive lifespan in women. *Nature*, 428, 178–181.
- Lee, R. D. (2003). Rethinking the evolutionary theory of aging: Transfers, not births, shape social species. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 9637–9642.
- Lee, R. D., & Kramer, K. L. (2002). Children's economic roles in the Maya family life cycle: Cain, Caldwell, and Chayanov revisited. *Population and Development Review*, 28, 475–499.
- Leonetti, D. L., Nath, D. C., Hemam, N. S., & Neill, D. B. (2004). Do women really need marital partners for support of their reproductive success? The case of the matrilineal Khasi of NE India. *Research in Economic Anthropology*, 23, 151–174.
- Leonetti, D. L., Nath, D. C., Hemam, N. S., & Neill, D. B. (2005). Kinship organisation and the impact of grandmothers on reproductive success among the matrilineal Khasi and patrilineal Bengali of Northeast India. In E. Voland, A. Chasiotis, & W. Schiefelhoevel. (Eds.), *Grandmotherhood: The evolutionary significance of the second half of female life* (pp. 194–214). New Brunswick: Rutgers University Press.
- Lewis, J. (1992). Gender and the development of welfare regimes. *Journal of European Social Policy*, 2, 159–173.
- Lovejoy, C. O. (1981). The origin of man. *Science*, 211, 341–350.
- Mace, R., & Pagel, M. (1994). The comparative method in anthropology. *Current Anthropology*, 35, 549–564.
- Mace, R. (1996). Biased parental investment and reproductive success in Gabbra pastoralists. *Behavioural Ecology and Sociobiology*, 38, 75–81.
- Marlowe, F. W. (2003). A critical period for provisioning by Hadza men—implications for pair bonding. *Evolution and Human Behavior*, 24, 217–229.
- Marlowe, F. W. (2005). Hunter–gatherers and human evolution. *Evolutionary Anthropology*, 14, 54–67.
- Masmas, T. N., Jensen, H., da Silva, D., Hoj, L., Sandstrom, A., & Aaby, P. (2004). Survival among motherless children in rural and urban areas in Guinea–Bissau. *Acta Paediatrica*, 93, 99–105.
- McDonald, P. (2000). The “toolbox” of public policies to impact on fertility—a global view. Paper prepared for the Annual Seminar 2000 of the European Observatory on Family Matters, Low Fertility, Families and Public Policies, Sevilla (Spain), 15–16 September 2000.
- Mosley, W. H., & Chen, L. C. (1984). An analytical framework for the study of child survival in developing countries. *Population and Development Review*, S10, 25–45.
- Muhuri, P. K., & Preston, S. H. (1991). Effects of family composition on mortality differentials by sex among children in Matlab Bangladesh. *Population and Development Review*, 17, 415–434.

- Over, M., Ellis, R. P., Huber, J. H., & Solon, O. (1992). The consequences of adult ill-health. In R. A. Feachem, T. Kjellstrom, C. J. L. Murray, M. Over, & M. A. Phillips. (Eds.), *The health of adults in the developing world* (pp. 161–207). Oxford: Oxford University Press.
- Pavard, S., Gagnon, A., Desjardins, B., & Heyer, E. (2005). Mother's death and child survival: The case of early Quebec. *Journal of Biosocial Science*, 37, 209–227.
- Pavard, S., Sibert, A., & Heyer, E. (2007). The effect of maternal care on child survival: A demographic, genetic and evolutionary perspective. *Evolution*, 61, 1153–1161.
- Ragsdale, G. (2004). Grandmothering in Cambridgeshire, 1770–1861. *Human Nature*, 15, 301–317.
- Reher, D. S., & González-Quñones, F. (2003). Do parents really matter? Child health and development in Spain during the demographic transition. *Population Studies*, 57, 63–75.
- Rogers, A. R. (1993). Why menopause? *Evolutionary Ecology*, 7, 406–420.
- Rohwer, S., Herron, J. C., & Daly, M. (1999). Stepparental behavior as mating effort in birds and other animals. *Evolution and Human Behavior*, 20, 367–390.
- Sear, R. (2007). Kin and child survival in rural Malawi: Are matrilineal kin beneficial in a matrilineal society? Manuscript under review.
- Sear, R., & Mace, R. (in press). Family matters: Kin, demography and child health in a rural Gambian population. In G. R. Bentley, & R. Mace (Eds.), *Substitute parents: Alloparenting in human societies*. New York: Berghahn Books.
- Sear, R., Mace, R., & McGregor, I. A. (2000). Maternal grandmothers improve the nutritional status and survival of children in rural Gambia. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 267, 461–467.
- Sear, R., Steele, F., McGregor, I. A., & Mace, R. (2002). The effects of kin on child mortality in rural Gambia. *Demography*, 39, 43–63.
- Shanley, D., Sear, R., Mace, R., & Kirkwood, T. (2007). Testing evolutionary theories of menopause. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 274, 2943–2949.
- Shanley, D. P., & Kirkwood, T. B. L. (2001). Evolution of the human menopause. *Bioessays*, 23, 282–287.
- Sigle-Rushton, W., & McLanahan, S. (2004). Father absence and child well-being: A critical review. In D. P. Moynihan, T. Smeeding, & L. Rainwater. (Eds.), *The future of the family* (pp. 116–158). New York: Russell Sage Foundation.
- Singer, J. D., & Willett, J. B. (2003). *Applied longitudinal data analysis: Modeling change and event occurrence*. Oxford: Oxford University Press.
- Sommestad, L. (1997). Welfare state attitudes to the male breadwinning system: The United States and Sweden in comparative perspective. *International Review of Social History*, 42, 153–174.
- Sorenson Jamison, C., Cornell, L. L., Jamison, P. L., & Nakazato, H. (2002). Are all grandmothers equal? A review and a preliminary test of the “grandmother hypothesis” in Tokugawa Japan. *American Journal of Physical Anthropology*, 119, 67–76.
- Strassmann, B. I., & Gillespie, B. (2002). Life-history theory, fertility and reproductive success in humans. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 269, 553–562.
- Thompson, B., & Rahman, A. K. (1967). Infant feeding and child care in a West African village. *Journal of Tropical Pediatrics*, 13, 124–138.
- Tsuya, N. O., & Kurosu, S. (2002). The mortality effects of adult male death on women and children in agrarian households in early modern Japan: Evidence from two Northeastern villages, 1716–1870. In R. Derosas, & M. Oris. (Eds.), *When dad died: Individuals and families coping with distress in past societies* (pp. 261–299). Bern: Peter Lang.
- Tymicki, K. (2006). The correlates of infant and childhood mortality: A theoretical overview and new evidence from the analysis of longitudinal data from Bejsce parish register reconstitution study 18th–20th centuries, Poland. Paper presented at Population Association of America Annual Conference 2006, Los Angeles.
- van Poppel, F. (2000). Children in one-parent families: Survival as an indicator of the role of the parents. *Journal of Family History*, 25, 269–290.
- Voland, E. (1988). Differential infant and child mortality in evolutionary perspective: Data from late 17th to 19th century Ostfriesland (Germany). In L. Betzig, M. Bergerhoff Mulder, & P. Turke. (Eds.), *Human reproductive behaviour: A Darwinian perspective* (pp. 253–276). Cambridge: Cambridge University Press.
- Voland, E., & Beise, J. (2002). Opposite effects of maternal and paternal grandmothers on infant survival in historical Krummhörn. *Behavioural Ecology & Sociobiology*, 52, 435–443.
- Voland, E., & Beise, J. (2005). “The husband's mother is the devil in the house”: Data on the impact of the mother-in-law on stillbirth mortality in historical Krummhörn (C18–19 Germany) and some thoughts on the evolution of postgenerative female life. In E. Voland, A. Chasiotis, & W. Schiefenhoevel. (Eds.), *Grandmotherhood: The evolutionary significance of the second half of the female life* (pp. 239–255). New Brunswick: Rutgers University Press.
- Walker, P. L., & Deniro, M. J. (1986). Stable nitrogen and carbon isotope ratios in bone-collagen as indexes of prehistoric dietary dependence on marine and terrestrial resources in Southern-California. *American Journal of Physical Anthropology*, 71, 51–61.
- Walker, R., Gurven, M., Hill, K., Migliano, A., Chagnon, N., De Souza, R., et al. (2006). Growth rates and life histories in 22 small-scale societies. *American Journal of Human Biology*, 18, 295–311.
- Waynforth, D. (2002). Evolutionary theory and reproductive responses to father absence: Implications of kin selection and the reproductive returns to mating and parenting effort. In C. S. Tamis-LeMonda, & N. Cabrera. (Eds.), *Handbook of father involvement: Multidisciplinary perspectives* (pp. 337–357). Mahwah, NJ: Lawrence Erlbaum Associates.
- Weisner, T. S., & Gallimore, R. (1977). My brother's keeper: Child and sibling caretaking. *Current Anthropology*, 18, 169–190.
- Winking, J. (in press). Are men really that bad as fathers? The role of men's investments. *Social Biology*.
- Winking, J., Gurven, M., & Kaplan, H. (2006). Measuring impacts of fathers among the Tsimane of Bolivia. Paper presented at the Human Behavior and Evolution Society Conference 2006, Philadelphia, USA.
- Woodbury, R. M. (1926). *Infant mortality and its causes*. Baltimore, MD: Williams and Wilkins.
- Yerushalmy, J., Kramer, M. S., & Gardiner, E. M. (1940). Studies in childbirth mortality: Puerperal fatality and loss of offspring. *Public Health Reports*, 55, 1010–1027.
- Zaba, B., Whitworth, J., Marston, M., Nakiyingi, J., Ruberantwari, A., Urassa, M., et al. (2005). HIV and mortality of mothers and children: Evidence from cohort studies in Uganda, Tanzania, and Malawi. *Epidemiology*, 16, 275–280.