

# Maternal grandmothers improve nutritional status and survival of children in rural Gambia

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Hypotheses for the evolution of human female life-history characteristics have often focused on the social nature of human societies, which allows women to share the burden of childcare and provisioning amongst other members of their kin group. We test the hypothesis that child health and survival probabilities will be improved by the presence of kin using a longitudinal database from rural Gambia. We find that the only kin to improve the nutritional status of children significantly (apart from mothers) are maternal grandmothers, and that this is reflected in higher survival probabilities for children with living maternal grandmothers. There is also evidence that the reproductive status of the maternal grandmother influences child nutrition, with young children being taller in the presence of non-reproductive grandmothers than grandmothers who are still reproductively active. Paternal grandmothers and male kin, including fathers, have negligible impacts on the nutritional status and survival of children.

**Keywords:** kin selection; child mortality; menopause; human social evolution

## 1. INTRODUCTION

The life history of human females differs in a number of ways from those of other primates. Human females begin reproducing at a relatively late age compared to the other apes but during their reproductive years they reproduce at a high rate. Human interbirth intervals average about three years in natural-fertility populations (e.g. the median interbirth interval in this Gambian population is 32 months; see also Hill & Hurtado (1996) and Wood (1994, p. 517)), compared to almost four years for gorillas, 5.5 years for chimpanzees and nearly eight years for orang-utans (Galdikas & Wood 1990). Then, women become unable to reproduce just halfway through their potential life span. Many evolutionary anthropologists agree that one factor in the evolution of these unusual characteristics is the highly social nature of human societies, which may allow women to draw upon the resources of other individuals when raising children. Kin-selection theory suggests that the most likely helpers will be close genetic relatives (Hamilton 1964) but there is some debate about which categories of kin provide most assistance. Some authors claim a pivotal role for fathers in the evolution of these traits (Hill 1993). There is evidence that paternal investment is high among certain human groups, with fathers in some societies providing important services to their children in the form of provisioning (Hill *et al.* 1985), direct childcare (Hewlett 1992) and protection from other males (Hill & Hurtado 1996). Others argue that the driving force behind these unusual features of human life history can be attributed to help from matrilineal kin (Hawkes *et al.* 1998). For example, authors have argued since the 1950s for the 'grandmother hypothesis' for the evolution of the menopause (Hamilton 1966; Williams 1957), which suggests that elderly women have a greater impact on their inclusive fitness by investing in their existing children and grandchildren rather than by continuing to reproduce themselves.

Evidence for the beneficial effects of older women on the nutritional status of children has been found in a hunter-gatherer population in Tanzania (Hawkes *et al.* 1997). Children in urban societies have also been shown to benefit from the presence of grandmothers, both in cognitive and health outcomes (Pope *et al.* 1993) and psychological and sociological well being (Alawad & Sonugabarke 1992; Wilson 1986). One study, which distinguished between maternal and paternal grandparents, found that maternal grandparents, particularly maternal grandmothers, were more solicitous of their grandchildren than paternal grandparents (Euler & Weitzel 1996). This was interpreted as a response to paternity uncertainty (in species with internal fertilization, maternity is certain whereas paternity is merely attributable), which lowers the probable genetic relatedness of children related through the male line. No previous study has found a direct fitness benefit to grandmaternal care; the only study to have looked for the effects of grandmothers on the survival rates of children found no difference between children with or without grandmothers (Hill & Hurtado 1996). We use a longitudinal database from The Gambia to determine which categories of kin improve nutritional status and survival probabilities of children in a natural-fertility, natural-mortality environment.

## 2. DATA

The data we use were collected by Sir Ian McGregor between 1950 and 1974 from two villages in rural Gambia, Keneba and Manduar (see McGregor (1991) for a detailed description of the study). Surveys were conducted at least annually in these villages during which anthropometric data and information on disease status were collected. A system was set up in 1950 in which literate villagers were chosen to record all births and deaths that occurred in their villages. These demographic data were supplemented by information on marriages, migration and residence collected during the annual surveys. Unique identification numbers for each individual

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allow us to link anthropometric and demographic data, and to link each individual with their parents, grandparents, siblings, spouses and children. Some medical treatment was given to villagers as required during the annual surveys, and short-term trials aimed at controlling certain parasitic diseases were attempted during the early years of the study. Overall, however, this project appeared to have little effect on mortality rates during the period of the study (Sear *et al.* 2001). Such comprehensive data from a natural-fertility and natural-mortality human population are exceedingly rare.

These data come from a patrilineal and patrilocal Mandinka farming community. Women were responsible for the farming of rice, the main subsistence crop, while men farmed groundnuts, a cash crop, and a few other subsistence crops. The majority of women married within their own village or neighbouring villages, which meant that their parents, as well as their husband's parents, were nearby during their married life (Thompson 1965). Both mortality and fertility were high during this period (Billewicz & McGregor 1981): women averaged a total of about seven live-born children but over 40% of these died before reaching the age of five years.

### 3. METHODS

#### (a) *Nutritional status*

We analysed anthropometric data from children aged between 0 and 59 months. Between 1950 and 1974, 8827 measurements were taken from 2018 children. Because the motivations and opportunities for kin to invest in children may differ over the first five years of childhood, we divided up the data set by age of child and ran a separate model for each of the first five years of life. Young infants are heavily dependent on their mothers while their major source of nourishment is still breast milk, but other caretakers may assume more importance in later childhood as children are weaned. We included only one height and one weight measurement for each child in each model to avoid biases due to non-independent observations. We restricted our analysis to data collected in the dry season because both adults and children show seasonal weight fluctuations due to variations in the availability of food, prevalence of disease and workloads (Billewicz & McGregor 1982). This resulted in a total sample size of 6153 measurements from 1998 children. In addition, we ran the same model for the whole five-year period, again using only one randomly chosen measurement from each child to avoid potential biases ( $n = 1998$ ).

We analysed nutritional status using ANCOVA models. We ran models for all age groups on both weight and height. To simplify the model and to avoid losing information from children with missing data in some categories, each category of parent and grandparent, except the maternal grandmother, was entered as a dummy variable. These dummy variables were coded 1 if the parent or grandparent had died before the survey and 0 for all other cases. The maternal grandmother variable was entered as a factor with three levels: maternal grandmother died before survey; maternal grandmother alive at time of survey but still reproductively active (defined as having had a birth in the year of the grandchild's birth or later); and all other cases. The reproductive status of maternal grandmothers was included in the model as grandmothers who have small children of their own are expected to direct most of their investment

towards their own children rather than their grandchildren, to whom they are less closely related. No paternal grandmothers were still reproductively active in this sample. The models had previously been run including an extra level for missing data for each category of kin but pairwise comparisons indicated that the missing data did not differ significantly from the other categories for any class of kin. All kin variables were entered as fixed factors. Both height and weight models included child's age, mother's body mass index (BMI, weight (kg)/height (m<sup>2</sup>)) and the age of all categories of kin at the time of the child's birth (for those kin who had died before the child was born their age at the child's birth had they been alive was included in the model) as covariates, and the child's sex and village as fixed factors. The weight model additionally included a covariate for height. The height model also included covariates for mother's height and father's height in an attempt to control for familial influences on height.

#### (b) *Mortality*

The sample of children used for this analysis included all children born between 1950 and 1974 where dates of birth and death (if applicable) were known to the month. This resulted in a sample size of 1691 children, of whom 622 died. Again, this data set was divided up by age of child, both because the effects of kin may vary across childhood and because the level and pattern of mortality vary throughout the first five years of life. Immediately after birth mortality rates are extremely high, nearly 7% of live-births in this data set died in their first month of life, but then mortality more or less declines until the end of the five-year period under study (Sear *et al.* 2001). The aetiology of mortality also differs between early and later childhood, with more deaths having endogenous causes (genetic defects, low birth weight) in the first few months of life but with exogenous causes (disease, accidents) predominating after the first year. We performed separate analyses on three groups of children: infant (0–11 months), toddler (12–23 months) and later childhood (24–59 months: there were too few deaths in the third, fourth and fifth years of life to justify analysing them separately).

We used multilevel discrete-time event history analysis to analyse the determinants of child mortality, using MLwiN software (Goldstein *et al.* 1998). Event history analysis models the duration of time until an event of interest occurs, in this case a death (Allison 1984). An advantage of this technique is that it allows the inclusion of time-varying covariates, such as the survival status of a grandparent, which may change over the child's lifetime. We entered each category of parent and grandparent as a time-varying dummy variable coded 1 if the relative was dead and 0 otherwise. For maternal grandmothers we included an additional dummy variable, which was coded 1 if the grandmother was still reproductively active and 0 otherwise. Also included in the model were a number of non-kin variables that are known to influence child mortality. The multilevel approach was used to control for the lack of independence of data points caused by including a number of children with the same mother (Goldstein 1995).

### 4. RESULTS

#### (a) *Nutritional status*

Table 1 shows the estimated marginal mean heights (table 1a) and weights (table 1b) of children in each age group by survival (and, in the case of maternal grandmothers, reproductive) status of each kin variable. For

Table 1. Estimated marginal mean heights in centimetres (a) and weights in kilograms (b) of children ( $\pm$  s.e.m.) for each age group by survival status of kin, controlling for child's age, height (in weight model), age of all parents and grandparents at child's birth, mother's and father's height (in height model) and mother's body mass index (Bold type indicates cells where the presence of kin had a positive effect on child height or weight. 'Alive' category includes missing cases. Asterisks indicate where child's height or weight is significantly different from 'alive' category. In no models were the 'maternal grandmother dead' and 'maternal grandmother reproductively active' categories significantly different from one another. \* $p < 0.05$ ; \*\* $p < 0.01$ .)

kin	survival/ reproductive status	sample size	age (months)					
			0-11	12-23	24-35	36-47	48-59	0-59
(a)	mother	alive	62.28 $\pm$ 0.44	<b>74.09 <math>\pm</math> 0.40</b>	<b>82.00 <math>\pm</math> 0.38</b>	89.39 $\pm$ 0.41	<b>96.59 <math>\pm</math> 0.41</b>	<b>75.86 <math>\pm</math> 0.38</b>
		dead	63.69 $\pm$ 1.32	<b>72.78 <math>\pm</math> 1.46</b>	<b>81.96 <math>\pm</math> 1.09</b>	90.87 $\pm$ 1.03	<b>96.25 <math>\pm</math> 1.05</b>	<b>74.99 <math>\pm</math> 0.99</b>
	father	alive	62.65 $\pm$ 0.65	<b>73.45 <math>\pm</math> 0.74</b>	<b>82.04 <math>\pm</math> 0.57</b>	<b>90.31 <math>\pm</math> 0.55</b>	<b>96.45 <math>\pm</math> 0.57</b>	75.42 $\pm$ 0.50
		dead	63.32 $\pm$ 1.03	<b>73.42 <math>\pm</math> 0.99</b>	<b>81.92 <math>\pm</math> 0.80</b>	<b>89.95 <math>\pm</math> 0.80</b>	<b>96.39 <math>\pm</math> 0.81</b>	75.42 $\pm$ 0.81
	maternal grandmother	non-reproductive	<b>63.36 <math>\pm</math> 0.75</b>	<b>74.03 <math>\pm</math> 0.79</b>	<b>82.74 <math>\pm</math> 0.61</b>	<b>91.18 <math>\pm</math> 0.59</b>	<b>97.55 <math>\pm</math> 0.60</b>	<b>76.32 <math>\pm</math> 0.57</b>
		reproductive	<b>62.36 <math>\pm</math> 0.87</b>	<b>73.27 <math>\pm</math> 0.95</b>	<b>81.28 <math>\pm</math> 0.83*</b>	<b>89.60 <math>\pm</math> 0.89</b>	<b>95.29 <math>\pm</math> 0.89**</b>	<b>74.55 <math>\pm</math> 0.76**</b>
		dead	<b>63.23 <math>\pm</math> 0.79</b>	<b>73.01 <math>\pm</math> 0.83**</b>	<b>81.93 <math>\pm</math> 0.67</b>	<b>89.60 <math>\pm</math> 0.66**</b>	<b>96.40 <math>\pm</math> 0.69*</b>	<b>75.40 <math>\pm</math> 0.63**</b>
	paternal grandmother	alive	<b>63.23 <math>\pm</math> 0.76</b>	<b>73.51 <math>\pm</math> 0.80</b>	81.92 $\pm$ 0.62	<b>90.19 <math>\pm</math> 0.61</b>	<b>96.54 <math>\pm</math> 0.63</b>	<b>75.43 <math>\pm</math> 0.59</b>
		dead	<b>62.73 <math>\pm</math> 0.78*</b>	<b>73.36 <math>\pm</math> 0.83</b>	82.05 $\pm$ 0.67	<b>90.07 <math>\pm</math> 0.67</b>	<b>96.29 <math>\pm</math> 0.69</b>	<b>75.41 <math>\pm</math> 0.63</b>
	maternal grandfather	alive	<b>63.46 <math>\pm</math> 0.77</b>	<b>73.51 <math>\pm</math> 0.81</b>	<b>82.13 <math>\pm</math> 0.63</b>	89.93 $\pm$ 0.62	96.37 $\pm$ 0.63	<b>75.47 <math>\pm</math> 0.60</b>
dead		<b>62.50 <math>\pm</math> 0.78**</b>	<b>73.36 <math>\pm</math> 0.83</b>	<b>81.84 <math>\pm</math> 0.67</b>	90.33 $\pm$ 0.67	96.46 $\pm$ 0.69	<b>75.37 <math>\pm</math> 0.62</b>	
paternal grandfather	alive	<b>62.99 <math>\pm</math> 0.77</b>	<b>73.62 <math>\pm</math> 0.81</b>	<b>82.26 <math>\pm</math> 0.63</b>	<b>90.31 <math>\pm</math> 0.62</b>	<b>96.44 <math>\pm</math> 0.63</b>	<b>75.46 <math>\pm</math> 0.60</b>	
	dead	<b>62.98 <math>\pm</math> 0.78</b>	<b>73.25 <math>\pm</math> 0.83</b>	<b>81.71 <math>\pm</math> 0.66</b>	<b>89.95 <math>\pm</math> 0.66</b>	<b>96.39 <math>\pm</math> 0.69</b>	<b>75.39 <math>\pm</math> 0.62</b>	
(b)	mother	alive	<b>6.17 <math>\pm</math> 0.10</b>	<b>8.57 <math>\pm</math> 0.09</b>	10.75 $\pm$ 0.10	<b>12.95 <math>\pm</math> 0.11</b>	<b>14.62 <math>\pm</math> 0.12</b>	<b>9.34 <math>\pm</math> 0.08</b>
		dead	<b>5.57 <math>\pm</math> 0.30*</b>	<b>7.81 <math>\pm</math> 0.35*</b>	11.17 $\pm$ 0.29	<b>12.56 <math>\pm</math> 0.28</b>	<b>12.49 <math>\pm</math> 0.30</b>	<b>8.91 <math>\pm</math> 0.22*</b>
	father	alive	5.85 $\pm$ 0.15	8.15 $\pm$ 0.18	10.93 $\pm$ 0.15	12.67 $\pm$ 0.15	14.42 $\pm$ 0.16	9.09 $\pm$ 0.11
		dead	5.89 $\pm$ 0.23	8.23 $\pm$ 0.24	10.99 $\pm$ 0.21	12.87 $\pm$ 0.22	14.69 $\pm$ 0.23	9.16 $\pm$ 0.18
	maternal grandmother	non-reproductive	<b>5.98 <math>\pm</math> 0.17</b>	<b>8.34 <math>\pm</math> 0.19</b>	<b>11.03 <math>\pm</math> 0.16</b>	<b>12.71 <math>\pm</math> 0.16</b>	<b>14.53 <math>\pm</math> 0.17</b>	<b>9.22 <math>\pm</math> 0.13</b>
		reproductive	<b>5.87 <math>\pm</math> 0.20</b>	<b>8.09 <math>\pm</math> 0.23</b>	<b>11.05 <math>\pm</math> 0.22</b>	<b>12.80 <math>\pm</math> 0.24</b>	<b>14.71 <math>\pm</math> 0.26</b>	<b>9.18 <math>\pm</math> 0.17</b>
		dead	<b>5.77 <math>\pm</math> 0.18**</b>	<b>8.13 <math>\pm</math> 0.20*</b>	<b>10.81 <math>\pm</math> 0.18</b>	<b>12.77 <math>\pm</math> 0.18</b>	<b>14.43 <math>\pm</math> 0.20</b>	<b>8.97 <math>\pm</math> 0.14**</b>
	paternal grandmother	alive	<b>5.93 <math>\pm</math> 0.17</b>	<b>8.24 <math>\pm</math> 0.19</b>	<b>10.97 <math>\pm</math> 0.17</b>	12.76 $\pm$ 0.17	<b>14.57 <math>\pm</math> 0.18</b>	9.12 $\pm$ 0.13
		dead	<b>5.81 <math>\pm</math> 0.18*</b>	<b>8.14 <math>\pm</math> 0.20</b>	<b>10.95 <math>\pm</math> 0.18</b>	12.76 $\pm$ 0.18	<b>14.54 <math>\pm</math> 0.20</b>	9.13 $\pm$ 0.14
	maternal grandfather	alive	5.87 $\pm$ 0.17	8.09 $\pm$ 0.19	10.90 $\pm$ 0.17	12.75 $\pm$ 0.17	14.54 $\pm$ 0.18	9.08 $\pm$ 0.13
dead		5.88 $\pm$ 0.18	8.29 $\pm$ 0.20**	11.02 $\pm$ 0.18	12.77 $\pm$ 0.18	14.58 $\pm$ 0.20	9.17 $\pm$ 0.14	
paternal grandfather	alive	5.84 $\pm$ 0.17	8.16 $\pm$ 0.19	10.90 $\pm$ 0.17	12.70 $\pm$ 0.17	14.56 $\pm$ 0.18	9.08 $\pm$ 0.13	
	dead	5.90 $\pm$ 0.18	8.22 $\pm$ 0.20	11.02 $\pm$ 0.18	12.82 $\pm$ 0.18	14.56 $\pm$ 0.20	9.17 $\pm$ 0.14	

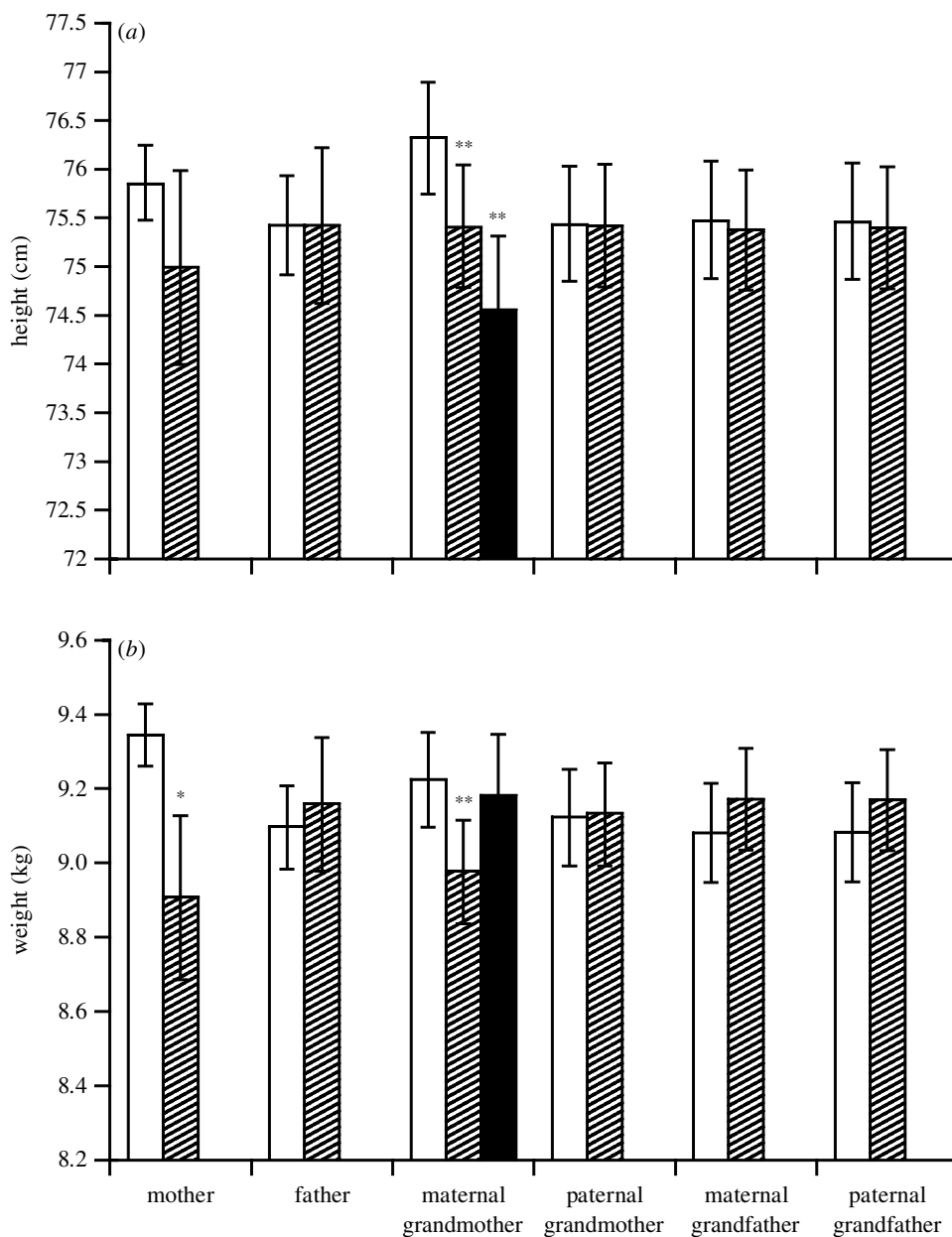


Figure 1. Estimated marginal mean heights (a) and weights (b), with standard errors, of children aged 0–59 months by survival status of kin, controlling for child's age, height (in weight model), age of parents and grandparents at child's birth, mother's and father's height (in height model) and mother's body mass index. For all categories of kin except maternal grandmothers open bars represent kin alive at time of survey (category includes missing cases) and hatched bars represent kin died before survey. For maternal grandmothers, open bars represent grandmothers alive and non-reproductive at time of survey (includes missing cases), solid bar represents maternal grandmothers alive and still reproductively active at time of survey, and hatched bars represent grandmother died before survey. Asterisks indicate whether categories were significantly different from alive category (\* $p < 0.05$ , \*\* $p < 0.01$ ).

both height and weight models the only kin to have a consistent positive effect on child nutritional status in all age groups were maternal grandmothers. These differences are significant for all ages, except height in the first year of life and weight in the first two years of life, and for the overall model. The reproductive status of the maternal grandmothers is also important for height. Overall, children with reproductively active maternal grandmothers were significantly shorter than those with non-reproductive grandmothers (figure 1a). When each age group of children is considered separately this difference is in the same direction across all age groups,

significantly so in the third and fifth years of life. In no models were the heights or weights of children with dead maternal grandmothers different from those of children with reproductively active maternal grandmothers.

In contrast, the evidence that paternal grandmothers improve the nutritional status of their grandchildren is weak. Though children with living paternal grandmothers were significantly taller and heavier than those without paternal grandmothers in the first year of life, this effect disappears in later childhood and is not significant in the overall models for either height or weight. Mothers broadly appear to improve the nutritional status

Table 2. *Parameter estimates ( $\pm$  s.e.m.) for kin variables from the multilevel discrete-time event history models of infant, toddler and later childhood mortality*

(Odds ratios indicate the risk of mortality relative to the reference category (reference category has an odds ratio of 1). Full model includes sex of child, year of birth, season of birth, village of birth, whether child was a twin, whether child was last born, birth order, length of preceding and succeeding birth intervals, mother's age at birth, survival status of previous sibling, whether child had living elder brothers and sisters, and marital status of mother and father. \*  $p < 0.05$ , \*\*  $p < 0.01$ .)

kin	survival/ reproductive status	sample size	age (months)					
			0-11		12-23		24-59	
			estimate	odds ratio	estimate	odds ratio	estimate	odds ratio
mother	alive	1553	0	1.00	0	1.00	0	1.00
	dead	30	2.59 $\pm$ 0.60**	13.36	2.45 $\pm$ 0.77**	11.65	0.23 $\pm$ 0.68	1.26
father	alive	1487	0	1.00	0	1.00	0	1.00
	dead	59	0.27 $\pm$ 0.76	1.31	-0.62 $\pm$ 0.74	0.54	-0.46 $\pm$ 0.47	0.63
maternal grandmother	non-reproductive	780	0	1.00	0	1.00	0	1.00
	reproductive	81	0.16 $\pm$ 0.31	1.17	0.45 $\pm$ 0.48	1.58	-0.32 $\pm$ 0.56	0.73
paternal grandmother	reproductive	222	0.15 $\pm$ 0.21	1.16	0.71 $\pm$ 0.27*	2.04	0.02 $\pm$ 0.27	1.02
	dead	440	0	1.00	0	1.00	0	1.00
maternal grandfather	alive	325	-0.22 $\pm$ 0.19	0.80	-0.16 $\pm$ 0.25	0.85	0.07 $\pm$ 0.23	1.07
	dead	532	0	1.00	0	1.00	0	1.00
paternal grandfather	alive	294	-0.09 $\pm$ 0.19	0.91	-0.01 $\pm$ 0.27	0.99	0.06 $\pm$ 0.24	1.07
	dead	161	0	1.00	0	1.00	0	1.00
maternal grandfather	alive	375	0.06 $\pm$ 0.17	1.06	-0.34 $\pm$ 0.24	0.71	-0.17 $\pm$ 0.22	0.84
	dead							

of their children. Overall, children were significantly heavier in the presence of mothers (figure 1*b*) and this difference is also significant between zero and 23 months. This effect does not persist into later childhood, nor are there any differences in the heights of children with and without mothers. This may be due to the small numbers of children who lost their mothers and survived to be measured; although there is a Mandinka saying 'as fat as an orphaned child', which suggests that orphaned children may be well cared for in this society, if they do survive.

Male kin appear to have a negligible impact on the nutritional status of children. There were no consistent effects of fathers or grandfathers on heights or weights, and no significant effects of fathers or paternal grandfathers at any age.

### (b) Mortality

Table 2 shows the effects of kin on child survival for all three multilevel models. The death of the mother had a strong effect on child survival rates during the first two years of life: children without mothers in the infant and toddler periods suffered risks of mortality 11 to 13 times greater than those whose mothers were still alive. After the second year, children with dead mothers did not have significantly higher chances of dying than those whose mothers were still living. Fathers had no consistent or significant effects on child mortality.

The presence of maternal grandmothers during the toddler period significantly increased the survival probability of the child (see figure 2). The trend is in the same direction in infancy and later childhood but these differences are not significant. Children whose maternal grandmothers were still reproductively active had slightly higher mortality in the infant and toddler periods than those whose grandmothers had stopped reproducing before their birth, but this did not reach statistical significance in either model. Paternal grandmothers, maternal grandfathers and paternal grandfathers all had no significant effect on child survival.

## 5. DISCUSSION

These analyses have shown a clear beneficial effect of maternal grandmothers on both child nutritional status and child mortality. The lack of any positive relationship between the other grandparents and mortality or nutritional status suggests that this effect is not the result of inherited effects but of some factor unique to the maternal grandmother, such as childcare. Maternal grandmothers provide the greatest protection from mortality during the second year of life. This coincides with the time that weaning begins in this society (Thompson 1965). Weaning allows the mother to delegate some of the responsibility for childcare and provisioning to other individuals, such as grandmothers. This delegation may allow human females to divert some of their resources into conceiving and raising another child more quickly, in contrast to other apes, where females are solely responsible for the care of their offspring.

The presence of male or patrilineal kin does not appear to improve the nutrition and survival of children. It is possible that the relatively small sample size of

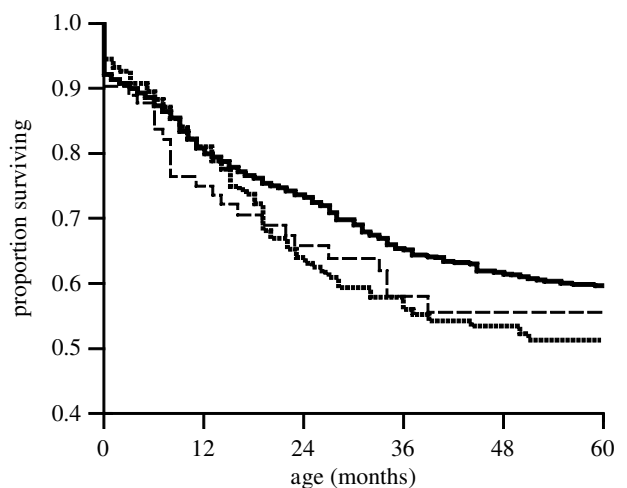


Figure 2. Kaplan–Meier plot showing survival of children whose maternal grandmothers died before their birth (dotted line) compared with those whose maternal grandmothers were alive at their birth and still reproductively active (dashed line) and those whose grandmothers were alive at their birth and non-reproductive (solid line).

children who lost their fathers may be obscuring any effect of paternal investment on child health and survival, but there is no evidence from the trends obtained from these analyses that the presence of fathers is beneficial to their offspring. The level of paternity uncertainty in a population may be a factor in determining the level of investment in children by males and patrilineal relatives (Emlen 1995). We have no quantitative information on paternity certainty in these villages, but there are considerable age differences between husbands and wives (the mean age at first birth differs by 11 years for men and women), and divorce and remarriage are not uncommon for either sex. The relative instability of marital bonds may reduce the inclination and opportunity for fathers, and other patrilineal kin, to invest in young children.

These results suggest that there may be fitness benefits to post-reproductive survival of women. At the median age of last birth in this population (39 years) women can expect to live almost a further 30 years, which is considerably longer than the period required to ensure their own infants' survival. Our analyses have shown that grandchildren enjoy fitness benefits from the presence of their maternal grandmothers. This suggests that older women are investing in their grandchildren after they have stopped reproducing themselves, a prediction expected from the 'grandmother hypothesis' for the evolution of menopause. These benefits to kin are not enough in themselves to drive the evolution of early reproductive cessation. There also needs to be some cost to continuing reproduction beyond the fifth decade of life. Some models have suggested that the increasing risks of death in child-birth with age are not sufficient by themselves for the evolution of menopause (Rogers 1993); but the evolution of such a trait is likely to be influenced by a number of factors. Our analyses have also suggested that there may be a cost to continued reproduction by grandmothers in the poorer nutritional status of grandchildren with reproductively active grandmothers compared to those whose grandmothers had stopped reproducing before their

birth. As this difference in nutritional status was not reflected in statistically significant differences in mortality rates, the evidence for this cost is not particularly strong. Nevertheless, given that we have observed the same trends in both nutritional status and mortality analyses, we suggest that this may be a real effect. It should be noted that maternal and grandmaternal reproduction rarely overlap in this society: 93% of children had maternal grandmothers who had stopped reproducing before their birth. The finding that orphanhood after the age of two years does not increase the probability of death for children illustrates the role of the extended matrilineal family in human child-rearing.

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