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Hamilton's Rule and Kin Competition: The Kipsigis Case

Running headline: **Hamilton's Rule and Kin Competition**

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ABSTRACT

Evolutionary studies of human behavior have emphasized the importance of kin selection in explaining social institutions and fitness outcomes. Our relatives can nevertheless be competitors as well as sources of altruism. This is particularly likely when there is local competition over resources, where conflict can lead to strife among non-dispersing relatives, reducing or even negating the effects of relatedness on promoting altruism. Here I present demographic data on a land-limited human population, utilizing large within population-variation in land ownership to determine the interactions between local resource competition and the benefits of kin in enhancing child survival, a key component of fitness in this population. As predicted, wealth affects the extent of kin altruism, in that paternal relatives (specifically father's brothers) appear to buffer young children from mortality much more effectively in rich than poor households. This interaction effect is interpreted as evidence that the extent of nepotism among humans depends critically on the resource availability. Further unanticipated evidence that maternal kin play a role in buffering children from mortality in situations where paternal kin control few resources speaks to the important role that specific local circumstance plays in shaping kin contributions to child welfare.

1.0 INTRODUCTION

Since the first applications of evolutionary theory to human behavior (Wilson 1975) kin selection has played a key explanatory role. Studies of parental investment (Daly and Wilson 1988), food sharing (Gurven et al. 2001), residence decisions and violence (Chagnon 1979) show that individuals favor close over distant (or non) relatives as targets of altruism, consistent with inclusive fitness theory (Hamilton 1964). However kin altruism can be disrupted if there is local competition over resources because this can lead to competition among non-dispersing relatives, reducing or negating the effects of relatedness on promoting altruism (Boyd 1982, Frank 1998, Hamilton 1967). While research on non-humans demonstrates that the extent of nepotism among kin can depend critically on resources available to parents or sibships in insects (Griffin, West, and Buckling 2004, West et al. 2001) our understanding of the sensitivity of human kinship relations to resource competition derives largely from folklore (Cindarella's scrubbing of the kitchen floor on the night of the Prince's ball at the behest of her stepsisters) or historical anecdote (the antics of the battling sons of Eleanor of Aquitaine).

Here I present demographic data from Kenya, leveraging large variation in land ownership among Kipsigis agropastoralists, to determine the interactions between local resource competition and the role of kin in enhancing child survival. As predicted, in this patrilineal, patrilocal population, where polygyny generates large co-resident aggregations of paternal relatives competing for inheritances, there is an interaction between resource availability and the extent to which paternal relatives apparently buffer young children from mortality. Additional unanticipated evidence suggests that maternal relatives also appear to protect children against mortality, although only in situations where paternal kin control inadequate resources to raise children. These results shed light on the ecological and social factors affecting when kin might affect the success of their relatives' reproductive careers. While there has been discussion of some of the possible contingencies influencing why certain categories of kin might (or might not) help (e.g., Beise 2005, Hames and Draper 2004, Leonetti et al. 2005, Sear and Mace 2006, Hrdy 2005) this study presents an empirical analysis of how the resources available to lineages affect the behavior of kin in such a way as to influence child survival outcomes.

To place the somewhat counterintuitive expectations that paternal Kipsigis kin are not necessarily very helpful when resources are strained I review some previous research on this population, adding ethnographic observations. Armed with the principal scholarly source on the Kipsigis (Peristiany 1939) I first arrived in a Kipsigis neighborhood (Tabarit) expecting to find strong localized patrilineages with marked patterns of respect and economic obligation. Almost immediately I learned of intense fraternal strife, conflicts over land and bridewealth (livestock) distributions, often taken to the neighborhood moots (or courts). When a young man from a neighboring community turned down funds to study journalism in Canada because of fear "that my brother and cousins will take my land and cattle if father dies in my absence" (Kab Gelegele resident, February, 1982) the truly pervasive influence of intralineage conflict dawned on me. Empirical analyses confirm the extent to which brothers hinder each others' marriage,

inheritance and reproductive chances (whereas sisters are an asset, Borgerhoff Mulder 1998).

Ethnographically the story is more complicated. Over the months I began to see instances of extraordinary cooperation over blood feuds, over the hosting of the all-important circumcision ceremonies, and in crises resulting from severe illness, theft or livestock loss. Agnates would appear from far away and deal with the disaster. Looking back into Peristiany I found he too saw the same things: "(T)he economic obligations between paternal relations are only enforced during moments of exceptional need" (1939:98) and "the solidarity of the paternal family can be seen functioning … in the case of a murder committed by one of its members" or "if the harvest is bad" (:98,:100).

With this knowledge of how paternal kin and lineages operate in contemporary and traditional Kipsigis communities, and receiving letters from Kipsigis friends whose lives were being destroyed by competitive kinsmen, I watched with some amazement a burgeoning literature on the cascades of positive kin effects on survival and growth (reviewed in Hrdy 2005, Sear and Mace 2006). Previous analyses of Kipsigis data had already shown negative effects of siblings (Borgerhoff Mulder 1998) and cowives (Borgerhoff Mulder 1990, 1997) on rates of child survival, indicative of intrafamilial resource competition. The motivation for the present study therefore lay in continuing to investigate such competition beyond the confines of sibships and polygynous marriages, guided by ongoing developments in kinship and reproductive skew theory to which I now turn.

1.1 Child mortality and social support

Although child mortality in the developed world is rare (6 deaths per 1000 livebirths), the developing world exhibits a 29-fold higher rate (175 per 1000 for Sub Saharan Africa (Black, Morris, and Bryce 2003)). This mortality level reflects the coincidence of an evolved set of life history traits, specifically the rapid production of altricial young requiring high levels of parental investment (Kaplan and Lancaster 2003), and the poor socioeconomic conditions typical of many regions within the developing world, including food insecurity, high pathogen exposure, low education and negative effects of global markets (Armelagos, Brown, and Turner 2005, Cesar et al. 2003). While within-population variation in child welfare and survival are clearly a function of household income, parental education, season of birth, maternal age, and child and maternal nutrition, public health scholars have recently extended their investigations to the importance of social support networks, often made up of kin, in promoting positive heath outcomes through buffering households against risk of food shortages (Cohen, Underwood, and Gottlieb 2000).

As regards such familial networks, biologists expect kin to assist their relatives in successfully raising offspring, even if at personal cost, because of inclusive fitness benefits. Hamilton's kin selection theory (Hamilton 1964) provides an explanation for such altruism: altruistic behavior is favored wherever $rb-c > 0$, where r is the genetic relatedness between actor and beneficiary, b the benefit of receiving the altruistic

behavior, and c the cost of performing the behavior. Evolutionary anthropologists have made specific tests of Hamilton's rule regarding nepotism and investment within human families (e.g., Alexander 1979, Chagnon 1982, Chagnon and Bugos 1979) and, in some cases, found quite close fits between predicted patterns of altruism and empirical data (Bowles and Posel 2005).

It is often forgotten that Hamilton also recognized the potential for competition among kin in viscous populations where dispersal is limited (Hamilton 1967). In studies of non humans competition between relatives over resources has been convincingly shown to reduce selection for cooperation among relatives (Griffin, West, and Buckling 2004, West et al. 2001), and to bias sex ratios away from the competing sex (Clarke 1978, Gowaty 1993); this is because although limited dispersal raises levels of relatedness among interacting individuals, it can also lead to more local competition among relatives (Frank 1998). And in a separate theoretical literature on reproductive skew some of the transactional models in which dominants are assumed to control the reproduction of subordinates, specifically the concessions model (Johnstone 2000, Keller and Reeve 1994), predict that relatedness within a group can exacerbate reproductive differentials among kin, leading to the prediction that some relatives can suffer from living in high aggregations of kin.

In humans, there is clear evidence that within-family inequities exist (Boone 1986, Hrdy and Judge 1993), and that families can be suffused with tension (Alexander 1979, Emlen 1995). Furthermore psychologists have explored health and educational differentials among siblings (Hertwig, Davis, and Sulloway 2002), in some cases within the framework of resource dilution (Downey 2001). Nevertheless, there has been no systematic examination of the implications of local resource competition for constraining the role of relatives as cooperators or competitors, with the exception of Hadley's (2004) study of Tanzanian Pimbwe in which he examined statistical interactions between socioeconomic status and kin effects. Ultimately a perspective focusing on the intersections of kin effects and resources could be brought to bear on explaining cross-cultural variation in kinship systems, but in this analysis I focus on the more tractable question of within population variability.

1.2 Predictions for a Kipsigis community

The Kipsigis of Kenya are a Nilotic agropastoral population, inhabiting the fringes of the White Highlands, living on now demarcated plots of land on which they keep livestock and grow crops for subsistence and cash. They have at least since the late 18th century been patrilineal, polygynous and patrilocal (Mwanza 1977). Marriages are sealed with a bridewealth payment from groom to bride's lineage, whereupon a woman moves from her natal to her husband's homestead and, as a new lineage member, becomes entirely dependent on her husband's resources (Peristiany 1939). A woman's sons inherit land exclusively from their father.

The study area on the borders of Kericho and Narok Districts was settled in the 1930s & 1940s by Kipsigis men and their families escaping the overcrowded "Native

Reserves" established by the British colonial government (Borgerhoff Mulder 1990). The non-traditional practice of land enclosure (through fencing, Manners 1967) that emerged throughout the century was exacerbated by a 1980s World Bank initiative for land registration in the area. Land ownership, together with rapid population growth and inter-ethnic territorial tensions, have to some extent inhibited the traditional pattern of married sons establishing farms adjacent to that of their father, and increasingly all sons settle on their father's land, or on a plot of land purchased by their father. Unsurprisingly many demographic traits are affected by size of a man's land holding, including polygynous marriage (Borgerhoff Mulder 1990), fertility and offspring survival (Borgerhoff Mulder 1987b). Perhaps unsurprisingly there can be intense competition among brothers over inheritances and reproductive opportunities, including bridewealth (Borgerhoff Mulder 1998). As cooperation among kin may be restricted when local competition is intense I predict that the effects of paternal kin on child survival will be stronger in wealthier than poorer households. This hypothesis predicts *wealth interaction* effects, not necessarily a reverse in the sign of the statistical relationship across wealth categories.

2.0 METHODS

2.1 Sample

Analyses are based on 785 births to 129 women and 107 men between 1945 and 1990, collected from retrospective interviews with members of all households in four neighborhoods (*kokwetinik*, sing. *kokwet*) intensively studied in 1982-1983 and 1990-91. Of these livebirths 15% failed to reach their fifth birthday, a percentage that varied over time: 19% of those born prior to 1980 (n=392) and 10% of those born in 1980 or later (n=393). As shown elsewhere, the principle causes of mortality for under fives is disease – malaria, diarrhea, measles and influenza (Borgerhoff Mulder 1987b) – all of which are treated with traditional and modern medicine. Consistent with analyses showing no sex-biased survival (Borgerhoff Mulder 1989) child sex dropped out of all the models.

Kipsigis households, as defined here, consist of a woman, her children and her husband. They are typically located within larger extended residential units of patrilineally related kin, units that include the households of a woman's cowives, of sons and their wives, and of the husband's father and his wives and that retain ultimate rights of ownership to land and livestock. Each woman owns her own hut; after a year or so of marriage she obtains rights of use to land and livestock, and builds her own granary. Reproductive histories were taken for all women in the four neighborhoods who had produced one or more children. Births to individuals deceased at the time of the interview were recorded (10 men [9.3% of sample] and 12 women [9.3% of sample]) women, by means of questions with a living spouse who fell in the sample.

2.2 Variables

Survival status or age at death, was determined for each birth. Of special interest were the survival status and residence of father's mother (FM) and father (FF), and the number of the father's brothers (FB), and the same for maternal kin – mother's mother

(MM), mother's father (MF) and mother's brothers (MB). The number and/or status of kin in these categories was determined from the full demographic sample (Borgerhoff Mulder 1987a, Borgerhoff Mulder 1987b). This was straightforward for paternal kin, given the strong patrilineal residence patterns among the Kipsigis, with men and their brothers very commonly living on the same or adjacent plots of land. Fortuitously systematic data on wives' relatives had been collected as part of a bridewealth study (Borgerhoff Mulder 1995). Additional kin effects considered in the model are the survival status of the focal child's mother and father.

Each of a child's parents and grandparents was coded as dead if this individual had died before or within the focal child's first five years of life. Because year of the specified relative's death could not always be narrowed down to month and year, this approximation seemed more appropriate than restricting analysis to better educated individuals with more precise recall of exact dates. The number of a child's father's brothers (FB) or mother's brothers (MB) was determined on the basis of questions regarding the number of currently living (1982-1983) brothers of the father and mother and their residential histories; it is therefore fixed for a sibset and can be considered only an approximation for any given child; these variables are accordingly treated as categorical variables (FBCAT, MBCAT). For FM, FF, MM and MF it was possible to determine whether this relative lived in the same set of adjacent *kokwetinik* as the child (generally within a 15 km range, an easy day's walk, termed "local"), or at a further distance (generally more than an easy day's walk, termed "distant"); even where relatives lived beyond the adjacent *kokwetinik* that constituted the sample of this study, the distance rarely exceeded 25 kms. In this sample the mode, median and range of ego's father's mother's residence and mother's mother's residence are (0km, 0kms, 0-11kms; 0km, 3kms, 0-128kms). Unless other information was available, it was assumed that residence patterns observed in 1982-1983 and confirmed in 1991 had been constant. Very infrequent land sales and minimal labour migration justify such an assumption.

To study the independent effects of kin factors on focal child survival, and their interactions with wealth, these measures were linked to the full demographic and socioeconomic records. Wealth is measured as land available to the child's mother, because of the significance of this factor in previous analyses of this population (Borgerhoff Mulder 1987b). Used as control variables were data on year of birth (for secular changes in survival), gender, twin status, mother's age at birth of child, previous birth interval, birth order, polygynous status of mother, mother's education, wealth (as defined above), and the number of the focal child's brothers (both full and half). These variables allow for both a finer determination of the effects of kin, and a more nuanced interpretation of the correlational results.

2.3 Analysis

Cox's regression, a form of event history analysis (Allison 1984), was used to determine probability of survival within the first 60 months of life, using STATA (v8.1). This method is appropriate in that it allows for the inclusion of censored cases, in this case children who have survived to various ages but not yet reached their fifth birthday.

Four analytical steps were taken. First, to identify unobserved variability between siblings born to the same mother all independent variables were investigated for shared frailty using the STATA "share" command, and entering the mother's ID as a covariate. Theta values (a single variance parameter that measures heterogeneity in survival times across the children of different mothers) were consistently very small (0.00 – 0.086) and never significant, indicating there is no inter-mother variance in frailty; in other words that all full sib sets have the same unobserved frailty (Gutierrez 2002). This results in part because many of the covariates of interest, such wealth, status of grandparents, number of siblings, etc., vary much less within families than between families. The same analysis with similar outcomes was conducted for shared fathers and shared lineages. Each of these terms was investigated in the full model, and again were observed to be very small, reflecting the fact that multiple independent variables capture much of the variation and leave little residue to be explained as unobserved heterogeneity. Since shared frailty parameters never contributed significantly to any of the models, they were dropped from the presentation of the final analyses.

The second step entailed identifying the effects of a range of control variables, defined as variables expected to affect survival times but not of primary interest in the current analysis. This was done by determining the increased probability of dying in the first five years of life as a function of a change in the specified independent variable. Models were fit using the Cox's proportional hazards model in STATA (see Table 1). Model A drops individuals for whom there is missing data, whereas Model B uses the full sample, dropping variables for which there is not complete information. The results are largely congruent. Interpretation of the proportional hazards ratio is as follows. The estimated hazard ratio of .974 for birth year (in the reduced sample, Model A) indicates that an individual born in any given year has a 2.6% reduced likelihood of dying than does an individual born in the preceding year (that is, the ratio of their respective hazards is .974). This ratio does not differ significantly from one, on the basis of a Wald chi-sq statistic (3.117) although it shows a statistically significant trend. Now consider birth intervals, coded as a categorical variable. Compared to children born after the shortest interval (the reference category underscored in the table) the 23-25 month group have a non significant 37% greater chance of dying, the 26-36 month group a 36% reduced chance of dying, and the longest category an even more (61%) reduced chance of dying. While only the ratio of the first to the last category is significantly different from one, there is an overall significant effect as indicated by the Wald chi-square statistic (11.741). Hazard ratios show that children with a later birth year are less likely to die (Table 1, panel 1), and that twins have higher mortality than single births (panel 3). Mortality declines with the length of the preceding birth interval (panel 5), among children of middle birth order (panel 6, Model A only), among children born to women with no cowives (panel 7, B only), with each year of maternal education (panel 8), with an intermediate number of full and half brothers (panel 9), and as the size of the land holding increases (panel 10). These are well-established and commonly observed effects found previously both in this and many other developing nation populations (Rutstein 1984, Rutstein 2000), and receive no further discussion here except with respect to their interactions with kin variables.

The third step entailed single-variate analyses of kin effects for the full sample of births (Table 2, Model C). The raw survival curves are presented in Figs. 1, 2, 3 & 4. The fourth step examined a series of multivariate models with control and kin variables considered together (Table 3, Model D), split by wealth (Model E) and with wealth interactions (Model F). The third and fourth steps are presented in the results section below.

3.0 RESULTS

3.1 Parental effects

As shown in the 1st panel of Table 2 a child is 77% less likely to die if his or her mother is alive during the first five years of life than if the mother dies during this period; living fathers have no significant effect on survival. This pattern is retained in the full model (Table 3, Model D), and holds in both the richer and the poorer (at marginal significance) halves of the population (Table 3, Model E). There is marginally significant interaction between mother and wealth, indicating that mothers' survival is more strongly associated with child survival in rich than poorer households, an unpredicted trend we return to in the discussion.

3.2 Paternal kin effects

The effects of paternal kin on survival (Fig. 1) are shown in the 2nd panel of Table 2. Single variate analyses (Model C) show children with a living father's mother and children with a living father's father are significantly less likely to die than those without these paternal kin.

The principle paternal grandparental effect lies between those who are deceased, and those who are alive and live either locally or distant. This indicates that for this category of kin the distance at which they live is not a major factor in providing support, conforming to ethnographic observations: paternal kin amass at times of conflict over land, interlineage conflicts, or family crises in current times, as they did in the early years of the 20th century (Peristiany 1939).

Examining paternal kin effects in a full model in which all demographic and economic variables are entered (Table 3, Model D) shows that both a surviving father's mother and the number of father's brothers are retained as significant factors reducing child mortality, though the latter is only marginally statistically significant. In other words paternal kin raise survival chances, independent of the positive effect associated with the number of *mother's* brothers (panel 3, and see below), and of control variables (see Table 3, panel 4), including wealth.

Splitting the sample by wealth shows clear wealth interactions. As expected the positive association between father's brothers (FBCAT) and child survival is stronger in the richer than the poorer section of the population (Fig. 2). Children with a large number of father's brothers show reduced mortality in the wealthier but not the poorer

half of the population. These results hold in the fully controlled model (Table 3, Model E), and there is a significant interaction effect between number of father's brothers and wealth (Model F). The reasons why the father's brothers might enhance survival in wealthy but not in poor households are examined in the discussion. A further wealth interaction indicates that the association between the father's mother and child survival is stronger in the poorer than the richer half of the population, another unexpected result address in the discussion.

3.3 Maternal kin effects

The effects of maternal kin on survival (Fig. 3) are shown in the 3rd panel of Table 2. Single variate analyses (Model C) reveals that the status of the mother's mother has no overall effect on child survival, and that for the mother's father and mother's brothers there is only a marginally significant trend.

These marginally statistically significant effects reflect low mortality (high proportional hazards ratio) in cases where the mother's mother and mother's father are alive but living beyond the neighborhood compared to those who are either deceased or alive and present. This suggests an unusual but ethnographically quite plausible maternal kin effect – a woman benefits if her parents live at some distance from her marital home. This "refuge" effect is explored in the discussion.

Examining the effects of maternal kin in the full analysis (Table 3, Model D) we find that statistically significant effects of neither the mother's mother nor the mother's father are retained in model. There is however a strong independent and positive effect of the number of mother's brothers on child survival. In other words, children whose mothers have three or more brothers experience a significantly reduced mortality risk, independent of whether the mother herself is alive (panel 1), of the effects of the father's mother and brothers (discussed above, panel 2), and other control variables (panel 4).

Splitting the sample by wealth shows that the apparently beneficial effects of the mother's brothers are in fact most marked in the poorer half of the population (Fig. 4). Statistically this is preserved in the full model (Table 3, Model E) where the number of mother's brothers is marginally significantly associated with child survival only in poorer households, yielding a marginally significant interaction between mother's brothers and wealth (Table 3, Model F). Adding to the model a further interaction term that identified whether the mother's brothers lived locally or not (as gauged by the location of the mother's parents) shows that the number of mother's brothers is associated with higher survival in poor households *when these brothers live at a distance* (Wald 9.17, df=3, $p<0.05$).

3.4. Control variables and the role of competition among kin

Analyses showing that nepotism towards grandchildren, nephews and nieces within patrilineages varies by wealth provides only *indirect* evidence that kin are motivated to help their relatives as a function of potential competition over resources

within the patrilineage. The most convincing evidence for this interpretation comes, unsurprisingly, from ethnographic observations (see Introduction and Discussion). Further indication of competition contributing to offspring survival in resource-stressed situations is found in the patterning of the effects of the control variables in these analyses. First, consistent with previous analyses, the number of a child's mother's cowives is negatively associated with child survival (Borgerhoff Mulder 1990, 1997), an effect that is observed in poorer but not richer households (although the interaction term is not significant). Second, again consistent with previous analyses (Borgerhoff Mulder 1998, Table B1, here just focus on *male* siblings – the most likely competitors), survival chances are negatively associated with the number of a child's full or half brothers. As with the analysis of mother's cowives, this effect is stronger in poorer than richer households (Model F).

Examining control variables in this way provides statistical support for the claim that competition within poorer patrilineages is modulated by wealth availability. On the other hand, it is important to stress that these imputed patterns of competition are not entirely accounted for by wealth since both the main effects and the wealth interaction terms are independent of the wealth covariate (ACRES). Furthermore an anticipated interaction between birthdate, wealth and child survival (reflecting increased competition over time with escalating land shortages) was not found, probably because in recent years child mortality has declined substantially and wealth nowadays shows higher correlations with fertility than with offspring survival (Borgerhoff Mulder 1987b).

The motivations for maternal kin to assist with the raising of grandchildren, nephews and nieces are more difficult to evaluate since we know less about their circumstances; this is because many of them reside outside of the study area. The present analyses do however indicate that these lineages help out their daughters when their daughters find themselves married to men with limited resources.

4.0 DISCUSSION

In this study demographic correlations between the existence and residence patterns of kin and the survival of children prior to their fifth birthday are presented to examine how kin cooperation affects reproduction in human societies. The principle finding is that paternal kin play a larger role in affecting child survival than maternal kin, no doubt reflecting patrilineal social institutions in the Kipsigis. As predicted by the local resource competition model, there is a significant interaction between wealth and number of father's brothers, suggesting that the apparently protective role of paternal uncles is stronger in richer than poorer lineages. An unanticipated finding is the apparent buffering effect of maternal kin in situations where paternal kin control limited resources.

The mechanisms whereby kin do, or do not, improve child survival are not identified in this study, but are likely to entail provision of food, labor and cash at critical family crises – food shortages, crop loss, cattle disease, political disputes, and acute illness. As mentioned in the Introduction, public health scholars are increasingly impressed with the importance of kin networks in promoting positive heath outcomes

(Cohen, Underwood, and Gottlieb 2000). My ethnographic observations with Kipsigis provide abundant evidence of the role kin often play in supporting one another in childrearing, whether this involves taking a child to a traditional or western health practitioner, providing money for care, slaughtering livestock in times of drought or temporary food shortage, helping with the tasks of firewood and water collection, assisting with agricultural work or providing direct childcare (Borgerhoff Mulder and Milton 1985). More diffusely, and as noted by Peristiany and myself, patrilineal kin amass at times of crisis, and provide critical assistance with events surrounding circumcision, weddings and blood payment negotiations (1939:98). Although neigborboods (*kokwetinwek*) have strong cooperative institutions for coordinating daily tasks (Peristiany 1939), relatives are usually the most reliable partners even within a neighborbood.

Though much of what we know about cooperative breeding in humans is based on correlational data (as reviewed in Sear and Mace 2006) we should caution that correlation is not causation. Since relatives share not only genes but many environmental factors, underlying heterogeneities between families may account for some of these correlations. To some extent this problem is mitigated here by the examination of the shared frailty parameters which, perhaps unsurprisingly, proved to be non significant given the number of independent variables available in this study. Furthermore if phenotypic correlations were important we would expect positive associations between child survival and all categories of equally related relatives, but this is not the case. A further problem with analyses of the type reported in this paper is that contingencies are not explored. In other words, no attempt is made to determine how the loss of one relative, for example a mother, might render other relatives more, or less, important in terms of affecting child survival; this could be the subject of further analysis and would undoubtedly add texture to our understanding of the facultative aspects of kinship behavior.

4.1 Evidence for local resource competition

Why do paternal kin, and specifically father's brothers, enhance survival in wealthy households but not in poor households? A man and his brothers and half brothers are direct competitors over their father's land and livestock. Kipsigis custom dictates an equal division of resources among sons, a practice that worked well in a traditional system in which livestock was the principle wealth source. During the colonial period the ownership of cultivable land became important. Unlike cattle, land is an inelastic resource, and plot sizes are shrinking across generations as population grows. Violent cases of strife over land among brothers, among brothers' wives, and among the co-wives married to polygynously married men were observed during fieldwork; cases including a man burning down the house of his brother, with wife and children inside, a woman attempting to poison the children of her husband's elder brother, attempts to "move" fences (effectively brush piles) over night prior to the formal delineation of fields, witchcraft accusations and local court cases. Equally notable were instances of supreme altruism and fraternal cooperation (such as shouldering the costs of a brother's children's medical expenses, or providing secondary school fees for a nephew or niece). The unexpected observation that living paternal grandmothers affect child survival in poor but

not rich households suggests that these grannies can perhaps buffer young children from mortality in patrilineages wrought with resource conflict.

The finding that kin cooperate more in richer than poorer patrilineages likely results from two specific features of Kipsigis society and ecology. First patrilineally related kin tend to be equivalent in wealth status, reflecting the traditional egalitarian inheritance system and limited access to off-farm employment in this population. Second, the relationship between resource availability and fitness shows diminishing marginal benefits as wealth increases (Borgerhoff Mulder 1987a). Under such circumstances a poor man might find that the inclusive fitness benefit (B) of making a resource transfer to a sick nephew or niece is eclipsed by the direct fitness cost (C) of the lost resource; conversely, for a rich man the marginal benefit of transferring resources to save the life of an ailing nephew or niece could outweigh the small direct fitness cost. *If* this is the logic underlying these empirical patterns, nepotism would indeed be more likely to trump direct fitness costs in richer rather than poorer lineages. This framework helps to explain why in a study of the Tanzanian Pimbwe Hadley (2004) found exactly the opposite pattern to the one reported here. The presence of mother's sisters in the village was positively associated with child weight-for-age scores only in families of low socioeconomic status, a more intuitively understood and possibly widespread pattern (e.g., Stack 1997, for African Americans). Why is the Pimbwe pattern so different from the Kipsigis? With little to no inherited possessions poorer families have few material assets to compete over, and much to gain from cooperation. In fact because close relatives can vary enormously in wealth, it is the rich individuals who report being pestered by their poorer relatives into providing a costly resource stream (Hadley 2004).

An alternative but unlikely explanation for the Kipsigis results is that it is not the B and C terms in Hamilton's equation that vary with wealth but rather r. Thus relatedness among agnatic kin might be higher in richer than poorer households, reflecting greater mate guarding potential on the part of husbands, or lower temptations to infidelity on the part of women. However extramarital affairs are heavily sanctioned in this population and lead to acute punitive outcomes for women which (anecdotally at least) appear unrelated to wealth. In so far as richer people tend to be more educated and cosmopolitan, one might expect (if anything) richer households to show lower r, although this is pure supposition.

These results can be placed in the broader framework of family conflict (Emlen 1995). Hill and Hurtado (1996), after failing to show effects on survival associated with individual relatives, turn to the use of the ratio of related helpers to potential recipients in the Ache to indicate kin assistance in the context of competing demands on their time. In Dominica Quinlan (2005) shows how the number of brothers in a community negatively affects reproductive success, a pattern elsewhere linked to competition over inheritance and marriage payments (East Africa, Mace 1996) and land inheritance (agrarian Sweden, Low 1994). Furthermore in many parts of the world strong negative effects of the number (Knodel, Havanon, and Sittitrai 1990) and sex (Parish and Willis 1994) of siblings are seen on health and educational outcomes (Garg and Morduch 1998, Downey, 2001) as parents strategize within offspring sets. Specific links can be drawn between parental

strategies and resource shortages in a historical German peasant population, where differential investment in sons and daughters is shown to vary in relation to habitat saturation (Voland and Dunbar 1995). The demographic evidence presented here on the Kipsigis, a population with a strong ethos of equal inheritance to sons and an almost exclusive reliance on inherited resources of land and livestock, demonstrates how the balance between apparent kin assistance and kin competition pivots on the availability of resources. On these grounds we might also expect that as rural populations become integrated into a cash economy (with wealth ultimately held individually in bank accounts) the importance of kin networks for resource transfers will decline, as is occurring in India (Shenk 2005); kin networks may nevertheless continue to play an important political role (Munshi and Rosenzweig 2005).

The implication of these results is that for humans, as with other species (Griffin, West, and Buckling 2004, West et al. 2001), patterns of dispersal and resource distributions are key to the development of more precise predictions regarding altruism. This might explain why in many domains of human behavior altruism is only loosely explained by relatedness; for example only one third of the variability in cash remittances in South Africa is attributable to a model of kin selection that includes reproductive value (Bowles and Posel 2005). Furthermore, local competition among kin over resources may explain why in some situations kin of equal relatedness but different categories, such as those related through maternal or paternal ties, may evince very different patterns of nepotism (Alvard 2003, Quinlan 2005).

4.2 The role of other kin in contributing to child welfare

We now turn to the effects (and lack thereof) of parents, of the maternal grandmother, and of other maternally related kin on child survival among the Kipsigis, and implications for understanding the role of kin as caretakers in human societies.

First, consider parents. Loss of a mother but not of a father is a strong determinant of offspring survival in the Kipsigis, as would indeed have been expected. Mother loss is an important influence on mortality in the first years of life in many populations (recently reviewed in Sear and Mace 2006). While mother loss does not precipitate infanticide in the Kipsigis (unlike in some populations, e.g., the Paraguayan Ache, Hill and Hurtado 1996), breastfeeding children are inevitably weaned rapidly, triggering potentially serious health complications that threaten survival, and weaned children move to the house of the deceased mothers cowife or sister-in-law where they are in direct competition with other children. Father loss, in contrast, has no evident survival costs. High mortality risks among children with a deceased father are most commonly attributed to the mother's new marriage, specifically the step parent (Daly and Wilson 1985, Voland 1988); indeed the stress of divorce may be more detrimental than death of father *per se* (Sear et al. 2002). In the Kipsigis remarriage does not occur. Widowed mothers are subject to "widow inheritance", a practice whereby the woman is effectively passed on to one of her brothers-in-law; the fact that widowed women do not remarry but cohabit with their late husband's brother likely contributes to the finding that widowed Kipsigis women do not experience higher child mortality than non-widowed women. Finally, the anomalous and

unanticipated finding that maternal loss is more prejudicial to child survival among the wealthy than the poor most likely reflects the fact that in this small sample children in the wealthy sector were somewhat older at their mother's death.

Second we examine the absence of a maternal grandmother effect. Generally maternal grannies are thought to be natural caretakers of their daughters' as opposed to their sons' children because of the greater certainty of relatedness, and across many studies their presence is found to be associated with positive survival outcomes (Sear and Mace 2006). In the Kipsigis, however, it is the paternal grandmother whose presence has a beneficial effect on the survival of small children, no doubt reflecting the strongly patrilineal organization of Kipsigis (see too Leonetti et al. 2005, Lycett, Dunbar, and Voland 2000, Gibson and Mace 2005). This suggests a facultative component to not only paternal grandparental behavior (as often surmised) but also, more surprisingly, to maternal grandparental roles.

We turn now to other maternal kin. In the Kipsigis the status of maternal kin, specifically maternal brothers, is associated with child survival only in the poorer half of the population. This suggests that maternal relatives provide help primarily in situations where limited nepotism from a child's father's lineage can be expected. This is the case despite the fact that there is very little cultural emphasis on matrilineal relatives in this population. These results speak to the obvious but often ignored fact that inheritance rules do not dictate behavior (Dickemann 1982), and also to the more specific point that patrilineal inheritance rules do not preclude an important role for maternal kin under certain circumstances, a phenomenon much appreciated by earlier ethnographers of African kinship (Radcliffe-Brown and Forde 1950), and indeed by Peristiany who singled out a mother's true brother as a person "of astounding importance" (1939:100) for the Kipsigis. The data presented here do indeed suggest that maternal kin can play a key role in situations where they observe a patrilineage unable or unwilling to provide adequate care to their grandchildren. A similar effect is found among the patrilineal Ethiopian Oromo, where maternal grannies work hard in their daughters' households; accordingly living maternal grannies tend to have taller granddaughters, although they have no significant effects on the survival of their daughters' children (Gibson and Mace, 2005).

Interestingly, the role of maternal kin as indirect providers of child welfare is only in evidence when they live at a distance (over a day's walk) from the mother's marital household. This is opposite to the Ethiopian pattern where child survival is enhanced by the presence of unspecified maternal kin in the village (Gibson & Mace 2005). An effect superficially similar to the Kipsigis is found for non-coresiding maternal grandmothers among the Northern Indian Khasi (Leonetti et al. 2005), but is attributed to self selection, specifically the decisions of grannies to live with otherwise disadvantaged daughters. The explanation in the Kipsigis is rather different (since women change residence at marriage not in grandmotherhood), and suggests a "refuge" hypothesis. In a cultural group where divorce is practically non-existent (Orchardson 1961, Peristiany 1939) women are typically unhappy during at least some period of their marital life. In such circumstances, and particularly when violence ensues, women run away (or at least take their children away) to the home of their parents, where their brothers also usually live. Several such

instances were observed during fieldwork. When the natal homestead is near to the marital homestead the husband and his kin arrive in person to demand the wife and her children back. When the natal homestead is at a distance such delegations demanding the wife's return, to the extent that they occur, are generally less successful. This is primarily because a patrilineage typically lacks political allies beyond the area where it is localized. I therefore view this effect as evidence of the wife finding safe haven, for herself and her children, with her natal family. To what extent absent kin play this role in other populations is not known.

5.0 IMPLICATIONS

How has this analysis of the implications of local resource competition for constraining the role of relatives as cooperators or competitors advanced our understanding of the evolution of the human family? Evolutionary anthropologists already know that across different societies distinct categories of kin assist mothers in the arduous tasks of childrearing. Indeed in many respects the greater role of paternal than maternal kin in the patrilineally organized Kipsigis was to be expected. Evolutionary anthropologists have speculated that this variation reflects a facultative response to different ecological and social conditions (e.g., Hames and Draper 2004) and to the distinct objectives of different sets of relatives (Sear, Mace, and McGreggor 2003). There has however been no application of general theory in regard to this variation.

To promote a more general model for which kin help and why, this study explored the role of resource competition in shaping kin effects, albeit presenting only correlational evidence. The principle finding is that the roles of maternal and paternal kin are conditioned by the wealth of the household into which the child is born. Clearly there are many factors likely to promote, or curtail, a facultative role for kin in promoting (or inhibiting) child survival. These include the availability of kin, the sensitivity of child survival to assistance from outside the nuclear family, and the potential for competition among kin, all of which are at least indirectly assayed in this study (through kin survival and residence patterns, wealth, and a count of competing siblings). Another important factor might be transaction costs, here and elsewhere modeled through residential propinquity, (although in this study it turned out that distance does not impede imputed patterns of patrilineal assistance and might actually enhance maternal kin contributions). Yet other factors that should be considered include competing demands on helpful kin, something that is difficult to measure without a very different sampling strategy.

While there are doubtless many factors promoting or inhibiting kin assistance, the importance of local resource competition (and enhancement) is analytically tractable and has potential generality, especially in systems where resources are inherited across generations. While this study has restricted focus to the significance of local resource competition for constraining the role of relatives as cooperators or competitors within a single population, the findings suggest that the variation in kin roles across societies will be strongly influenced by the elasticity of the resource base, the pattern of inheritance, and the divisibility of the inherited resources. We now need to shift scholarly attention that has focused primarily on the factors responsible for the cohesiveness of kin groups

(Hughes 1986, Jones 2000) to the source of their fragmentation, to situations in which relatives transmute from friend to potential foe.

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TABLE 1. NON-KIN VARIABLES AND CHILD SURVIVAL – MULTIVARIATE ANALYSES

	Model A (a)			Model B (b)		
Variable	N	Proportional hazards ratio and Z score significance level (c)	Chi-Square Wald and significance level	N	Proportional hazards ratio and Z score significance level	Chi-Square Wald and significance level
1. Birth year (d)	582	.974	3.117 (t)	785	.957	15.975***
2. Sex (e)			.002			0.492
Male	300			404		
Female	282	1.012		381	.882	
3. Twins			7.419**			31.987***
Single	568			756		
Twin	14	3.793**		29	6.304***	
4. Mother's age at birth (f)			0.571			1.341
12-20 years	105			253		
21-27 years	249	.795		286	.696	
28-47 years	228	.975		246	.715	
5. Previous IBI (g)			11.741**			
10-22 months	147					
23-25 months	147	1.373				
26-36 months	164	.640				
37 – 150 months	124	.389 *				
6. Birth order (h)			6.050 (t)			3.382
1-2	99			255		
3	94	.696		111	.989	
4-6	228	.363**		248	.649 (t)	
7-14	161	.601		171	1.152	
7. Polygyny (f)			3.211			10.120**
Cowives 0	254			391		
Cowives 1	264	1.555(t)		317	1.841**	
Cowives >1	64	1.804		77	2.376**	
8. Education (g)						
Years of education (d)	582	.930	3.463(t)			
9. Number of full and half sib brothers			7.213*			11.028**
0-3	112			140		
4-8	338	.557*		411	.600(t)	
9-15	132	1.130		234	1.330	
10. Acres (d)	568	.978	6.183**	785	.974	11.606***
Full model Chi Square Likelihood statistics	60.371, df = 17, p<0.001			78.715, df = 13, p < 0.001		

(a) Reduced sample: individuals dropped with missing data
(b) Full sample: variables dropped with missing data
(c) *** p<0.001, ** p<0.01, * p<0.05, (t) p<0.10, and in all upcoming tables
(d) Covariate
(e) Reference category underlined, in all upcoming tables
(f) Calculated at time of birth of child
(g) Data on previous IBI missing for 146 observations, and on education for 87 observations. These two variables are dropped from Model B, leaving an N of 582 (there is an overlap in cases with missing values)
(h) Birth order categorized this way to maximize capture of inverted U shape survival by parity

TABLE 2. KIN VARIABLES AND CHILD SURVIVAL – SINGLE VARIATE ANALYSES

		Model C	
	N	Proportional hazards ratio & Z score significance level	Chi-Square Wald and significance level
1. Parental survival			
Father (dead)	19		0.09
Father (alive)	766	1.235	
Mother (dead)	23		19.85 ***
Mother (alive)	762	.228 ***	
2. Paternal Kin			
FM (deceased)	117		29.73 ***
FM (distant)	214	.294 ***	
FM (local)	454	.354 ***	
FF (deceased)	193		6.98 *
FF (distant)	219	.581 *	
FF (local)	373	.600 *	
FBCAT (0-1)	215		3.95
FBCAT (2)	177	.892	
FBCAT (3)	202	.604 (t)	
FBCAT (4-6)	191	.745	
3. Maternal kin			
MM (deceased)	84		3.93
MM (distant)	381	.582 (t)	
MM (local)	320	.740	
MF (deceased)	147		4.77 (t)
MF (distant)	342	.672	
MF (local)	296	1.054	
MBCAT (0-1)	112		6.23 (t)
MBCAT (2)	320	.732	
MBCAT (3)	292	.550 *	
MBCAT (4-7)	61	.448 (t)	

TABLE 3 KN VARIABLES, CONTROL VARIABLES AND CHILD SURVIVAL (MODEL D), WITH DATA SPLIT BY WEALTH (MODEL E), AND WITH WEALTH INTERACTION TERMS (MODEL F)

		Model D		**Model E**				**Model F** (a)
				Poor		Rich		
	N	Prop. Hazards Ratio and Z Sig. level	Chi Sq Wald and Sig. level	Prop. Hazards Ratio and Z Sig. level	Chi Sq Wald and Sig. level	Prop. Hazards Ratio and Z Sig. level	Chi Sq Wald and Sig. level	Chi Sq Wald and Sig. level
1. Parental survival								
Father (dead)	19		1.49		1.39		.01	2.40
Father (alive)	766	2.350		2.660		4.269		
Mother (dead)	23		20.72***		2.73 (t)		18.07***	3.51 (t)
Mother (alive)	762	.164***		.357(t)		.053***		
2. Paternal Kin								
FM (deceased)	117		19.50***		10.58**		2.74	6.40 *
FM (distant)	214	.294***		.173***		.537		
FM (local)	454	.337***		.481(t)		.227		
FF (deceased)	193		3.26		1.12		2.04	.358
FF (distant)	219	.574(t)		.589		.455		
FF (local)	373	.713		.629		1.304		
FBCAT (0-1)	215		7.35(t)		3.29		10.11**	15.25 **
FBCAT (2)	177	.721		1.620		.186*		
FBCAT (3)	202	.502*		1.683		.079**		
FBCAT (4-6)	191	.494*		.747		.162**		
3. Maternal kin								
MM (deceased)	84		3.59		0.30		3.65	1.39
MM (distant)	381	.727		.781		.503		
MM (local)	320	.478(t)		.720		.189 (t)		
MF (deceased)	147		3.35		3.27		0.25	2.05
MF (distant)	342	.873		.664		.698		
MF (local)	296	1.544		1.485		.963		
MBCAT (0-1)	112		10.82*		7.14 (t)		4.75	6.77 (t)
MBCAT (2)	320	1.790		1.314		2.189 (t)		
MBCAT (3)	292	.838		.561		1.321		
MBCAT (4-7)	61	.588		.214		.602		
4. Control variables								
Co-wives 0	391		10.18**		4.58 (t)		2.25	1.21
Cowives 1	317	2.012**		1.843(t)		2.007		
Cowives >1	77	2.359**		2.332		1.481		
Birth year	785	.940***	26.35	.948	7.56**	.922**	9.87 **	3.56 (t)
Single	756		27.00***		9.97**		18.70 ***	2.46
Twin	29	5.802***		6.760**		9.314***		
Acres	785	.968***	11.36***	.925	2.31	.954	3.16 (t)	NA
Full or half brothers 0-3	140		4.34 (t)		5.65 (t)		.86	4.46 (t)
Full of half brothers 4-8	411	.998		1.393		1.164		
Full or half brothers 9-15	234	1.813		3.318		2.078		
Full model Log Likelihood Chi-square	785	138.001, df=23, p<0.001		78.34, df=23, P<0.001		107.27, df=23, p<0.001		

(a) Model F is not strictly a single model. It results from a rerunning of Model D twelve times, each time with a wealth interaction terms added for the specified variable.

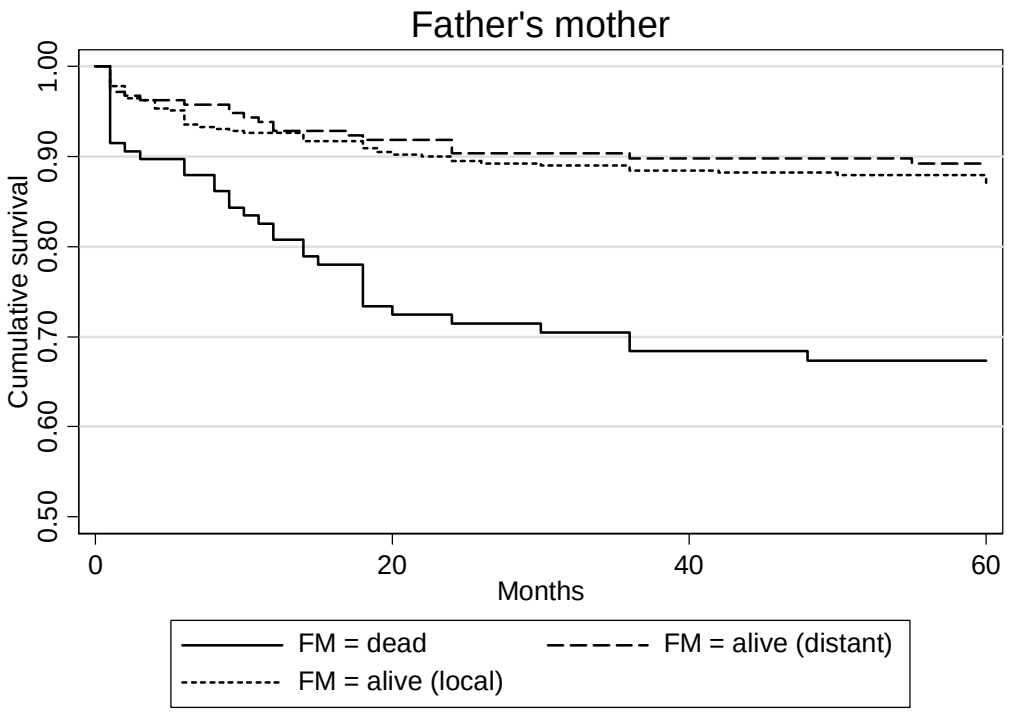
Figure 1.
The effects of a) father's mother, b) father's father, and c) the number of father's brothers on child survival (<60 months). For statistical tests see Table 2 (single variate analyses) and Table 3 (multivariate model).

Figure 2.
The effects of the number of father's brothers on child survival (<60 months) splitting the population into a poorer and richer half. Compared to the baseline (FBCAT 0 to 1) the proportional hazards ratio for 2, 3 and 4-6 father's brothers are .996, 1.161 and 1.973 (Wald chi-square: 6.173) for the poorer households, and .861, .232 and .124 (Wald chi-square: 18.603, $p<0.001$) for richer households, yielding a significant interaction (Wald chi-square: 20.823, $p<0.001$). For the multivariate model statistics, see Table 3.

Figure 3.
The effects of a) mother's mother, b) mother's father, and c) the number of mother's brothers on child survival (<60 months). For statistical tests see Table 2 (single variate analyses) and Table 3 (multivariate model).

Figure 4.
The effects of the number of mother's brothers on child survival (<60 months) splitting the population into a poorer and richer half. Compared to the baseline (MBCAT 0 to 1) the proportional hazards ratio for 2, 3 and 4-7 mother's brothers are .730, .409, and .197 (Wald chi-square: 9.539, $p<0.05$) for the poorer households, and 1.264, 1.425, and 1.837 (Wald chi-square: 0.777, ns) for the richer households, yielding a significant interaction effect (Wald chi-square: 6.681, $0.05<p<0.10$). For the multivariate model statistics, see Table 3.

Figure 1


Father's mother
Cumulative survival
1.00
0.90
0.80
0.70
0.60
0.50
0
20
40
60
Months
FM = dead
FM = alive (distant)
FM = alive (local)

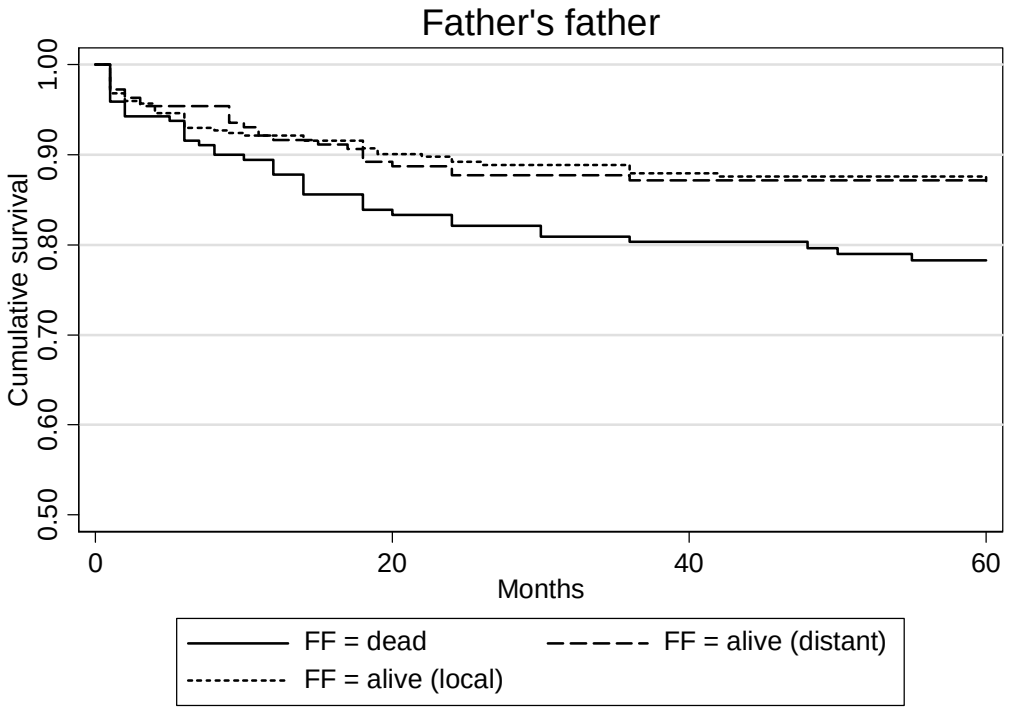

Father's father
Cumulative survival
1.00
0.90
0.80
0.70
0.60
0.50
0
20
40
60
Months
FF = dead
FF = alive (distant)
FF = alive (local)

Figure 1 continued

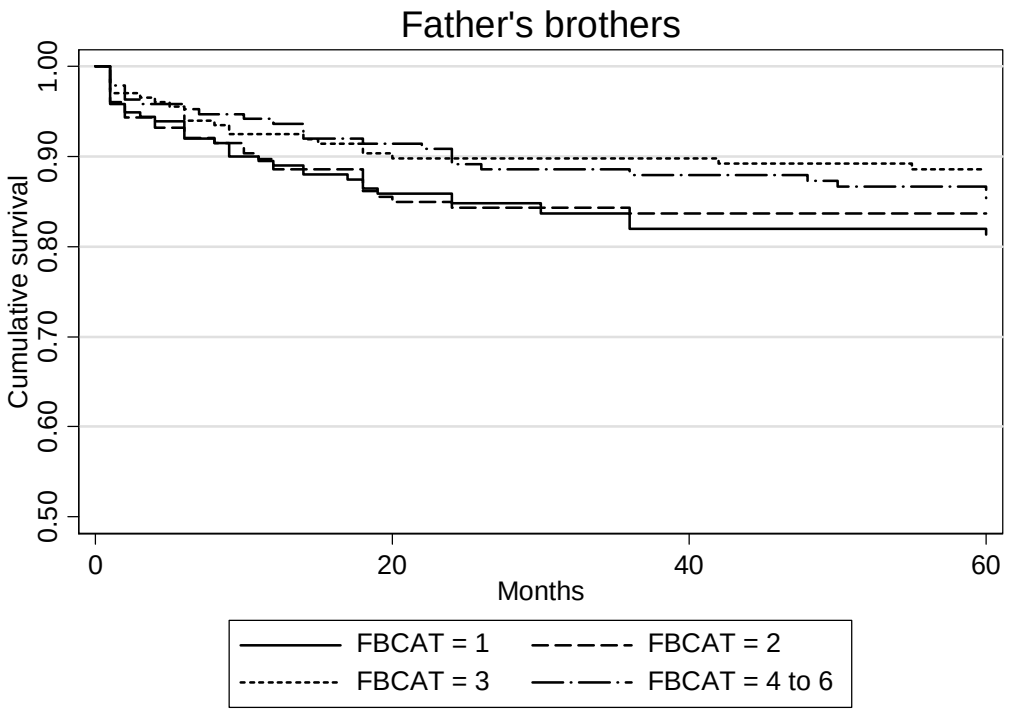
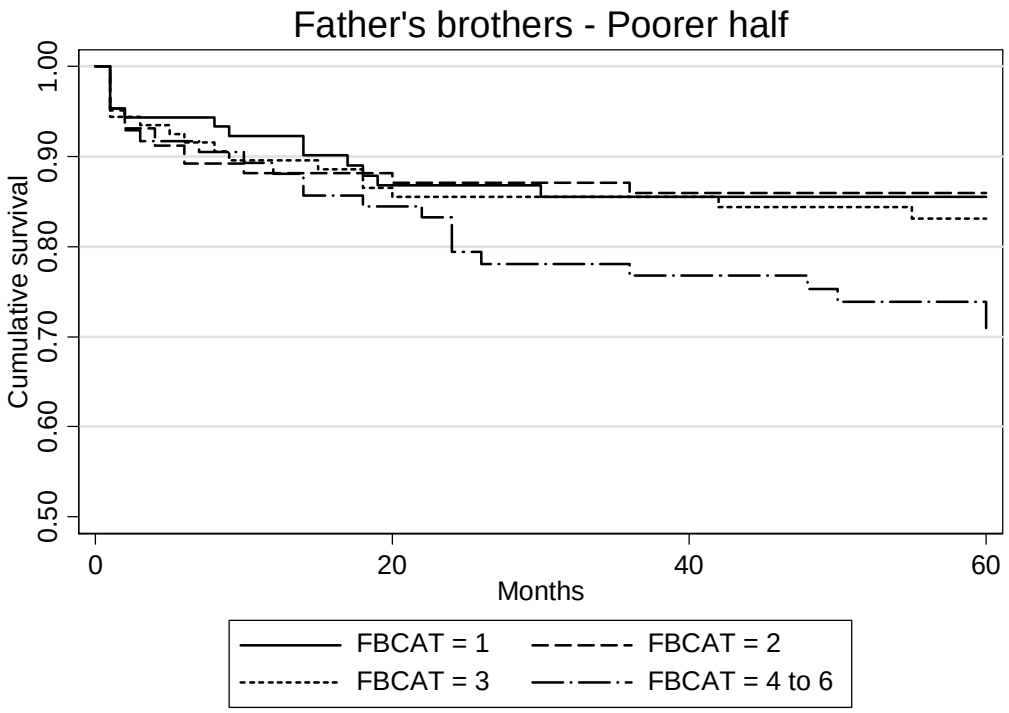


Figure 2


Father's brothers - Poorer half
Cumulative survival
1.00
0.90
0.80
0.70
0.60
0.50
0
20
40
60
Months
FBCAT = 1
FBCAT = 2
FBCAT = 3
FBCAT = 4 to 6

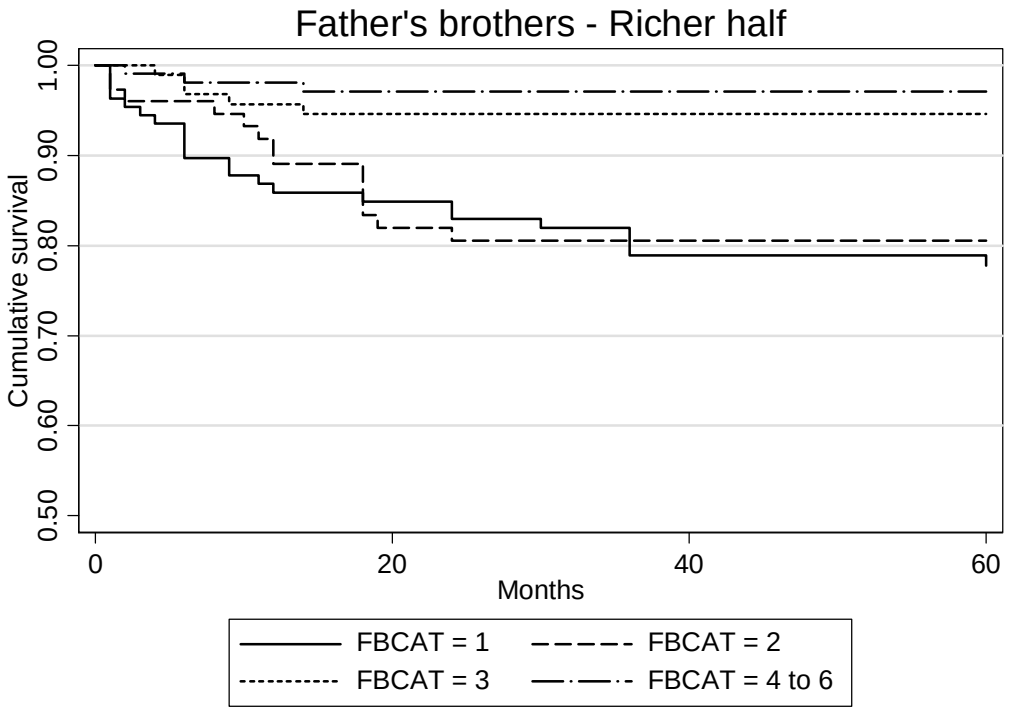
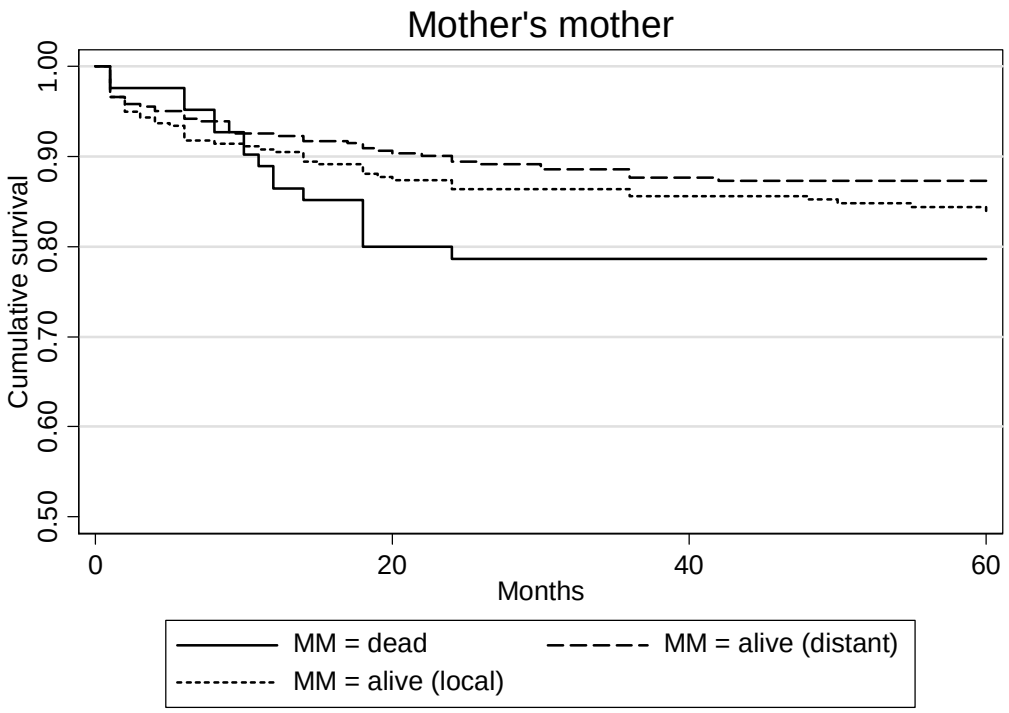

Father's brothers - Richer half
Cumulative survival
1.00
0.90
0.80
0.70
0.60
0.50
0
20
40
60
Months
FBCAT = 1
FBCAT = 2
FBCAT = 3
FBCAT = 4 to 6

Figure 3


Mother's mother
Cumulative survival
1.00
0.90
0.80
0.70
0.60
0.50
0
20
40
60
Months
MM = dead
MM = alive (distant)
MM = alive (local)

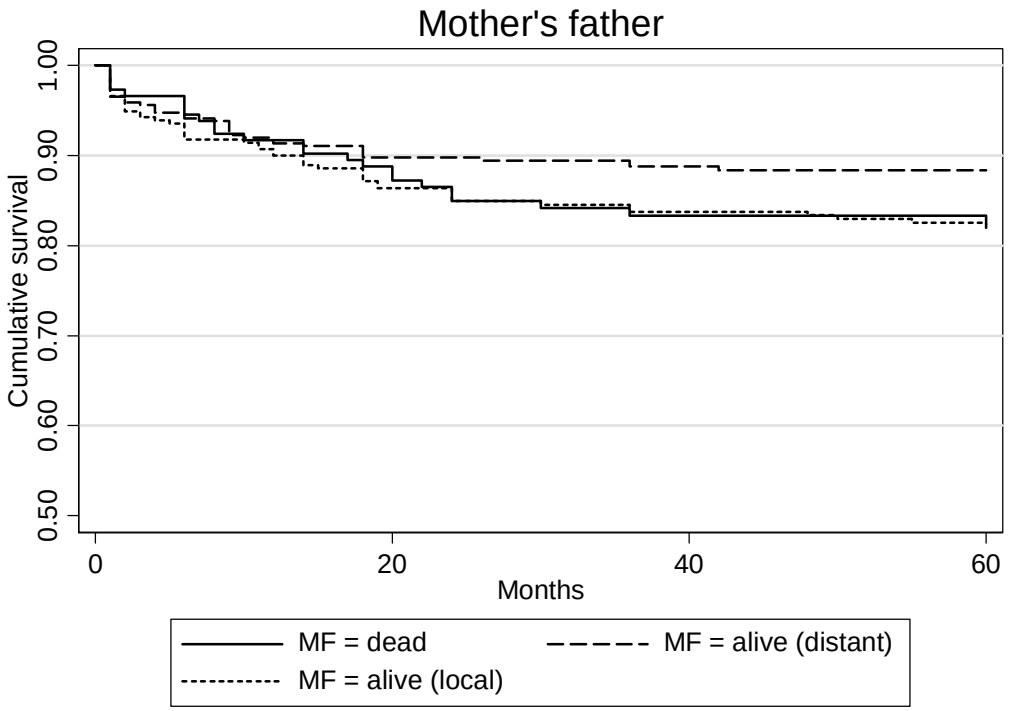

Mother's father
Cumulative survival
1.00
0.90
0.80
0.70
0.60
0.50
0
20
40
60
Months
MF = dead
MF = alive (distant)
MF = alive (local)

Figure 3 Continued

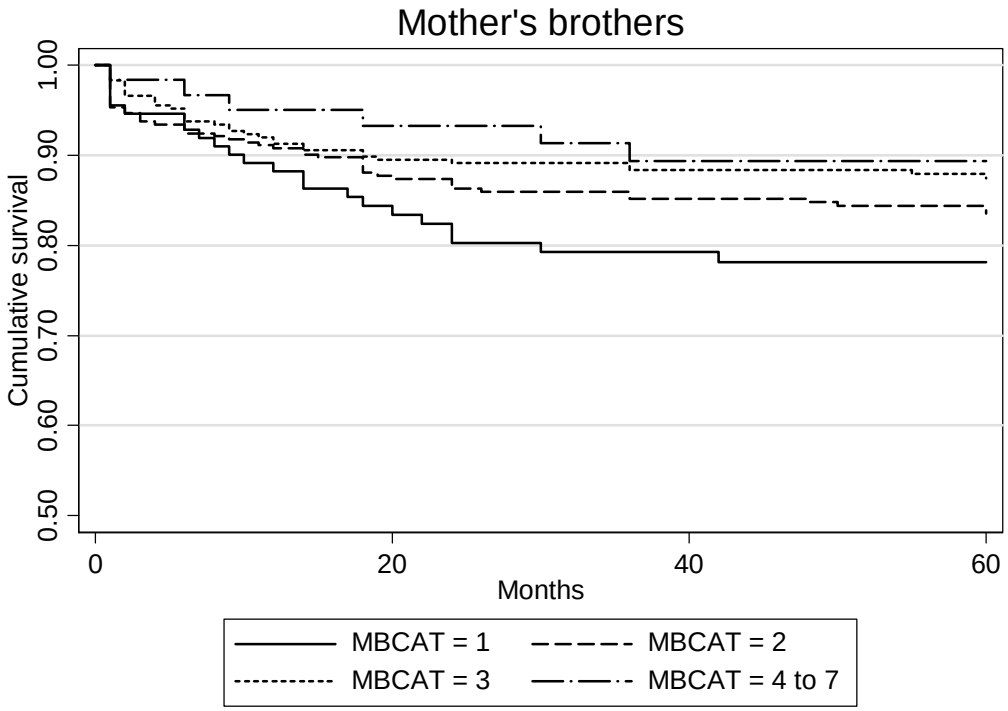
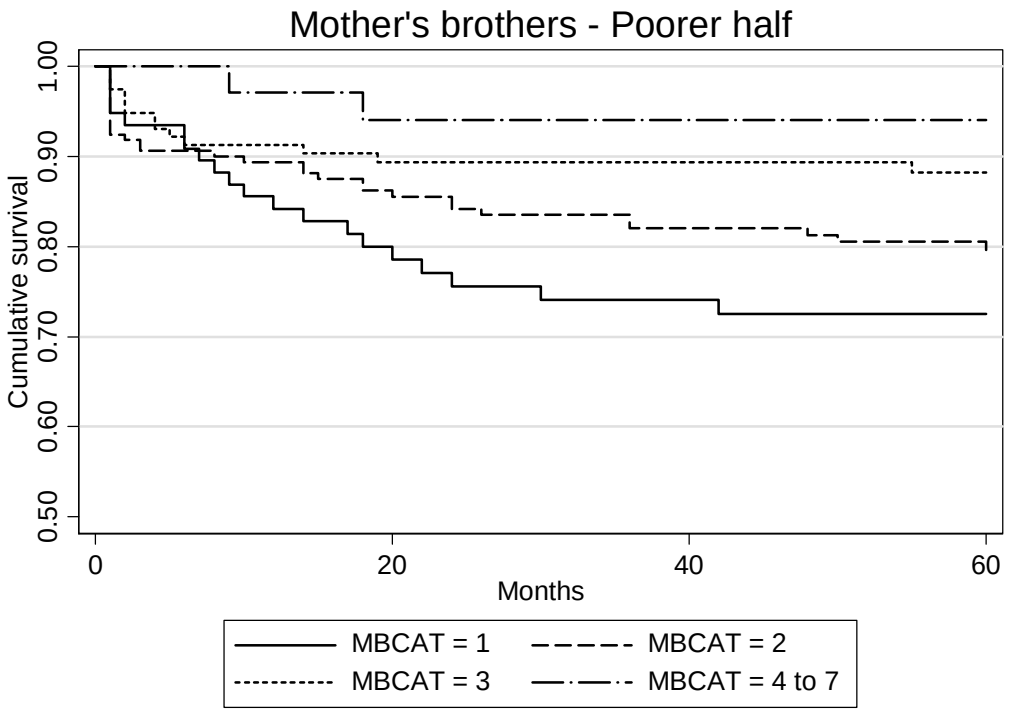
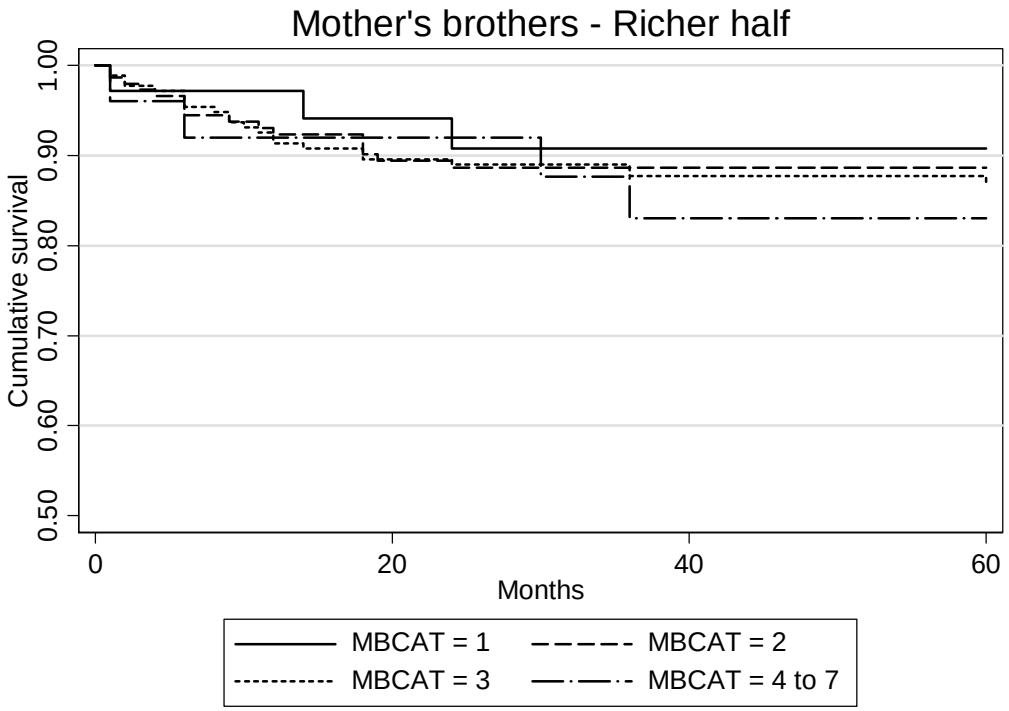


Figure 4


Mother's brothers - Poorer half
Cumulative survival
1.00
0.90
0.80
0.70
0.60
0.50
0
20
40
60
Months
MBCAT = 1
MBCAT = 2
MBCAT = 3
MBCAT = 4 to 7


Mother's brothers - Richer half
Cumulative survival
1.00
0.90
0.80
0.70
0.60
0.50
0
20
40
60
Months
MBCAT = 1
MBCAT = 2
MBCAT = 3
MBCAT = 4 to 7