

Hamilton's rule and kin competition: the Kipsigis case[☆]

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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 nondispersing 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 in poor households. This interaction effect is interpreted as evidence that the extent of nepotism among humans depends critically on 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.

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1. 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 & Wilson, 1988), food sharing (Gurven, Allen-Arave, Hill, & Hurtado, 2001), residence decisions, and violence (Chagnon, 1979) show that individuals favor close relatives over distant ones (or nonrelatives) 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 nondispersing relatives, reducing or negating the effects of relatedness on promoting altruism (Boyd, 1982, Frank, 1998, Hamilton, 1967). While research on nonhumans demonstrates that the extent of nepotism among kin can depend

critically on resources available to parents or sibships in insects (Griffin, West, & Buckling 2004; West, Murray, Machado, Griffin, & Herre, 2001), our understanding of the sensitivity of human kinship relations to resource competition derives largely from folklore (Cinderella'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 coresident 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

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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 & Draper, 2004; Hrdy, 2005; Leonetti, Nath, Heman, & Neill, 2005; Sear & Mace, 2006), 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 that are 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 other’s 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 (1939), I found that he, too, saw the same things: “(T)he economic obligations between paternal relations are only enforced during moments of exceptional need” (p. 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” (pp. 98 and 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 & 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 live births), the developing world exhibits a 29-fold higher rate (175 per 1000 for sub-Saharan Africa; Black, Morris, & 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 & 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, & 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 health outcomes through buffering households against risk of food shortages (Cohen, Underwood, & 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 is the benefit of receiving the altruistic behavior, and c is 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 & Bugos, 1979) and, in some cases, found quite close fits between predicted patterns of altruism and empirical data (Bowles & 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 nonhumans, competition between relatives over resources has been convincingly shown to reduce selection for cooperation among relatives (Griffin et al., 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). 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 & 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 & Judge, 1993) and that

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