

No evidence that polygynous marriage is a harmful cultural practice in northern Tanzania

David W. Lawson^{a,1}, Susan James^b, Esther Ngadaya^c, Bernard Ngowi^c, Sayoki G. M. Mfinanga^c, and Monique Borgerhoff Mulder^{b,d}

^aDepartment of Population Health, London School of Hygiene and Tropical Medicine, London, WC1E 7HT, United Kingdom; ^bSavannas Forever Tanzania, Arusha, Tanzania; ^cNational Institute for Medical Research, Muhimbili Medical Research Centre, Dar es Salaam, 11101, Tanzania; and ^dDepartment of Anthropology, University of California, Davis, CA 95616

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Polygyny is cross-culturally common and a topic of considerable academic and policy interest, often deemed a harmful cultural practice serving the interests of men contrary to those of women and children. Supporting this view, large-scale studies of national African demographic surveys consistently demonstrate that poor child health outcomes are concentrated in polygynous households. Negative population-level associations between polygyny and well-being have also been reported, consistent with the hypothesis that modern transitions to socially imposed monogamy are driven by cultural group selection. We challenge the consensus view that polygyny is harmful, drawing on multilevel data from 56 ethnically diverse Tanzanian villages. We first demonstrate the vulnerability of aggregated data to confounding between ecological and individual determinants of health; while across villages polygyny is associated with poor child health and low food security, such relationships are absent or reversed within villages, particularly when children and fathers are coresident. We then provide data indicating that the costs of sharing a husband are offset by greater wealth (land and livestock) of polygynous households. These results are consistent with models of polygyny based on female choice. Finally, we show that village-level negative associations between polygyny prevalence, food security, and child health are fully accounted for by underlying differences in ecological vulnerability (rainfall) and socioeconomic marginalization (access to education). We highlight the need for improved, culturally sensitive measurement tools and appropriate scales of analysis in studies of polygyny and other purportedly harmful practices and discuss the relevance of our results to theoretical accounts of marriage and contemporary population policy.

evolutionary anthropology | public health | family structure | child health | food security

Recent years have witnessed growing recognition of the importance of gender in all aspects of international development (1). This shift includes domestic and international efforts to abolish so-called “harmful cultural practices,” a term used to describe practices of, typically nonwestern, cultures deemed detrimental to well-being, most often with regard to women and children (*SI Text*). Most attention has focused on female genital cutting and on child and forced marriage (2, 3). In many policy-orientated texts, this label is also given to polygynous marriage (hereafter polygyny). For example, the United Nations Convention on the Elimination of All Forms of Discrimination Against Women states that polygyny “contravene[s] a woman’s right to equality with men and can have such serious emotional and financial consequences for her and her dependents that such marriages ought to be discouraged and prohibited” (2). Such statements are frequently presented as stylized facts and made without discussion of supporting evidence. However, a recent spate of articles, mostly based on large-scale African Demographic and Health Surveys (DHS), conclude that polygyny is indeed harmful, reporting that children in polygynous households are consistently more likely to be of ill health or die in early childhood than children in monogamous households (4–8). Reviews of the literature have also informed

policy in developed countries, including via the presentation of expert evidence in a recent retrial of the legal prohibition of polygyny in Canada (9).

Historically, more than 80% of preindustrial societies permitted polygyny (10). Today it is most prevalent in sub-Saharan Africa (11). If women and children do not benefit from polygyny then why is it so common? Evolutionary anthropologists have long puzzled the costs and benefits of polygyny (12). This literature, drawing on small-scale field studies of specific cultural contexts, reaches a consensus on the benefits of polygyny to men; polygynous men generally have higher reproductive success than their monogamous counterparts (13–16). The potential benefits of, and motivation for, polygyny for women are less clear. The “polygyny-threshold model” posits that polygyny occurs when the costs of sharing a husband are offset by equal or greater resource access than could otherwise be obtained via monogamy (17, 18). Supporting this model, polygynous men are typically wealthier than monogamous men (19, 20), and several studies show no apparent deficit in reproductive success or child health for polygynously married women (19, 21). However, in other cases, polygyny is associated with relatively poor child health (20, 22–24). Poor outcomes for women and/or children do not necessarily imply a rejection of the polygyny threshold model (12, 19). However, these findings have been interpreted as evidence of sexual conflict, with polygyny maximizing total reproductive success for men at the cost of suboptimal outcomes for individual wives and children (25).

Significance

Polygynous marriage is commonly regarded as a harmful cultural practice, detrimental to women and children at the individual and group level. We present counterevidence that polygyny is often positively associated with food security and child health within communities and that, although polygyny and health are negatively associated at the group level, such differences are accounted for by alternative socioecological factors. These results support models of polygyny based on female choice and suggest that, in some contexts, prohibiting polygyny could be costly for women and children by restricting marital options. Our study highlights the dangers of naive analyses of aggregated population data and the importance of considering locally realizable alternatives and context dependency when considering the health implications of cultural practices.

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¹To whom correspondence should be addressed. Email: david.lawson@lshtm.ac.uk.

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Drawing generalizable conclusions regarding the potential costs of polygyny from the anthropological literature alone is difficult (25, 26). Findings are mixed, study sites are rarely regionally or nationally representative, and small sample sizes raise issues of statistical power. Given these problems, the consistency of findings presented in recent large-scale, representatively sampled demographic studies of polygyny and child health is seductive (4–8). However, as we will argue, studies relying on highly aggregated data bring their own, often overlooked, methodological problems (27), problems that are acute when contrasting polygynous and monogamous households, in part because the former tend to be most common in remote and/or marginalized groups facing numerous socioecological barriers to health (*SI Text*).

Not only policy, but also grand theory, is built on the view that polygyny is harmful. It has been argued that cultural shifts to “socially imposed monogamy” in modern stratified societies can be accounted for by detrimental effects of polygyny at the group level, including costs to child health (28, 29). Most recently, Henrich et al. (28) assert that monogamy evolves by cultural group selection, with normative polygyny (*i*) incentivizing strategies of reduced paternal care, so that male effort is diverted into accumulating wives rather than raising offspring, and (*ii*) increasing the propensity for social unrest driven by a larger pool of unmarried men. To support the specific claim that polygyny has negative group-wide consequences for children, Henrich et al. (28) rely on data from large-scale demographic studies, as well as on selected population-specific contrasts where children in polygynous households experience relatively poor well-being. Consistent with the claim of greater social unrest in polygynous groups, the authors review evidence that the proportion of unmarried men positively predicts national rates of rape, murder, assault, theft, and fraud. However, such crude comparisons have limited inferential value in the face of many potential confounds. A recent review reveals no clear association between adult sex ratio, a likely correlate of the proportion of unmarried men, and violent crime (30).

Given the significance of the purported harmful effects of polygyny for both policy and our understanding of marriage systems, we conducted an innovative study addressing both individual and group-level relationships between polygyny, food security, and child health. We draw on multilevel data from 56 villages in northern Tanzania (*Fig. S1*). Tanzania experiences a high burden of food insecurity and malnutrition; 45% of children are stunted by World Health Organization (WHO) standards (31), a measure of developmental potential predictive of both later physical and cognitive functioning (32). One in four married women in rural Tanzania have at least one cowife (31), and female status is poor; internationally Tanzania scores 124/152 on the Gender Inequality Index (33). In many respects, our study combines the relative strengths of prior large-scale demographic and small-scale anthropological studies (*SI Text*). We sampled more households ($n = 3,584$) than the Tanzanian DHS for the same regions (34). However, unlike DHS studies, we incorporate data on ethnicity and livelihood-specific measures of household wealth (i.e., land cultivated and livestock owned), and, crucially, sufficient village-level data to enable a statistically robust consideration of within and between-village variation. Four main ethnic groups reside in the area, including the highly polygynous Maasai and Sukuma, the moderately polygynous Rangi and the predominantly monogamous Meru (34) (*Tables S1* and *S2*). This setup provides a unique opportunity to consider relationships between polygyny and health in a context of varied and transitioning marital norms.

Results

Contrasting Monogamous and Polygynous Households. We first estimate relationships between polygyny, food security and the heights and weights of children under 5 y using linear regression aggregating data across all villages (*Table S3*). This method is analytically equivalent to existing studies of large-scale demographic surveys, which routinely ignore both ethnic variation and

village-level spatial clustering of health (*SI Text*). Consistent with such studies, polygynous households have lower food security than monogamous households ($\beta = -1.56$, 95% confidence intervals (95%CI) = -2.31 ; -0.81 , $P < 0.001$) and, using WHO standardized z-scores, lower child height-for-age (HAZ, $\beta = -0.21$, 95%CI = -0.34 ; -0.08 , $P < 0.01$). Child weight-for-height (WHZ) did not significantly differ between polygynous and monogamous households ($\beta = -0.06$, 95% CI = -0.16 ; 0.05 , $P > 0.1$).

However, there is a clear tendency for relatively polygynous villages and ethnic groups (particularly the Maasai) to have poor food security and child health (*Fig. 1*) (see ref. 34 for a comprehensive analysis of ethnic differences in food security and child health). Accounting for this variance by including a random effect for village demonstrates that neither food security nor child health are significantly associated with polygyny when contrasted within villages (food security: $\beta = 0.26$, 95% CI = -0.47 ; 0.98 , $P > 0.1$; HAZ: $\beta = -0.07$, 95% CI = -0.20 ; 0.06 , $P > 0.1$; WHZ: $\beta = 0.00$, 95% CI = -0.12 ; 0.11 , $P > 0.1$; *Table S3*). As such, multilevel analysis reveals a Simpson's paradox (27), i.e., village-level differences obscure underlying relationships between polygyny, food security, and child health within villages.

Polygynous men generally resided with their first wife (*SI Text*), and in only 10% of male-headed polygynous households did multiple wives coreside (most commonly among the Sukuma, where 17% of polygynously married male household heads lived with multiple wives). Second or later cowives and their children typically lived in separate, but often adjacent, dwellings to their husbands. Distinguishing between these household types reveals that male-headed polygynous households have significantly higher food security than monogamous households within villages ($\beta = 0.86$, 95% CI = 0.01 ; 1.70 , $P < 0.05$). Stratified analysis confirms that a trend toward higher food security for male-headed polygynous households is present in all three ethnic groups with a substantial prevalence of polygyny (*Fig. 2*), although this is only statistically significant in the Sukuma ($\beta = 2.00$, 95% CI = 0.68 ; 3.32 , $P < 0.01$). Furthermore, in both the Sukuma and Rangi, children in male-headed polygynous households also had higher WHZ (Sukuma: $\beta = 0.21$, 95% CI = 0.03 ; 0.39 , $P < 0.05$; Rangi: $\beta = 0.33$, 95% CI = -0.01 ; 0.67 , $P = 0.06$). Overall, female-headed polygynous households had lower food security than monogamous households within the same village ($\beta = -1.16$, 95% CI = -2.34 ; 0.01 , $P = 0.05$), although this pattern did not approach statistical significance in stratified analyses (*Fig. 2* and *Tables S3* and *S4*).

Polygyny and Wealth. Wealth was measured by an asset-based household wealth index (*SI Text*), a generic measure favored by large-scale surveys and used across rural and urban contexts (35). This measure indicates minimal differences in wealth between monogamous and polygynous households. However, livelihood-specific measures of wealth reveal that polygynous households, particularly when male-headed, both cultivate more land ($\beta = 0.22$, 95% CI = 0.14 ; 0.31 , $P < 0.001$) and own more livestock ($\beta = 0.49$, 95% CI = 0.36 ; 0.62 , $P < 0.001$) than monogamous households (*Fig. 3*). These differences are apparent in all major ethnic groups in stratified analyses and are robust to statistical adjustment for the number of adults and young dependents in the household (*Tables S5* and *S6*). Thus, consistent with the polygyny threshold model, higher wealth presents a strong candidate mechanism for superior food security and child nutrition in male-headed polygynous households.

Contrasting Monogamous and Polygynous Villages. We next consider how village characteristics predict individual measures of food security and child health using multilevel regression including village-level random and fixed effects (*SI Text* and *Table S7*). Independently of individual marital status, each 10% increase in the proportion of polygynous households sampled per village is associated with an estimated -1.52 unit decrease in food security ($\beta = -1.52$, 95% CI = -2.09 ; -0.95 , $P < 0.001$), a -0.15 reduction in child HAZ ($\beta = -0.15$, 95%

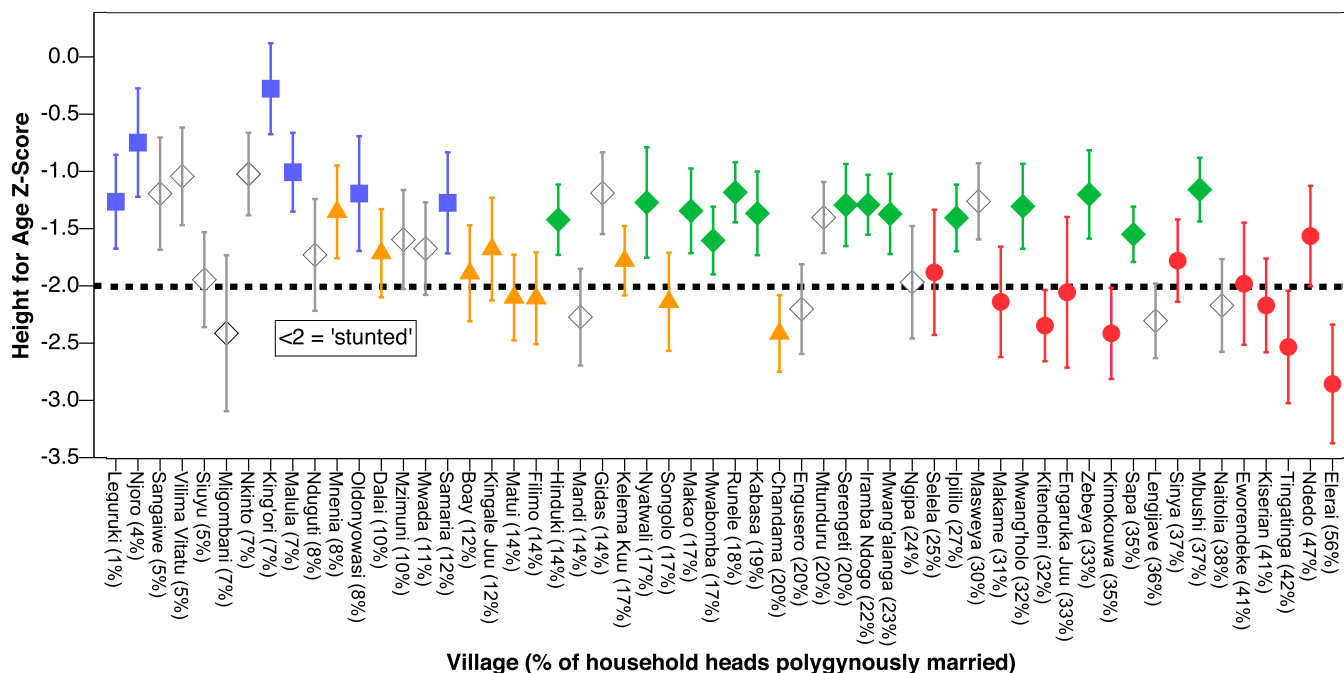


Fig. 1. Child height-for-age by village sorted by polygyny prevalence. There is strong ethnic and village-level variation in child health. Relatively monogamous Meru villages tend to have relatively good child health, whereas relatively polygynous Maasai villages tend to have relatively poor child health. The dashed line represents the WHO cutoff for chronic malnutrition. Ethnicity is coded as the majority ethnic group residing in each village. Error bars represent 95% CIs. Red circle, Maasai; green diamond, Sukuma; orange triangle, Rangi; blue square, Meru; white diamond, other ethnicity.

CI = -0.25; -0.05, $P < 0.001$), and a -0.07 reduction in child WHZ ($\beta = -0.07$, 95% CI = -0.15; 0.01, $P < 0.1$). However, once we adjust analyses for village-level proxies for ecological vulnerability (annual rainfall) and socioeconomic marginalization (distance to district capital and the proportion of household heads with nonzero education), these associations dramatically attenuate and become statistically nonsignificant in the case of food security and child HAZ, whereas the proportion of polygynous households in a village becomes positively associated with child WHZ ($\beta = 0.08$, 95% CI = -0.01; 0.18, $P = 0.09$; Fig. 4). As such, our analyses do not support the idea that polygyny has negative group-level consequences on well-being.

Discussion

We challenge the widespread notion that polygyny is harmful to children. Consistent with prior studies (4-8), polygyny is predictive of relatively low food security and poor child health in aggregated data. However, such associations are driven entirely by the tendency of polygyny to be more common in marginalized and ecologically vulnerable villages and ethnic groups. Within villages,

polygynous households, at least those headed by males, often had higher food security and better child outcomes than monogamous households. Polygynous households were also wealthier in terms of livelihood-specific forms of wealth (land and livestock), although not in asset ownership, which is the foundation of wealth indices favored by national demographic surveys (35). These findings are consistent with classic evolutionary and economic models suggesting that sharing a husband can be in a woman's strategic interest, at least in contexts where women depend on men for resources, by enabling access to equal or greater wealth than could be achieved by opting for monogamy (17, 18). Our results also highlight the inherent weaknesses of highly aggregated samples such as the DHS, the primary data source for population scientists studying family structure and health in sub-Saharan Africa (36).

That polygyny is associated with better outcomes for specifically male-headed households indicates that cowives resident with their husband are most likely to benefit from polygyny. Female-headed polygynous households in contrast may often lose cowife conflicts over shared resources. We found that female-headed polygynous

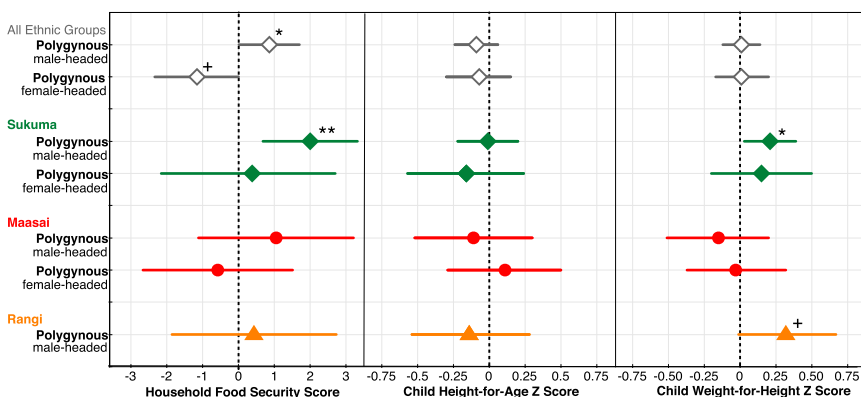


Fig. 2. Food security and child health by household type. Within villages polygyny is associated with relatively high food security when households are headed by a male and relatively low food security when headed by a female (typically later wife households). Stratified analysis confirms higher food security in the Sukuma and relatively improved child weight-for-height in both the Sukuma and Rangi, for male-headed polygynous households. The reference category (dashed line) is male-headed monogamous households (Table S4 for full model output). $^+P < 0.1$, $^*P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.001$.

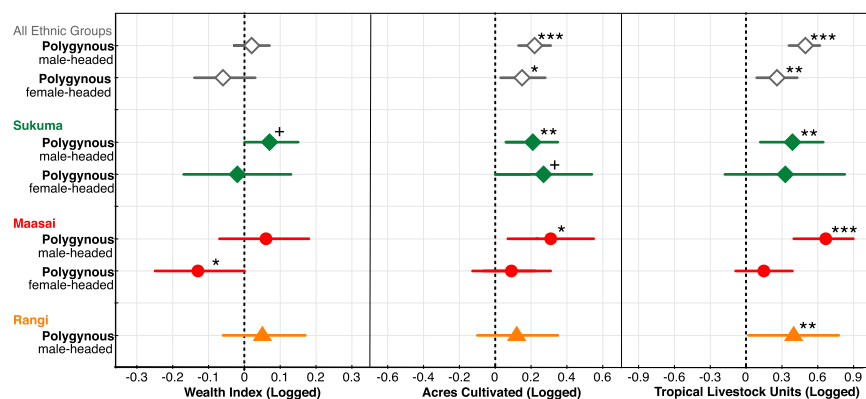


Fig. 3. Wealth index, land cultivated, and livestock owned by household type. Within villages polygynous households, particularly when headed by males, cultivate more land and own more livestock than monogamous households. The reference category (dashed line) is male-headed monogamous households (Table S6 for full model output). $^+P < 0.1$, $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$.

households had lower food security than monogamous households when considering the sample as a whole, although child health did not differ (Fig. 2). In this context, first wives are most often co-resident with their husband. Advantages to first wives have been reported elsewhere (13, 24). In rural Ethiopia, Gibson and Mace (13) found first wives were in better physical health and had more surviving offspring than monogamously married women and that relatively poor child health was only associated with polygyny for second or later cowives. This result may reflect selection effects, i.e., women of good health/social standing are less likely to enter polygynous marriages as later wives, such that differences in child outcomes, or indeed food security, cannot be seen as consequences of polygyny itself (13, 16). Alternatively, first wives may benefit from exclusivity before sharing their husband and subsequent seniority over later wives. Thus, to the extent that deficits in child health or food security are unequally portioned among wives, we note that polygyny may, in some instances, be considered harmful.

We demonstrate ethnic variation in the relationship between polygyny and health. Findings from prior small-scale studies suggest such variation, but comparing results across studies is hampered by methodological differences (25). Specifically, we detect an advantage of being raised in male-headed polygynous households for the Sukuma (the largest ethnic group in Tanzania) and the Rangi, but not for the Maasai. Although our stratified analyses here have relatively low statistical power, at least two factors may account for these differences: low status of Maasai women and the relative poverty of this ethnic group. Previous studies emphasize low female status in the Maasai (37), restricting women's control over their marital arrangements (including divorce and the addition of cowives) and/or preventing women from effectively allocating household resources to children (38). The Maasai also suffered the greatest burden of food insecurity and poor health in our study (34). Borgerhoff Mulder (39, 40) found that polygyny was negatively associated with child survival only in the poorest households in Kenyan Kipsigis. Strassmann (22) observed negative associations between polygyny and child health in the Dogon of Mali in all but one "exceptionally large and wealthy village" (p. 10,897). Thus, it might be that polygyny fails to provide better circumstances in conditions of relative resource scarcity where children are most vulnerable to biased intrahousehold resource allocation, accounting for the differences between the Maasai and neighboring ethnic groups.

Our analyses do not support the assertion that polygyny has group-wide costs on child health (28). Instead, it seems parsimonious that highly polygynous, predominantly Maasai, villages do poorly not because of polygyny, but because of vulnerability to drought, low service provision, and broader sociopolitical disadvantages. Highly monogamous, predominantly Meru, villages on the other hand occupy the relatively high rainfall, fertile slopes of Mount Meru close to Arusha city, benefiting from improved health care and education infrastructure (34). It is possible that polygyny has negative group-level consequences on unmeasured aspects of

well-being. However, we are skeptical of the theoretical foundation of such arguments. Recent reformulations of sexual selection theory emphasize facultative responses to partner availability, predicting that the more common sex will cater to the preferences of the rarer sex to acquire and retain mates. As such when polygyny leads unmarried women to be in relatively short supply we might expect higher not lower levels of paternal investment (30, 41). Consistent with this perspective, our adjusted analyses found that child WHZ was marginally higher in the most polygynous villages (Fig. 4).

If polygyny does not bestow group-level costs on women and children, as suggested by Henrich et al. (28), how can we account for observed transitions to socially imposed monogamy with economic development? In Tanzania, the spread of both Islam and Christianity have clearly influenced marital norms. Missionary influence may be partially responsible for the ubiquity of monogamy among the Meru (42). However, explanations based solely on religion are unsatisfactory because religious prescriptions and marriage patterns most likely coevolve, constrained to some extent by systems of production (43). Fortunato and Archetti (44) propose that monogamy evolves via the maximization of individual, not group benefits, and is best understood as an inheritance strategy favored when intergenerational resource transfers are critical to descendant success. Monogamy may thus be beneficial to both men and women when returns to parental investment favor offspring quality over quantity. In line with this account, the Meru were early adopters of relatively intensified agriculture (42), where productivity is limited by land inheritance, as opposed to low intensity agriculture and pastoralism, which may be relatively labor limited. The Meru also have the highest educational attainment (34), which is associated with transitions to low fertility. Once individuals opt for smaller family sizes, a pattern best understood as motivated by economic rather than reproductive success (45), the reproductive advantages of polygyny are likely outweighed by novel opportunities to invest more per child, e.g., via formal education.

Although we make important methodological advancements, our study shares several limitations with prior studies of polygyny. Our use of the standard demographic household definition (*SI Text*) often cleaves polygynous families into distinct survey units, preventing direct contrasts of children of first and later wives sharing the same husband. Cross-sectional data also limit our ability to infer causality, preventing explicit consideration of the impact of additional wives on previously monogamous women and their children. A recent retrospective study in Bolivia reports that although women in polygynous marriages had lower fertility than women in monogamous marriages overall, the addition of a second wife did not impact on the fertility of the first wife in intra-individual analyses (16). Self-selection may thus be responsible for reported effects of polygyny in some cross-sectional studies (13). We also caution that the relatively small number of female-headed polygynous households (at least for the Sukuma and Rangi; *Table S1*) in our study may have resulted from disagreement between the

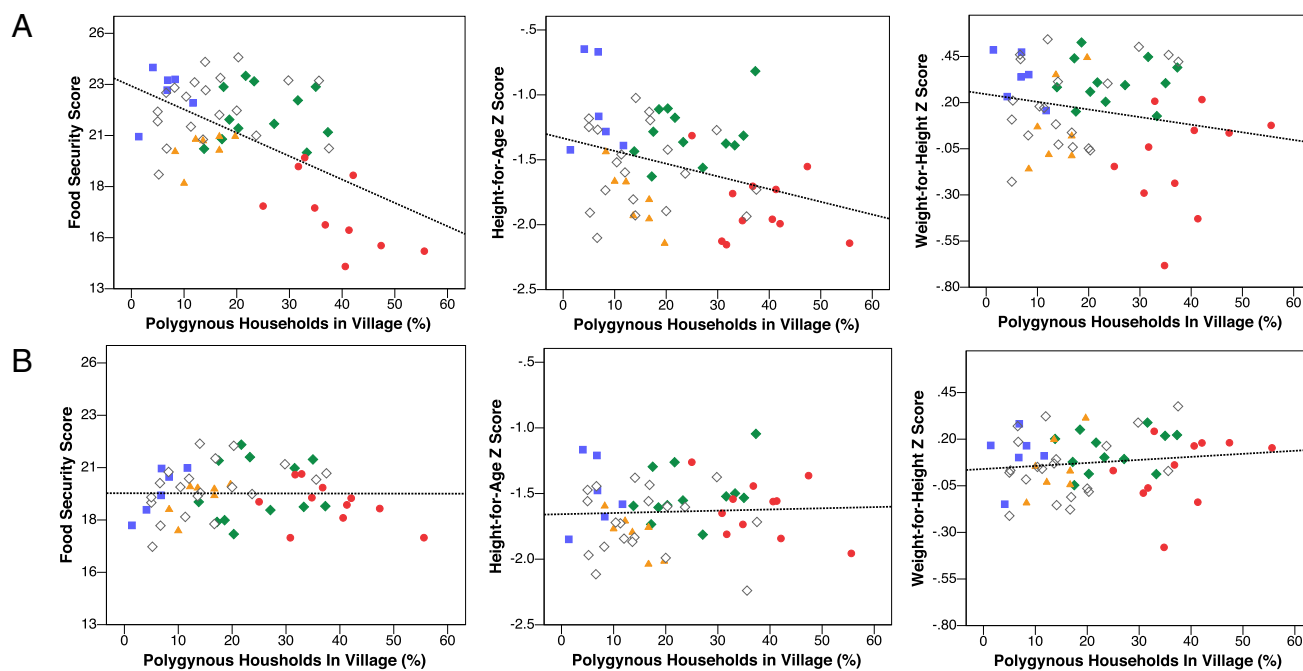


Fig. 4. Village differences in food security and child health by polygyny prevalence. Predicted village intercepts before (A) and after (B) adjustment for village-level differences in ecological vulnerability (annual rainfall) and socioeconomic marginalization (distance to district capital and proportion of household heads with nonzero education). After adjustment, polygyny prevalence is unrelated to food security and HAZ, and positively predicts WHZ. Intercepts are mean/mode centered for household characteristics. See text for estimated coefficients and Table S7 for corresponding model output. Red circle, Maasai village; green diamond, Sukuma village; orange triangle, Rangi village; blue square, Meru village; white diamond, other ethnicity village.

village register sampling frame and household definition used by enumerators on the ground. If unsampled and sampled households systematically differ this may bias our estimates. The common use of rigid household definitions is coming under increasing criticism for obscuring the measurement of complex demographic phenomena, and we support recent calls (46) for experimentation with alternative survey methodologies that more accurately cater to the reality of African family structure.

Our study concerns food security and child health and cannot tell us about the wider potential of polygyny to cause harm. Other aspects of physical and mental well-being may be influenced by polygyny (47). Recent studies counter simple intuition. Polygyny is associated with lower HIV prevalence at both national and regional levels across Africa. Reniers and colleagues (48) suggest polygyny increases individual exposure, but selective recruitment of HIV-positive women into polygynous marriages where coital frequency is lower isolates transmission risks from the wider population. A recent study in Tanzania also found no evidence for an association between polygyny and maternal anxiety and depression (49). Whatever the outcome, we do not anticipate universal relationships between polygyny and well-being. We have demonstrated variation in the estimated consequences of polygyny both between women (by coresidence with husband) and between ethnic groups. Moreover, the vital insight of both economic and anthropological theory is that cultural diversity in marriage practices stems in large part from context-dependency in the pay-offs to alternative behavioral strategies (50). As anthropologists have long emphasized, polygyny itself is also a diverse institution with considerable cultural variation in associated norms of spousal recruitment and residence (51).

We particularly advocate that policy makers distinguish low female autonomy from polygyny rather than treat the latter as a definitive indicator of the former. Where women have control over marital placements, we do not anticipate costs to polygyny. Indeed, if there are large differences in male wealth, prohibiting polygyny may be disadvantageous to women by restricting marital options.

Levirate marriage or widow inheritance, whereby a woman marries the close male relative of her deceased spouse as a polygynous bride, is also likely to offer women and their children substantially better prospects than living as a single widow in many contexts (52). On the other hand, if female autonomy is low, and/or when polygyny is not associated with differences in male wealth, marital placements may logically be prone to negative impacts of male coercion. We also recommend future research prioritizes data analysis at the level of social groups (i.e., villages, neighborhoods). Institutions for marriage and child-raising are rapidly changing across the globe, and their gendered impacts are increasingly taking center stage in discussions of international development (1). Policy analysts concerned with these transformations need to consider appropriate comparison groups, selection effects, and broader community confounds. Only by making meaningful contrasts, which capture alternatives readily available to individuals, and by taking into account the distribution of specific traditions across different communities and ecologies, can we expect to achieve a true understanding of the health implications of cultural practices.

Materials and Methods

Data (Dataset S1) were collected between 2009 and 2011 as part of the Whole Village Project (WVP), coordinated by Savannas Forever Tanzania, the University of Minnesota (UM), and the Tanzanian National Institute of Medical Research (NIMR). The WVP received ethical approval from the UM Institutional Review Board (code 0905565241) and NIMR. Between 60–75 households were randomly selected from 56 villages (Fig. S1), leading to a sample of 3,584 households, 2,268 of which contained children under 5 y of age. Nearly half (45%) provided anthropometric data on more than one child (two children, 35%; three or more children, 10%). Four ethnicities, the Maasai, Sukuma, Rangi, and Meru, make up 65% of households. Maasai are traditionally seminomadic pastoralists but have recently diversified into cultivation. Sukuma, Rangi, and Meru are all characterized as agro-pastoralists. Rangi and Meru primarily identify as Muslims and Protestants, respectively. Sukuma and Maasai identify with either Christian or indigenous religions (34). Our analysis is limited to households with a married head of at least 16 y, bringing our working sample to 1,764 households, containing 2,833 children (averaging 32 households

and 51 children per village). The Household Food Insecurity Access Scale assesses food insecurity during the last month on a 27-point scale. We reversed this measure so that a higher score indicates greater food security (mean: 16.9; SD: 7.0). Anthropometrics were WHO standardized. HAZ assesses chronic malnourishment (mean: -1.6; SD: 1.6) and WHZ assesses acute malnourishment (mean: 0.2; SD: 1.3). Z-scores less than -2.0 indicate stunting and wasting, respectively. Relatedness data are available for villages 15–56 only: 80% of children were biological children of the head, 14% were grandchildren, 6% were other relatives. A wealth index was calculated by principal component analysis applied to the ownership of 37 assets. Acres cultivated and livestock units were recorded separately. Wealth measures were transformed ($\log x + 1$) to approximate normal distributions. Village mapping was used to compute distance to district capital and estimated annual rainfall. *SI Text* provides further information on

child, household, and village data. Regressions were fit using maximum likelihood estimation and include controls for child age and sex, age of household head, and hunger season (for details, see *SI Text* and *Tables S3–S7*).

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