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Research

Understanding the nature of wealth and its effects on human fitness

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Studying fitness consequences of variable behavioural, physiological and cognitive traits in contemporary populations constitutes the specific contribution of human behavioural ecology to the study of human diversity. Yet, despite 30 years of evolutionary anthropological interest in the determinants of fitness, there exist few principled investigations of the diverse sources of wealth that might reveal selective forces during recent human history. To develop a more holistic understanding of how selection shapes human phenotypic traits, be these transmitted by genetic or cultural means, we expand the conventional focus on associations between socioeconomic status and fitness to three distinct types of wealth—embodied, material and relational. Using a model selection approach to the study of women's success in raising offspring in an African horticultural population (the Tanzanian Pimbwe), we find that the top performing models consistently include relational and material wealth, with embodied wealth as a less reliable predictor. Specifically, child mortality risk is increased with few household assets, parent nonresidency, child legitimacy, and one or more parents having been accused of witchcraft. The use of multiple models to test various hypotheses greatly facilitates systematic comparative analyses of human behavioural diversity in wealth accrual and investment across different kinds of societies.

Keywords: fitness; child mortality; wealth; Pimbwe; human behavioural ecology; multi-model inference

1. INTRODUCTION

Biologists strive to understand natural selection in wild populations in order to understand variability in traits within and between populations and species. Evolutionary social science embraces similar aims, recognizing that cultural [1], ecological [2] and material [3] transmission supplement genetic transmission in contributing to trait distributions. The specific contribution of human behavioural ecology to understanding the role of natural selection in human populations lies in determining the consequences for genetic fitness of specific behavioural, physiological and cognitive traits, and in exploring the adaptive flexibility of humans across traditional and modern contexts [4,5]. Though human behavioural ecology (*aka* evolutionary anthropology) cannot easily demonstrate evidence of genetically transmitted adaptations [6], it offers a useful and perhaps unique naturalistic window through which we can study the operation of selection in natural populations [7].

To understand the operation of natural selection in human populations, evolutionary anthropologists have, for several decades, studied the sources of fitness variation, aiming to specify the phenotypic traits on which natural selection may have acted over recent human history, the selective pressures that have shaped human evolution, as well as the culturally transmitted strategies whereby men and women maximize their fitness (e.g. [8]). Initially, attention was directed to the importance of access to material resources in assuring fertility and survival, attracting multiple spouses and stabilizing marriage (e.g. [9–11]). Such patterns are neither restricted to agricultural and pastoral populations [12], nor indeed to men [13]. Despite contrary expectations for modern populations, derived from the fact that the European demographic transition started and was most pronounced among the wealthy [14,15], recent analyses confirm the importance for successful reproduction of both material resources [16–18], and the training whereby such resources are attained (such as formal education [19]). As such, there is considerable support for evolutionary anthropologists' claim, first posited by Irons [11], that men and women strive for cultural goals, such as wealth, in order to achieve reproductive fitness, and the corollary that people in different societies will redefine their goals and values over time such that these motivate behaviour and dispositions that favour fitness; here cultural goals serve as proximate mechanisms whereby individuals, consciously or not, achieve ultimate fitness objectives. In support of this claim, a recent overview indicates that selection coefficients on wealth accrual in humans are of parallel magnitude to those on competitive ability in other species [18].

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One contribution of 14 to a Theme Issue 'Evolution and human behavioural diversity'.

Increasingly, evolutionary anthropologists recognize that the nature of 'wealth' is far more diverse than early studies focusing on material goods might suggest. Attention initially expanded to the importance of status [20,21], then to skills (such as hunting [8,22]) and physiological characteristics (such as height [23,24]), and most recently to kin networks [25,26] and the presence of (or assistance from) particular relatives such as grandparents [27]; there has, in addition, been considerable debate over the relative importance of mates (typically husbands [28–30]). As yet, however, studies are mainly piecemeal, with ethnographers investigating the sources of wealth that they suspect are most important in their populations, such as land ownership, size of livestock herds, hunting success or grandmothers, with other variables only sometimes included in the model as controls. There is little principled investigation of the diverse sources of wealth which might reveal the phenotypic traits selected across different socioecological systems during recent human history.

To develop a more integrated understanding of how selection may have shaped human phenotypic traits, be these transmitted by genetic or cultural means, Kaplan [31] recasts human life-history theory in terms of investment in stocks of embodied and extrasomatic wealth, with the former including a person's strength, skills, knowledge and other abilities, and the latter including such items of stored value as land, livestock and cash. In an expansive overview, Kaplan & Lancaster [32] (see also [33]) show how investments in these different kinds of stock might potentially structure major historical trends in fertility, mating and parental investment across different societies in response to large-scale shifts in socioecology, but conclude that our understanding of these dynamics is very incomplete. Indeed, there are no systematic and empirical studies of how different kinds of wealth in concert shape reproductive outcomes. Kaplan & Lancaster [32] identify new frontiers for research in examining how individuals make decisions about life-history allocations within differing socioecological contexts, for which a first step must lie in determining how different types of wealth affect fitness.

Here, we pursue this agenda. Rather than testing specific hypotheses about particular fitness determinants, we adopt a more holistic approach to determining which types of wealth are most important to fitness. We build on recent comparative work that attributes the widely varying extent of inequality across foragers, pastoralists, horticultural and small-scale agricultural societies to the nature of the wealth that is most important for making a living in that society [34–36]. As in the previous work, we classify the principal types of wealth that are important in small-scale societies into three categories—embodied, material and relational wealth. Embodied wealth encompasses the stocks of health, skill and productive knowledge embodied in people, paralleling [31] usage. Material wealth consists of the productive capital that an individual owns, either personally or by dint of membership of a household or kin group, and typically comprises land, livestock and household or private assets (for many examples, see [37]). Relational wealth consists of the social ties on which an individual can draw, ties that derive from social position, trust, reputation, kinship and symbolic goods [38,39]. We propose that an approach that evaluates individual fitness variability in relation to the suite of different kinds of wealth that an individual can accrue in a given society lays the groundwork for a systematic comparative study of how natural selection operates on human wealth accrual strategies (with wealth defined in the broad sense above), thereby providing a principled approach to the comparative study of behavioural diversity. Furthermore, from our previous study, we would predict that relational and embodied wealth would be particularly important for fitness in foraging and horticultural populations, and material wealth in pastoral and agricultural populations.

To identify the principal phenotypic traits associated with fitness in an African horticultural community, we conduct an inductive analysis of fitness differentials among individuals in relation to these three wealth types. The Bantu Pimbwe village under study is in many ways typical of horticultural communities worldwide [40,41], with a livelihood based on farming with hoes, fishing, hunting and seasonal foraging of wild foods. We make the specific prediction that embodied and relational wealth will be of greater significance for fitness than material wealth. This is based on Gurven *et al.*'s [41] examination of the contribution of these sources of wealth to variation in household well-being among four horticulturalist populations in East Africa, West Africa, the Caribbean and lowland South America. In each of these populations embodied wealth was rated (qualitatively by the ethnographers) to be twice as important for family well-being as relational wealth, and relational wealth to be somewhat more important than material wealth; furthermore, the estimate of intergenerational transmission (based on an age-independent, unit-free regression statistic) for material wealth ($\beta = 0.09$) was also much lower than for relational ($\beta = 0.26$) and embodied ($\beta = 0.17$) wealth.

We focus here on women and on a single component of their fitness—the survival of their children to age five. Keeping children alive is a key component of fitness in rural populations in the developing world, and a major challenge to any Pimbwe family, where one in five livebirths fail to reach their fifth birthday. The universality with which selection acts on prereproductive survival in age-structured populations such as humans, particularly survival prior to the fifth birthday [42], suggests that there should be species-specific adaptations to parenting and the promotion of child survival. A two-stage model selection based on Akaike Information Criterion (AIC) is used to estimate the relative importance of different kinds of wealth in affecting mortality prior to age five. The merits of this approach are considered in §4.

2. METHODS

(a) *Ethnographic context*

Research was conducted in the village of Mirumba lying in the Rukwa Valley of western Tanzania,

whose inhabitants belong primarily to the Pimbwe and very closely related ethnic groups of Bantu origin; the area is called Mpimbwe. Originally farmer-foragers, the Pimbwe's gradual loss of much of their traditional territory resulting from colonial and postcolonial land protection policies [43] has increased reliance on hoe-based farming, though hunting, fishing, beekeeping and a variety of other crafts based on natural resources continue to contribute both subsistence and cash to the household economy. Traditionally subject to a system of chiefs [44], the largely autonomous households have since the 1970s been governed by elected and appointed village officials. Owing to the remote location, the village infrastructure is limited to a poorly supplied dispensary with no trained personnel, no surfaced road, reliance on seasonal rivers and shallow wells, and no electricity. Monogamous households are the norm, forming either in the village (or neighbourhood) of the husband (patrilocal) or the wife (matrilocal), or in a village with no close relatives (neolocal). However, marriages are unstable [45], single parent households are common, day-to-day life is characterized by high levels of food insecurity [46] and maternal anxiety [47], and children show very poor levels of growth for their age [48]. Fragile marriages lead to many children changing households across years, although children under 5 years of age usually reside with their mothers. Finally, there are many seams of mistrust among villagers, arising from conflicts relating to failed kin obligations, theft, nascent economic development initiatives, multi-party political campaigning, and conflicts of interest between farmers and agro-pastoral Sukuma households settled adjacent to the village. As elsewhere in Tanzania conflicts over land, health (typically HIV-free status), food, political influence and even sheer good luck are often construed as disputes over a 'limited good' ([49], 'limited' in the sense of being in short supply and attainable only from others), and often take the form of witchcraft accusations [50].

(b) *Data*

Analyses are based on a longitudinal study of all inhabitants of the village of Mirumba, a village characteristic of the ancient Mpimbwe chiefdom and more broadly of Bantu horticulturalists of Central-Eastern Africa [44], although also affected by inevitable impacts of the Tanzanian state and global economy. At each of seven censuses (between 1995 and 2006), every household in the village was visited. Across years there was some household attrition from the sample, and new households formed through emigration, divorce, immigration and remarriage. Demographic data (reproductive records, marital histories, survival) were collected at each round, as well as measures of household economic productivity and capital possessions. Additionally, anthropometric data (weights and heights) are available for all individuals who attended a biennial 2–4 day measurement session administered at the village clinic building and various more-distant outposts (with a meal for compensation). All witchcraft cases openly discussed in the village between 1995 and 2009 were noted, along with identity of the accused witch and his/her victim(s); these were uncovered through participation in village gossip networks, not systematic questioning during household interviews, which could bias reports to cases of misfortune (specifically child death).

The sample consists of 376 women who produced 916 livebirths between July 1994 and June 2006; these women have resided for some or all of this period in Mirumba and their reproductive careers have been consistently monitored longitudinally, even during intermittent absences. Information on the fathers of these children is available for 76 per cent of the sample (220 children). The fate of all children born in this period is tracked, with 173 (19%) dying before their fifth birthday. Life-table analyses on a larger Pimbwe sample (1750 livebirths, covering a period of approx. 40 years) show survival levels for the period between birth and fifth birthday to be 0.81, dropping only to 0.77 by age 15 (M. Borgerhoff Mulder 2006, unpublished data). The sample is therefore representative of the larger Pimbwe population, and encompasses the principal period of juvenile mortality (infancy and early childhood). All variables were examined for secular (in this case annual) effects in child mortality rates, parental education, material wealth, etc., but no changes over time were detected, reflecting the relatively restricted temporal span of this cohort of births (1995–2006).

(c) *Wealth measures*

The survival of a woman's children was tracked in relation to a suite of independent variables designed to best capture the woman's embodied, material and relational wealth. A woman's embodied wealth was measured using her education (*education*) and height (*height*); education is not strongly associated with material wealth in this population because of the lack of formal occupational opportunities, but women with some primary (or secondary) education are likely to have more knowledge regarding treatment of disease and to provide higher quality care as a result of greater exposure to national development messages, as reflected in national statistics showing associations between maternal education and child survival [51].

A woman's material wealth is ideally best measured using multiple indices, since at least in Western industrial populations income, expenditure and capital assets are neither closely correlated nor entirely substitutable (e.g. [52]). In Mpimbwe, annual income (derived from a broad mix of small-scale seasonal, and often very intermittent, activities) is not easily measured; accordingly we determine the cash value of a woman's household assets (*household assets*, which include buckets, torch/lamp, bicycle, livestock, drum, tin roof, farm implements, radio, watch, etc.; some of these assets women own, others they get partial access to through their current husband). We also use a binary variable capturing house quality (*house quality*, based on the presence of baked bricks that allow for cleaner walls and floor, windows, a fitted door, etc.; houses with unbaked mudbricks are known as 'bescoti' because they crumble like biscuits

in the rain, creating muddy and unsanitary living conditions). These indices were assessed as time-varying covariates in the statistical analysis because of the high inter-annual variation in household assets, and indeed household of residence (as children and their mothers are often located in different houses across years).

Relational wealth is measured in four ways. First, we use the number of households in the village containing a woman's relatives (*relatives*) and her child's father's relatives (*child's father's relatives*), classified as 'none', '1–6' or 'more than 6' The second measure is the whereabouts (in relation to the child) of the woman (*residence status*) and her child's father (*child's father's residence status*) at each census, classified as 'present in the household', 'present in the village', 'elsewhere/unknown' or 'deceased'. Third, we use a binary code to indicate whether the woman conceived the child in marriage or with an extrapair partner (*child's conception status*). Finally, because of the devastating social, economic and psychological effects of being accused of practicing witchcraft, we include an indicator of whether the woman (*witch*) or her child's father (*child's father witch*) has been implicated in a village witchcraft case, either as 'victim' (of witchcraft) or 'accused perpetrator' (of witchcraft), since 1994.

Several points need to be clarified regarding the three types of wealth. First, there is necessarily some ambiguity regarding these classifications [36]. Although the classification of education and height as embodied, and cash assets and house quality as material is relatively straightforward, relational wealth is more complex and multifaceted. In a socioecology where harvests, cash assets and general fortune are highly unpredictable across years, women view relational capital as important, at least in an idealized way. They elaborate on the importance of their natal families, their sisters and their mothers (if still active) as important social allies while at the same time recognizing that these people can be a drain on their own time and resources. This was clearly shown in Hadley's [53] study of child growth in a nearby Pimbwe village, where wealthy women benefitted less in terms of their children's weight for age scores from the availability of kin than did poorer women. A Pimbwe woman also thinks strategically about her children's fathers and their kin; she might, for example move to a village where one or more of her children have paternal kin even if she has divorced the father. Women must also balance their own desires to remarry and move against the fate of children who may either be left with natal kin, with their father's kin or brought to live with a new husband. While these dynamics merit detailed analysis in their own right, for the current purposes we simply capture relational wealth with variables measuring number of relatives, residence, child's conception status and witchcraft. Second, the measures of each wealth type (embodied, material and relational) are not, for the most part, indicators of some common underlying quantifiable dimension that might be aggregated; by similar token, there is little multi-collinearity among measures, with highest associations observed between child's father's residence status and child's conception status (0.40), household assets and house quality (0.34), firstborn status and being conceived out of marriage (−0.25), education and height (0.23), and own and child's father's status as a witch (0.23) (electronic supplementary material, table S1). Third, there are potential interactions among wealth types [36], the significance of which is raised in §4.

Finally, mortality prior to fifth birthday is controlled for child's gender and birth order (among maternal sibs, classified as first, second to fourth, or later). Child's age-adjusted weight and height (measured as *Z*-scores calculated using Epi-Info http://www.cdc.gov/epiinfo/) as averaged across years were available for a smaller sample.

(d) *Analysis and modelling strategy*

The effects of the full suite of independent variables on mortality were examined using survival analysis. The hazard (or odds) ratio (Exp(B)) of each variable in predicting the mortality of a woman's children was determined through Cox's proportional hazards regression run in R (using the survival package). Survival analysis is appropriate for two reasons. First, many children were 'right censored', that is they had not yet reached 5 years by the last observation in September 2006. This method computes the regression coefficient using uncensored cases only, but includes all cases to estimate the baseline hazard. Second, Cox models can incorporate time-dependent covariates. Thus, variation in the wealth of a child's household can be examined as this changes across years, in a manner analogous to a panel study; for this purpose, multiple records were created for each individual to capture the time-varying covariates over a 5 year period. Cox's regression is a semi-parametric method, and assumes no particular distribution for the shape of the hazard function, other than proportional hazards (tested and confirmed following [54]); results were also examined for highly influential cases.

To prepare for a model selection analysis, we made several modifications to the dataset. First, to combine categories with small sample sizes the residence status variables were compacted, without any substantial loss of information. All other residence categories were compared against the category 'dead', while for the child's father's residence the category 'dead' was combined with 'absent/unknown' and 'in household' with 'in village'. Second, a woman's witchcraft status and that of her child's father were combined, because effects on child mortality were so similar (electronic supplementary material, table S2) and because of low numbers of accused witches and victims. Third, to avoid possible sources of bias [55,56], missing values were multiply imputed in R using the chained equations algorithm available in the Multivariate Imputation by Chained Equations (MICE) package; all predictor variables described above, as well as parent ethnicity, were used to impute missing values. For each missing data point, three values were generated, each produced after 20 iterations of regression imputation to ensure a stable sampling distribution (if imputation predictors were themselves missing for a particular census year, MICE sampled randomly from their complete cases). This resulted in three

distinct imputed datasets, with which the reported analyses were conducted (as recommended by [56]). Bivariate estimates for the three imputed datasets did not differ substantially in direction, size of effect, or levels of significance in comparison with those of the complete-case analysis, and is presented in the electronic supplementary material, table S2.

The results (tables 1–3) were produced by model selection based on comparing AIC scores. We initially generated a list of 1023 models representing the various possible combinations of covariates (including both gender and birth order as controls). Though such a large model space is undesirable, each model represents a plausible relationship between covariates such that we could not exclude any, and the ratio of observations to parameters remains very high. One simplifying constraint we imposed on the model space was to include the measure for a child's father for residence and number of relatives whenever we included the equivalent measure for the focal mother, and vice versa. After specification, each model was fitted to each of the three imputed datasets, and each dataset was ranked according to its AIC score. We found it computationally efficient to limit further analysis to those models within the first 99.99 per cent of aggregate AIC weight for each dataset, and the results reported in table 2 are from this second, smaller round of model selection. For the first imputed dataset, this included only 24 models, and for the remaining two imputed datasets, 31 models. The model-averaged hazard ratio estimates from this second round for each variable potentially affecting child morality are reported in table 1. In table 2, we report the top 14 models in the first missing data imputation, and include comparable information from the second and third imputations. Finally, in table 3 we compare AIC weights for models that include only material, only relational and only embodied wealth; control variables were not included.

3. RESULTS

The hazard ratios in both the bivariate analysis (electronic supplementary material, table S2) and the multivariate AIC model-averaging approach (table 1) show that multiple measures of embodied, material and relational variables predict child mortality in Mpimbwe. As a control variable gender has no observed effects on survival; although boys have 12 per cent higher odds of dying than girls (see table S2 in electronic supplementary material for odds ratios), the effect is not significant, neither in the bivariate nor in the multivariate analysis. As a second control variable, birth order affects survival, with first births showing a hazard ratio double (1.5) that of middle births (2nd–4th born), which do not differ from later births.

For embodied wealth, education reduces a mother's chance of losing a child, with children of secondary educated mothers having a considerably lower risk (61%) of dying than those of uneducated mothers, but the results are not statistically significant in either the bivariate or multivariate models because of low statistical power. A woman's height (and weight, not shown) is consistently associated with a declining risk of mortality for her children, although again the effects are not statistically significant.

For material wealth, cash value of assets of the household in which a woman raises her child (a value that varies across years as both the fortune of the household and the residence of the child changes) shows a strong negative effect on mortality risk (figure 1*a*). For each 1000 Tanzanian shillings (US$0.84, as averaged for the period under study), the risk of morality declines by 0.3 per cent (table 1). The effect retains statistical significance with the multivariate AIC model-averaged estimates. House quality shows no statistically significant effect on survival.

For relational wealth there are multiple influences on survival. Given the high mobility of children across households, a key variable is where the child's parents chose to live. Women generally live with their children under 5 years of age; however, in cases where the mother has died her children have a high probability of dying, as seen both in the bivariate and in the multivariate models (figure 1*b*); the fact that no children died when their mother was absent or in the village reflects the likelihood that caretakers of an ailing child call on the mother to return. Considering the residential status of the child's father, mortality is highest if the father is either dead or absent/unknown (figure 1*c*); whether he resides in the child's household or merely in the village is immaterial; this effect is retained in the multivariate model. Turning to the full count of relatives a woman has in the village we see that the best chances for child survival are when she has no relatives in the village, and that mortality increases with number of relatives; a similar pattern holds for the relatives of the child's father, although neither effect reaches statistical significance. Whether the child was born in or out of wedlock had no discernible impact on his or her probability of survival in the bivariate model, but in the AIC model-averaged estimates children born in legitimate marriages showed mortality 1.6 times higher than those born to a lover outside of (or before) marriage (figure 1*d*). Finally, women accused of witchcraft since 1994, or women whose children are fathered by men accused of witchcraft in that period, have children who are more than three times more likely to die than the children of parents who are not so accused (figure 1*e*).

Child weight for age *Z*-score is available for 516 children of 256 mothers. In a reduced model, entering only those predictors significant in a full model that includes child's weight for age, there were three significant predictors of mortality: child's weight for age (Exp(B) = 0.553, s.e. = 0.169, $p < 0.001$, $n = 516$), household assets (Exp(B) = 0.998, s.e. = 0.001, $p = 0.04$) and mother's residence (Exp(B) = 6.264, s.e. = 1.001, $p = 0.07$). This result suggests that most of the covariates that predict mortality risk do so through weight loss, indicating a significant role for food competition, compromised child care, and disease rather than accidents.

Using the first missing data imputation, 99 per cent of the AIC weights are accounted for by 14 models; these are shown in table 2 in the first 11 columns. On the right-side panels of this table, we show how

Table 1. Hazard ratio (Exp(B)) estimates, 95% confidence intervals and statistical significance (p) for each independent variable in predicting childhood mortality, averaged over the highest ranked models for each of the three imputed datasets (24 for imputation 1, 31 for imputations 2 and 3) by AIC weight.

	imputation 1			imputation 2			imputation 3		
variable, reference category (sample sizes in parentheses)[a]	Exp(B)	95% CI[b]	p[b]	Exp(B)	95% CI[b]	p[b]	Exp(B)	95% CI[b]	p[b]
control variables									
sex (879), ref. category 'female' (439), male (440)	1.003	(0.923, 1.089)	0.95	1.014	(0.922, 1.115)	0.78	1.032	(0.907, 1.175)	0.63
birth order (880), ref. category '2nd–4th birth' (407)									
1st birth (196)	1.750	(1.151, 2.660)	0.01	1.676	(1.104, 2.545)	0.02	1.677	(1.120, 2.511)	0.01
5th–12th birth (277)	1.365	(0.938, 1.989)	0.10	1.310	(0.900, 1.906)	0.16	1.345	(0.921, 1.964)	0.12
embodied wealth									
education (853), ref. category 'none' (144)									
lower primary (177)	0.979	(0.876, 1.094)	0.71	0.991	(0.911, 1.077)	0.82	0.983	(0.883, 1.095)	0.76
upper primary (499)	0.965	(0.870, 1.070)	0.49	0.978	(0.906, 1.057)	0.58	0.967	(0.873, 1.070)	0.51
some or finished secondary (33)	0.932	(0.701, 1.239)	0.63	0.944	(0.753, 1.185)	0.62	0.934	(0.706, 1.236)	0.63
height (in cm) (619)	0.996	(0.980, 1.011)	0.57	0.994	(0.977, 1.012)	0.53	0.998	(0.988, 1.008)	0.75
material wealth									
household assets (in 1000 s TZ) (770)[c]	0.997	(0.996, 0.998)	0	0.997	(0.996, 0.998)	0	0.997	(0.996, 0.998)	0
house quality (770), ref. category 'no baked bricks' (256)[c] baked bricks (514)	1.179	(0.953, 1.460)	0.13	1.201	(0.960, 1.502)	0.11	1.078	(0.925, 1.258)	0.34
relational wealth									
residence status (792), ref. category 'village/house/absent' (781)[c] dead (11)	4.062	(1.995, 8.269)	0	4.279	(2.153, 8.504)	0	3.503	(1.783, 6.884)	0
child's father's residence status (792), ref. category 'village/house' (592)[c] absent/unknown or dead (200)	2.199	(1.556, 3.109)	0	1.993	(1.389, 2.860)	0	2.031	(1.439, 2.868)	0
relatives (760), ref. category 'none' (48)									
1–6 (275)	1.490	(0.695, 3.197)	0.31	1.535	(0.699, 3.371)	0.28	1.318	(0.621, 2.800)	0.47
over 6 (437)	1.720	(0.778, 3.802)	0.18	1.787	(0.786, 4.063)	0.17	1.627	(0.739, 3.586)	0.23
child's father's relatives (619), ref. category 'none' (84)									
1–6 (162)	1.283	(0.855, 1.924)	0.23	0.938	(0.645, 1.365)	0.74	1.135	(0.764, 1.686)	0.53
over 6 (373)	1.381	(0.877, 2.173)	0.16	0.979	(0.627, 1.528)	0.93	1.246	(0.787, 1.975)	0.35
child's conception status (916), ref. category 'born outside of/before marriage' (259)									
born inside marriage (657)	1.678	(1.115, 2.527)	0.01	1.634	(1.077, 2.480)	0.02	1.615	(1.079, 2.419)	0.02
own/child's father witch (916), ref. category 'uninvolved' (863)									
accused perpetrator (20)	3.597	(2.007, 6.445)	0	3.785	(2.148, 6.670)	0	3.703	(2.103, 6.521)	0
victim (33)	0.255	(0.064, 1.018)	0.05	0.265	(0.066, 1.067)	0.06	0.257	(0.064, 1.025)	0.05

[a]Using imputed missing values (see text).
[b]Calculated for robust standard errors clustered by child.
[c]Time-dependent covariates.

Table 2. Akaike Information Criterion (AIC) weighting for the top 14 models predicting child mortality. Presence of variable in model indicated by grey, absence by white. Models are shown for imputation 1; corresponding rankings and AIC weights and delta weights are shown for imputations 2 and 3.

imputation 1[a]											imputation 2			imputation 3		
rank	AIC	AIC weight	education	height	house quality	household assets	own/child's father's residence status	own/child's father's relatives	child's conception status	own/child's father's witchcraft status	rank	ΔAIC	AIC weight	rank	ΔAIC	AIC weight
1	13782.73	0.25		■		■	■	■	■	■	1	0	0.26	4	1.23	0.10
2	13782.78	0.25				■	■	■	■	■	2	0.27	0.23	1	0	0.18
3	13784.71	0.09		■		■	■	■	■	■	3	1.62	0.12	6	1.97	0.07
4	13784.74	0.09				■	■	■	■	■	4	1.81	0.10	3	0.67	0.13
5	13784.87	0.09	■			■	■	■	■	■	5	3.06	0.06	8	2.44	0.05
6	13785.83	0.05	■	■		■	■	■	■	■	6	3.67	0.04	13	4.20	0.02
7	13786.43	0.04					■	■	■	■	7	4.53	0.03	2	0.64	0.13
8	13786.86	0.03	■		■		■	■	■	■	9	4.66	0.03	11	3.20	0.04
9	13786.99	0.03		■			■	■	■	■	10	4.90	0.02	7	2.12	0.06
10	13787.82	0.02	■	■	■		■	■	■	■	11	5.33	0.02	15	5.00	0.01
11	13788.39	0.01					■	■	■	■	12	6.11	0.01	5	1.37	0.09
12	13788.50	0.01	■				■	■	■	■	16	7.32	0.01	10	2.99	0.04
13	13788.96	0.01		■			■	■	■	■	14	6.54	0.01	9	2.92	0.04
14	13789.90	0.01	■	■			■	■	■	■	19	8.42	0	14	4.88	0.02

[a]Birth parity appears in all 14 models, gender appears in 6 out of 14.

Table 3. Akaike Information Criterion weighting for relational, material and embodied wealth as predictors of child mortality. Models are shown for imputations 1, 2 and 3.

	imputation 1			imputation 2			imputation 3		
model	rank	AIC	AIC weight	rank	AIC	AIC weight	rank	AIC	AIC weight
all relational	1	14036.94	99.81	1	14036.94	1.00	2	14046.11	10.01
all material	2	14049.47	0.19	2	14049.47	0	1	14041.72	89.98
all embodied	3	14228.25	0	3	14228.25	0	3	14226.54	0

these top 14 models are ranked in two subsequent imputed datasets, and find that they account, respectively, for 93 and 96 per cent of the AIC weights. The clearest conclusion to draw from this table is that the top models consist either of all three kinds of wealth, or of material and relational wealth alone.

Turning more specifically to the role of each variable, shown as grey or white in table 2, we find that each of the four relational wealth measures, and one of the material wealth measures (household assets) are included in each of the top 14 ranked models. The other measure of material wealth (house quality) appears in just over half the models, which together takes the vast majority of the AIC weight. The two measures of embodied wealth (education and height) appear in half of the models, most of which have negligible (5% or less) AIC weight.

Finally we compared three models, consisting exclusively of embodied, material and relational wealth, respectively, to determine the best predictor of a woman's ability to keep her children alive. In two of the three imputations, relational wealth is the best predictor of mortality, with an AIC weight of 99 and 100 per cent, respectively; in the third imputation material wealth is the strongest predictor, with a weight of 89 per cent. A mother's embodied wealth clearly plays a weaker role in predicting child survival in Mpimbwe than do her material assets or her relational wealth.

4. DISCUSSION

Results suggest that elements of a woman's material and relational wealth play key roles in assuring fitness in Mpimbwe, as measured by child survival to age 5; embodied wealth is also an important predictor, but with less weight than material and relational wealth. The variables with conventional statistical significance levels are more limited: in the multivariate models child mortality risk is associated with fewer household assets, with the mother (or the child's father) being dead or absent, with the child's legitimacy and either parent being accused of witchcraft. Note however that while each category of wealth matters for offspring survival, the direction of some effects is unexpected. The fact that a woman's children are more likely to survive if she, and the child's father, has no relatives in the village, indicates that in Mpimbwe kin may be a drain rather than an asset (see discussion below), and thus that relational 'wealth' actually constitutes an absence of relatives! Similarly, the counterintuitive enhanced survival of illegitimate children points to the unimportance of legitimacy in this population (and, perhaps to strategic extrapair mating by women, as discussed below). As a result, our measures of embodied, material and relational wealth cannot be thought of as constituting a *single* dimension that could be summed or averaged. In short, the best prospects for a Pimbwe woman successfully raising children is to have access to household assets, to conceive children out of wedlock, to keep the father around (at least in the village), to avoid being encumbered with other distant relatives (even from her natal family), and to keep herself and the child's father out of witchcraft trouble.

Our initial hypothesis was that embodied and relational wealth might be more important than material wealth to a woman's success in raising surviving children. This was drawn from Gurven *et al.*'s [41] analysis of the relative importance of different wealth types for variability in household welfare in horticultural populations (including the Pimbwe). The results here are not entirely supportive insofar as household assets are an important predictor of child survival. We do not think that this reflects a discrepancy between household well-being (Gurven *et al.*'s focus) and child survival (our focus), since the successful raising of children is central to the well-being of the household. Rather, we suspect that material wealth is increasingly eclipsing relational and embodied wealth among the Pimbwe as they obtain greater market access for cash crops, as traditional institutional networks weaken, as more individuals store wealth in cash, and as witchcraft accusations escalate; these developments are contingent on the rapid economic liberalization of the Tanzanian economy and disintegration of traditional values since the late 1990s. In support of this interpretation, note that in our measure of relational wealth, we actually find that family members are important in their *absence*, as noted above.

Our findings on control variables are typical of populations of this type: gender is not an important influence on child survival in most sub-Sahelian populations where sons and daughters play key roles in household provisioning and child care [57]. With respect to birth order, mortality is somewhat elevated in first borns, indicative of the immature reproductive systems of young mothers (that lead to underweight babies); a U-shaped pattern is common in developing countries (e.g. [58]), a pattern that tends to shift (to inverted J and then linear functions) as national levels of child mortality decline [59]. Mpimbwe is clearly transitional in this respect.

Turning now to the three wealth types, our measures of embodied wealth (education and height)

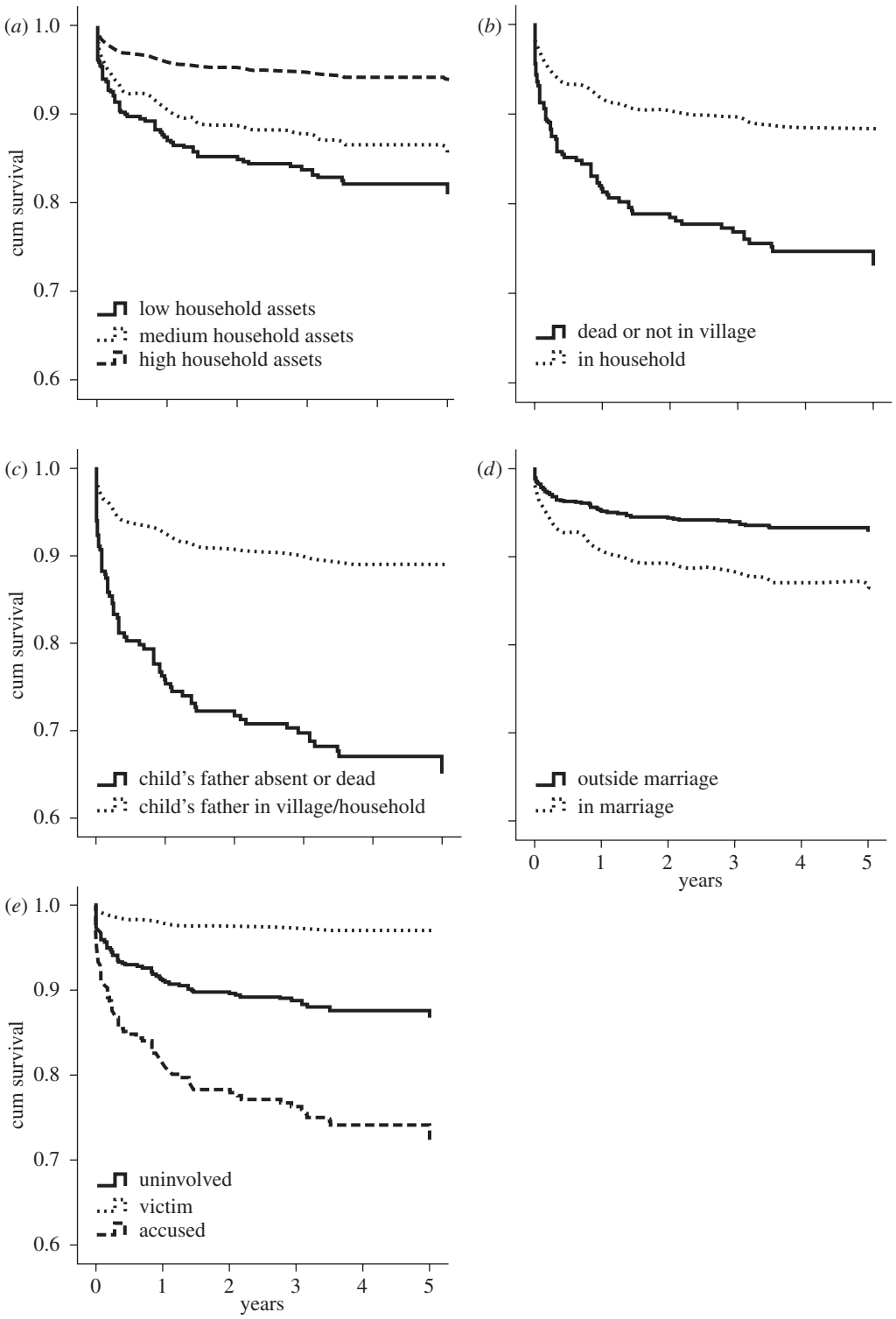

Figure 1. The cumulative survival of children in the first 5 years of life as predicted by a proportional hazards model, with the effects of all variables included in the models shown in table 1 controlled. (*a*) Household assets (divided into terciles, as averaged over time periods); (*b*) residence status (modal over time periods); (*c*) child's father's residence status (modal over time periods); (*d*) child's conception status; and (*e*) own/child's father's witch status.

predict child mortality, but less consistently than do material and relational wealth, appearing in only about half of the top AIC-ranked models. A woman's education, much discussed as a cause of reduced infant and child mortality [60], typically enhances women's skill and knowledge in effectively using the available health and community development resources; it may also increase a woman's autonomy within the household in advocating for her children's health, as shown in Mpimbwe with respect to family planning [61]. Typically, education effects become stronger when schooling leads either to more effective use of healthcare services or reliable cash employment, neither of which exists to any significant extent in the village; this may account for the weak effects in Mpimbwe. Height, another measure of embodied wealth, is also commonly found to positively affect child survival in developing nation contexts,

particularly among women with low levels of education [62], most probably because taller women are generally healthier and stronger, and they also give birth to heavier babies. The relatively weak effect observed in Mpimbwe, where health insults are so prevalent, was unexpected and deserves further study.

Regarding material wealth, household assets predict a woman's success in raising her children to age 5, despite the fact that among horticulturalists there are few durable goods that can be held exclusively by households [41] or that are reliably transmitted across generations [34]. While studies in more socially differentiated communities show distinct effects of different measures of material wealth on health and survival outcomes [52], here we use a composite measure of the value of household assets as an indicator of relative freedom from material stresses, insofar as only households with a food surplus can afford to buy extensive household durable goods (buckets, bicycle, corrugated iron roofing, etc.), and such items are rapidly dispensed of in times of duress. The value of household assets is closely associated with measures of food security in this population [46], and previous research in other Pimbwe villages shows the importance of food security in promoting child growth [48] and maternal emotional stability [47,63]. We therefore interpret the consistent entry of household assets into all of the heavily AIC-weighted models as clear indication of the importance of material wealth in contributing to a Pimbwe woman's fitness. The association between living in a mud house without baked bricks (rather than the more easily cleaned and ventilated baked brick house) and the enhanced survival of a woman's children is difficult to explain, and suggests collinearity (0.34, see electronic supplementary material, table S1).

Measures of relational wealth appear consistently in all of the top ranked models. Mothers are more likely to keep their children alive if they survive for 5 years after the child's birth. They are also more successful in raising surviving children if the father of the child is present in the household or village, and if they and the father of the child are free of witchcraft accusations. Rather unexpectedly, a mother is also more likely to have her children survive if both she and the child's father have no kin in the village. The importance of mothers for child survival is documented in every population where this has been looked at quantitatively, and a child's father's presence is also very important in some but not all populations [26]. The prejudicing effect on child survival of relatives is more unusual, particularly given the current evidence for humans as cooperative breeders (e.g. [64]), and clearly deserves closer attention in terms of differentiating specific categories of kin. A woman's in-laws may want their son's wife to reproduce faster than is optimal for the woman herself, as suspected in a Gambian farming population where a similar effect was found (see also [65,66]). Poor child outcomes for women with numerous natal kin are not typically observed, although Quinlan & Flinn [25] find a curvilinear relationship in Dominica. The pattern is nevertheless somewhat consistent with Hadley's [53] quantitative and qualitative data from another Pimbwe village showing women's awareness of how the demands of assistance from their kin can erode family welfare and child growth (as also seen in Kenyan Kipsigis agropastoralists for patrilineal relatives [67]). Given the apparent reluctance of nuclear households to share food (and labour) in this population, and the lack of effective third party institutions for social control, Pimbwe are stereotyped as 'stingy' and mistrusting. This caricature seems apt for both kin and non-kin relationships, and is captured in results of an Ultimatum Game study, which showed Pimbwe making very low initial offers and retaliating with very high rates of punishment of low offers [68]. Suspicion, mistrust and punishment in this population frequently takes the form of witchcraft accusations [44] that are here shown, for the first time to our knowledge, to be associated with devastating effects on child survival, no doubt reflecting the severe psychological and economic consequences of being labelled a witch, and often banished to outlying areas of the village land. Note that children of victims of witchcraft (that is, the children of those who accuse others of witchcraft) do not show enhanced mortality, ruling out an explanation of reverse causality—namely that witchcraft explains child death (a common explanation). Rather, such children show substantially *lower* mortality than those whose parents are not involved in witchcraft accusations at all; the reasons for this finding are as yet unclear, although perhaps only well-connected individuals can afford to make such accusations. More generally, being trusted and/or well-connected in rural Tanzanian villages plays an important role in assuring family welfare [69].

A final variable to affect child survival is the child's conception status. Unexpectedly, children born in marriage have 60 per cent higher odds of dying than children born to men other than the mother's current spouse; this is consistent with the finding that women with multiple sequential spouses have higher fitness than those with a single spouse [45]. While this might be interpreted as evidence that women seek men with high genetic quality in extrapair relationships [70], possible intervening effects deserve further attention in future analyses.

Here we used model selection for predicting one component of fitness, offspring survival. An alternative approach towards uncovering the complexity of factors affecting fitness lies in investigating the means, whereby various wealth types influence subsequent outcomes. For example, a remarkable dataset that provides social and biological variables at birth for a Swedish cohort born between 1915 and 1925 Goodman & Koupil [16] shows how biological (embodied) factors operate through social pathways. The advantage of such an analysis is that it allows clear specification of how, in the Swedish case, biological factors (such as birth weight) influence fitness through social processes (such as marriage), or alternatively how material factors (such as wealth) might influence embodied outcomes (such as weight or height) that subsequently affect fitness. The disadvantage is that such models quickly become highly complex and population-specific, and therefore difficult to use in a systematic comparative endeavour.

5. POTENTIAL OF THIS APPROACH FOR COMPARATIVE STUDIES

Comprehensive understanding of human behavioural variation requires a systematic analysis of the determinants of fitness across populations. This is because individuals are likely to strive most ardently to acquire (entrain or cultivate) the kinds of wealth (material, embodied or relational) that are most important in that particular socioecological context [11]. In addition, parents will strive to ensure transmission to their offspring of those kinds of wealth that most reliably predict the well-being (and presumed fitness) of their offspring's families; comparative evidence for this latter expectation comes from a study of intergenerational transmission in 21 foraging, horticultural, pastoralist and agricultural societies where parent–offspring similarities in wealth were most marked for the resources deemed to be most important to household well-being in that particular type of society [34].

There are many human behavioural ecological studies of individual variation in fitness on which a more general comparative understanding of human behavioural variation can be based. Recent comparative reviews of these studies are valuable, but focus only on a single type of wealth (e.g. material [18]) or on a single kind of society (e.g. foragers [8]). Here we offer a multivariate approach that provides a robust and easily replicable way of ranking the importance of wealth types for fitness across different societies. This approach can incorporate different measures of wealth as appropriate, such as hunting skill, number of relatives or herd size. With very simple modifications, it can be applied to the genders separately, and to different components of fitness such as completed fertility or reproductive success, or the production and survival of grandchildren. Child survival was used here because of the availability of longitudinally monitored year-by-year survival of all livebirths born over an 11 year period with corresponding economic and demographic covariates, but a similar approach could be taken to a post-reproductive individual's fertility or number of surviving offspring (with necessarily a greater reliance on reported data).

The advantage of the model selection approach is that it allows us to directly compare the hypotheses embodied in the regression models. If we had simply included all variables in a full regression model, the resulting parameter estimates would represent the relationship between our independent variables and measures of fitness only given the *a priori* validity of the full model itself. Standard null-hypothesis testing allows no principled way to evaluate the merits of this assumption, nor address the problem of overfitting, leaving open the possibility that our estimates are a consequence of the idiosyncrasies of Mirumba rather than actual associations among Bantu horticulturalists more broadly. Modern model selection procedures have the additional advantage of a rigorous foundation in information theory (in the case of AIC, as an approximation of the Kullback–Leibler distance). Because models are penalized for additional parameters in ways grounded on information theory, AIC-based metrics strike an effective balance between the conflicting demands of maximizing explained variance and avoiding overfitting. For these reasons, AIC-based models are better suited than traditional null hypothesis testing for exploratory analysis when multiple variables (>9) are being investigated in an inductive manner [71]. This approach is straightforward, flexible and easily replicable whereby researchers working in different populations can test various hypotheses about the relationship between wealth measures and fitness.

We view this model selection approach as complementary to the recent work on life-history trade-offs, which examine the costs and benefits of different life-history allocations between embodied investment and current reproduction, fertility and (grand) parental care, sons and daughters, etc. (reviewed in e.g. [72]). This is because with a more systematic understanding of the various influences on fitness differences across different types of human populations, we can better model the life-history trade-offs that men and women must make in different social and economic contexts, and thence ultimately the institutions that emerge for the facilitation and control of reproduction.

With this approach, general hypotheses can be derived regarding which wealth types are likely to be most important to fitness in different kinds of societies, contingent on the importance of each wealth class to variations in household well-being [34]. Relational wealth, for example, may be particularly important to fitness in populations where material assets are not reliably transmitted to the next generation, and where networks of allies are key to obtaining access to key resources, such as water holes in the Kalahari !Kung [73]. Embodied wealth may be particularly important where a heavy reliance on hunted resources demands skill, stamina and knowledge, as in the Ache [22,31]. Material wealth may be key where property norms facilitate the persistence of sharp wealth differentials among individuals and, commonly, over generations, as in many herders (e.g. [74]) and farmers (e.g. [75]). The analysis is also open to further improvements in functional form of the included models. Because there is good reason to think that the three kinds of wealth are complements, for example, wealth type interactions might be used to predict measures of fitness, and compared across populations. The claim here then is that by analysing a suite of wealth types, we provide a foundation for conducting comparative analyses of fitness determinants across human populations, as initiated in a recent comparative investigation [18] of men's holdings of material wealth, thereby providing a key piece to the analysis of human behavioural diversity.

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