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Science **326**, 682 (2009);
DOI: 10.1126/science.1178336

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Intergenerational Wealth Transmission and the Dynamics of Inequality in Small-Scale Societies

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Small-scale human societies range from foraging bands with a strong egalitarian ethos to more economically stratified agrarian and pastoral societies. We explain this variation in inequality using a dynamic model in which a population's long-run steady-state level of inequality depends on the extent to which its most important forms of wealth are transmitted within families across generations. We estimate the degree of intergenerational transmission of three different types of wealth (material, embodied, and relational), as well as the extent of wealth inequality in 21 historical and contemporary populations. We show that intergenerational transmission of wealth and wealth inequality are substantial among pastoral and small-scale agricultural societies (on a par with or even exceeding the most unequal modern industrial economies) but are limited among horticultural and foraging peoples (equivalent to the most egalitarian of modern industrial populations). Differences in the technology by which a people derive their livelihood and in the institutions and norms making up the economic system jointly contribute to this pattern.

Investigations of the dynamics of economic inequality across distinct economic systems have been limited by the paucity of data on all but contemporary market-based industrial societies. They are also hampered by the lack of an empirically based model applicable to the differing institutions and technologies characteristic of the broad range of economic systems, ranging from hunter-gatherers through pastoral and agrarian societies to modern economies. Here we present empirical estimates of the extent of inheritance of wealth across generations and of the degree of wealth inequality, along with a descriptive model of the relation between the two. We support our model with data on three distinct wealth classes—material, embodied, and relational, to be defined below—in 21 contemporary and recent hunter-gatherer, horticultural, pastoral, and agricultural populations.

The key thesis to be explored is that for some kinds of wealth and some economic systems (but not others) the parents' wealth strongly predicts the wealth of the offspring. In particular, the cattle, land and other types of material wealth of pastoral and agricultural economies are directly transmitted by simple transfers, often buttressed by social conventions of inheritance. By contrast the somatic wealth and skills and the social network ties central to foraging and horticultural livelihoods are more subject to the vagaries of learning, genetic recombination, and childhood development. Moreover, in foraging and horticultural economies, such material wealth as exists tends to circulate through broad social networks rather than being vertically transmitted to offspring. A corollary of the thesis is that, if our model is correct, economies in which material wealth is important will show substantial levels of wealth inequality.

Both the thesis and the corollary find strong support in our data. We focus on small-scale societies because they offer the greatest variation in both the technologies by which a livelihood is gained and the basic institutions that provide the incentives and constraints regulating economic life, including the dynamics of inequality and the inheritance process. (We use the term "small-scale" to refer to populations in which the influence of modern national states is limited). These societies thus provide the most powerful lens for exploring hypotheses concerning the importance of technologies (kinds of wealth) and institutions (kinds of society) in explaining the dynamics of inequality and, thus, may also illuminate long-term trends in contemporary and future economies.

The connection between wealth inheritance and wealth inequality (explained more precisely in the model below) is the following: If wealth is strongly transmitted across generations, chance shocks to the economic fortunes of a household due to disease or accident, luck in a hunt or harvest, and other environmental disturbances or windfalls will be reproduced in the next generation. These effects will thus accumulate over time and thereby counteract the widely observed inequality-dampening tendency of regression to the mean (*1*–*3*). We seek to understand the effects of this process by examining how the offsetting effects of random shocks and imperfect transmission across generations jointly determine a steady-state distribution of wealth for differing kinds of wealth and across the four different economic systems (*4*). The institutions and norms that characterize distinct economic systems and the nature of the wealth class alike will affect the degree of intergenerational transmission. The extent of shocks will also differ across wealth classes and economic systems.

For a number of modern economies, there are quantitative estimates and comparisons of the intergenerational transmission of education, occupational prestige, nonhuman physical capital, and other forms of embodied and material wealth (*3*, *5*, *6*). For small-scale populations, associations between reproductive success and material forms of wealth have been studied (*7*), and there exist piecemeal estimates of intergenerational transmission of, for example, fertility (*8*) and height (*9*). But there are no estimates allowing a comparison across populations of the inheritance of the distinctive kinds of wealth that are central to the livelihoods of small-scale communities of foragers, horticulturalists, herders, and farmers. Here we present a new set of data and conduct a quantitative comparative analysis of the transmission of distinct types of wealth among the 21 populations shown in Fig.1 and Table 1. Further information is provided in (*4*).

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The dynamics of wealth inequality. To clarify our model, we initially consider just a single type of wealth and show that the degree of inequality in its steady-state distribution depends on the extent to which wealth is transmitted across generations. Suppose that a household's wealth is acquired in two ways. The first is transmission directly from the parents, in the form of material bequests, clients, skills, private information, genotype, conditions affecting development, network connections, and so on. The second way of acquiring wealth is from the resources available to all members of the population, in the form, say, of equal access to common resources or public information.

We summarize these two influences on a household's wealth by expressing the expected wealth of household i as $\beta w_{ip} + (1 - \beta)\underline{w}$, where wealth is measured in natural logarithms, w_{ip} is the wealth level of household i's parents, and $\underline{w}$ is the population-average wealth level (normalized to be the same across generations). The intergenerational transmission coefficient, β ($0 \leq \beta < 1$), measures the extent to which the wealth of a household in one generation depends on the wealth in the previous generation, and $(1 - \beta)$ represents regression to the mean as introduced by Galton in his study of human stature (*10*).

In each generation, the realized wealth of a household is its expected wealth (above) plus a disturbance term, λ, reflecting exogenous shocks that over time are assumed to be independent of the wealth of previous generations, with mean zero and variance σ_λ^2:

$$w_i = \beta w_{ip} + (1 - \beta)\underline{w} + \lambda_i \quad (1)$$

We are interested in the variance of the logarithm of a population's wealth (a standard unit-free measure of inequality) in the long run. To determine this, we use Eq. (1) to write the variance of wealth in generation t as:

$$\text{var}(w_{it}) \equiv \mu_t = \beta^2 \mu_{t-1} + \sigma_\lambda^2 \quad (2)$$

where μ_{t-1} is the variance of the logarithm of wealth in the parental generation. We then solve for μ, the steady-state (stationary, or long run) variance of the logarithm of wealth, by setting $\mu_{t-1} = \mu_t = \mu$, giving:

$$\text{var}(w_i) \equiv \mu = \sigma_\lambda^2/(1 - \beta^2) \quad (3)$$

This steady-state level of wealth inequality may be interpreted as the effect of stochastic shocks (the numerator), blown up by the intergenerational transmission multiplier, $(1 - \beta^2)^{-1}$, which is increasing in β, the extent of intergenerational transmission of wealth. As β approaches one, the effects of windfalls of wealth, accidents of health, theft, and the like, dissipate more slowly over time so that the shocks of even the distant past contribute to inequality in a given generation, resulting in high levels of steady-state inequality. For $\beta > 1$, there is no steady state, and inequality will increase over time. The determination of this steady state is illustrated in Fig. 2.

A population exposed to greater wealth shocks is represented by a larger intercept on the vertical axis (σ_λ^2), whereas greater intergenerational transmission of wealth is represented by a steeper solid line [the slope of which is β^2, see Eq. (2)]. To use this model, we need not assume that the steady-state wealth distribution is typically attained. What is important for our approach is that, for a given society, the fluctuations around the steady-state value are small relative to the differences in steady-state inequality across societies characterized by different economic systems and different kinds of wealth.

By a household's wealth, we mean any of its attributes that contribute to its well-being as measured by consumption levels, social status, or other ends that are valued in the particular society. To take account of many kinds of wealth simultaneously, we define the importance of each class of wealth as follows. Let E, M, and R be positive numbers representing the amount of a household's embodied, material and relational wealth. The well-being of the household, W, is a weighted product of these classes of wealth, the weights being the relative importance of each wealth class in the economic system in which the household lives:

$$W = \gamma E^e M^m R^r \quad (4)$$

where γ is a positive constant and the exponents e, m, and r (the weights) are the derivatives of the logarithm of well-being with respect to the logarithms of the three respective wealth classes or, equivalently, the percent difference in well-being associated with a 1% difference in the amount of each class of wealth. The weighted product is preferred (to the weighted sum, for example) because it implies, plausibly, that the wealth classes are complements; that is, the contribution of each class of wealth to individual well-being is enhanced by the extent of the other classes of wealth.

We assume constant returns to scale (doubling the amount of all three classes of wealth of a household will double its well-being) implying that $e + m + r = 1$. This motivates our interpretation of these exponents as weights indicating the relative importance of each class of wealth. We refer to these weights as $\alpha \equiv \{e, m, r\}$. To combine this information on the importance of wealth classes with our measures of the extent of transmission of each wealth class across generations, we estimate an α-weighted average β for each economic system. We also calculate an α-weighted average measure of wealth inequality (the Gini coefficient) for each economic system (see below).

Ideally, one would have comparable measures of the relative importance (α) and degree of transmission (β) of each class of wealth, the degree of inequality in the distribution of each kind of wealth (Gini), and the extent of wealth shocks (σ_λ^2). Measuring the last-mentioned is difficult in any economy and impossible in the economies under study, as the estimate requires long time-

Fig. 1. Populations studied. Note: Circle indicates hunter-gatherers; star, horticulturalists; square, pastoralists; and triangle, agriculturalists.

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series data for individual wealth, which, with few exceptions, are simply nonexistent. We are able, however, to measure the other three quantities, and this permits us to gauge the extent to which intergenerational wealth transmission allows the effect of shocks to accumulate over time, and to explore differences in both intergenerational wealth transmission and wealth inequality across economic systems and wealth classes.

The nature of wealth and the varieties of economic systems. Since the development of human capital theory a half-century ago, it has been conventional to treat wealth as a multidimensional attribute, as evidenced by the adjectives now routinely applied to the word "capital," namely, social, somatic, material, cultural, and network (*11*–*13*). We identified three broad classes of wealth in our populations, namely, embodied

Table 1. Population characteristics and estimates of the intergenerational transmission of 43 measures of embodied, relational, and material wealth across 5 hunter-gatherer, 4 horticultural, 4 pastoral and 8 agricultural populations. For wealth type, the number of parent-child pairs is in parentheses. β ± SE.

Economic system and population	Wealth type	Wealth class	β	General description (ref.)
Hunter-gatherer				
Ache	Hunting returns (49)	E	0.081 ± 0.273	Mobile foragers (Paraguay 1982–2008) (*30*)
Ache	Body weight (137)	E	0.509 ± 0.128	
Hadza	Body weight (227)	E	0.305 ± 0.076	Mobile foragers (Tanzania 1982–2008) (*31*)
Hadza	Grip strength (196)	E	–0.044 ± 0.050	
Hadza	Foraging returns (33)	E	0.047 ± 0.193	
Ju/'hoansi	Exchange partners (26)	R	0.208 ± 0.114	Mobile foragers (Botswana 1973–75) (*32*)
Lamalera	Quality of housing (121)	M	0.218 ± 0.099	Sedentary fishers, trade, and some farming (Indonesia 2006) (*33*)
Lamalera	Boat shares (121)	M	0.122 ± 0.093	
Lamalera	Food share partners (119)	R	0.251 ± 0.052	
Lamalera	Reproductive success (121)	E	0.161 ± 0.174	
Meriam	Reproductive success (91)	E	0.088 ± 0.247	Sedentary fishers, some farming (Australia 1998) (*34*)
Horticultural				
Dominicans	Land (62)	M	0.137 ± 0.140	Subsistence farming, fishing, bay oil production, limited wages (Dominica 2000–08) (*35*)
Gambians	Body weight (1274)	E	0.391 ± 0.041	Subsistence rice and cash farmers (Gambia 1950–80) (*36*)
Gambians	Reproductive success (967)	E	0.088 ± 0.086	
Pimbwe	House/farm utensils (283)	M	0.107 ± 0.318	Subsistence farming, some cash farming, some foraging (Tanzania 1995–2006) (*37*)
Pimbwe	Farming skill (217)	E	–0.015 ± 0.097	
Pimbwe	Body weight (148)	E	0.377 ± 0.096	
Pimbwe	Reproductive success (599)	E	–0.057 ± 0.107	
Tsimane	Household utensils (110)	M	0.024 ± 0.071	Subsistence farming, some foraging (Bolivia 2002–08) (*38*)
Tsimane	Labor cooperation (67)	R	0.181 ± 0.106	
Tsimane	Allies in conflict (45)	R	0.338 ± 0.103	
Tsimane	Knowledge/skill (181)	E	0.111 ± 0.094	
Tsimane	Grip strength (490)	E	0.070 ± 0.042	
Tsimane	Body weight (383)	E	0.253 ± 0.069	
Tsimane	Hunting returns (26)	E	0.384 ± 0.130	
Tsimane	Reproductive success (849)	E	0.128 ± 0.073	
Pastoral				
Datoga	Livestock (135)	M	0.622 ± 0.127	Transhumant pastoralism, some farming (Tanzania 1987–89) (*39*)
Datoga	Reproductive success (133)	E	0.066 ± 0.060	
Juhaina Arabs	Camels (21)	M	0.535 ± 0.226	Transhumant pastoralism (Chad 2003) (*40*)
Sangu (Ukwaheri)	Cattle (108)	M	0.957 ± 0.424	Pastoralism, some farming (Tanzania 1997–2000) (*41*)
Yomut (Charwa)	Patrimony (livestock) (22)	M	0.564 ± 0.167	Transhumant pastoralism, some farming (Turkmenistan/Iran 1965–74) (*42*)
Agricultural				
Bengali	Reproductive success (382)	E	–0.074 ± 0.057	Farmers with wage labor (India 2000–01) (*43*)
Bengaluru	In-law networks (249)	R	0.114 ± 0.073	Farmers, merchants, wage labor, urban (India 1910–1973) (*44*)
East Anglians	Estate value (land) (210)	M	0.642 ± 0.073	Farmers, wage labor, merchants; rural and urban (England 1540–1845) (*45*)
East Anglians	Reproductive success (200)	E	0.171 ± 0.150	
Khasi	Reproductive success (650)	E	0.165 ± 0.045	Farmers with wage labor (India 2000–01) (*43*)
Kipsigis	Land (270)	M	0.357 ± 0.041	Farmers with livestock (Kenya 1981–1990) (*46*)
Kipsigis	Livestock (270)	M	0.635 ± 0.098	
Kipsigis	Cattle partners (102)	R	0.041 ± 0.139	
Kipsigis	Reproductive success (270)	E	0.213 ± 0.106	
Krummhörn	Land (1602)	M	0.610 ± 0.043	Farmers with diverse off-farm occupations (German 17th to 19th century) (*47*)
Skellefteå	Reproductive success (2515)	E	0.010 ± 0.028	Farmers with diverse off-farm occupations (Sweden 1800–88) (*48*)
Yomut (Chomur)	Patrimony (land) (58)	M	0.528 ± 0.147	Farmers with livestock (Turkmenistan/Iran 1965–74) (*42*)

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(body weight, grip strength, practical skills, and, in predemographic transition populations, reproductive success); material (land, livestock, and household goods); and relational (social ties in food-sharing networks and other forms of assistance). We have no measures of other heritable determinants of well-being such as ritual knowledge, an important source of institutionalized inequality in some populations. By linking the level of wealth of parents and adult offspring, measured as appropriate for individuals (e.g., body weight) or households (e.g., land), we are able to estimate the degree of intergenerational persistence for particular types of wealth and then to create averages for each broad class of wealth.

We classify economic systems according to the conventions of anthropology (*14*). Hunter-gatherer economic systems are those that make minimal use of domesticated species (either plant or animal), whereas pastoralists rely heavily, though rarely exclusively, on livestock kept for subsistence and sometimes commercial purposes. Although both horticulturalists and agriculturalists use domesticated plants and animals, horticulturalists do not typically use ploughs, their cultivation is labor- not land-limited, and land markets are absent or limited. As with all classificatory systems, there are some ambiguities of assignment of our populations to these classes, but the least improbable reclassifications do not affect our results [see (*4*), section 4].

Transmission of wealth across generations need not take the form of bequests, or the literal passing on of physical objects (such as when land is transmitted from father to son). What matters for the long-run dynamics of inequality is anything that results in a statistical association between the wealth of parents and children. This statistical association may be enhanced by positive assortment in mating or in economic pursuits as occurs when skilled hunters pursue prey together, or when successful herders cooperate in livestock management. The same is true of increasing returns or other forms of positive feedbacks, for example when those who invest a substantial amount earn higher than average returns, or when childhood developmental effects associated with modest genotypic differences result in substantial phenotypic differences. Negative feedbacks, such as sharing norms that extract substantial transfers from the wealthy, or wealth shocks that are inversely correlated with one's wealth (such as occur when cattle thieves target large herds), by contrast, heighten regression to the mean by reducing β, thereby attenuating the persistence of inequality over time and hence reducing steady-state inequality.

Our three wealth classes differ in the extent to which these transmission mechanisms—transfers, assortment, and positive feedbacks in development or accumulation—are at work. Material wealth is readily transferred to the next generation by bequests sanctioned by cultural rules. Moreover, because it is typically observable, material wealth can facilitate deliberate marital or economic assortment. For some types of material wealth (storage facilities, herds of livestock, and irrigated land, for example), the correlation of material wealth levels across generations is further enhanced by the presence of increasing returns to scale or other positive feedbacks. Network ties can easily be passed from parent to child, but the offspring of less well-connected parents can usually gain access to allies and helpers more readily than a landless son in a farming community can acquire land, for example, through savings or systems of patronage. As a result we expect the intergenerational transmission of relational wealth to be limited, at least by comparison with material wealth.

Embodied wealth is transmitted by a combination of genetic inheritance, socialization, and parent-offspring similarity in the conditions affecting childhood development. The knowledge component of embodied wealth is readily transmitted to offspring, but, unless restricted by religious or other constraints, it is typically available to other members of a population as well (the common knowledge of the behavior of prey species, for example, or farming practices). Genetic and psychometric evidence from industrial societies suggests that parent-offspring transmission of economically relevant personality and behavioral characteristics, such as risk-taking, trustworthiness, conscientiousness, and extroversion is limited (*4*). We do not have similar evidence across generations in the small-scale populations under study, but industrial-society estimates support our expectation that the degree of intergenerational transmission will differ markedly among our three wealth classes, with substantial transmission of material wealth and more limited transmission of relational and embodied wealth.

Ethnographic evidence suggests that the four economic systems also differ in the importance of

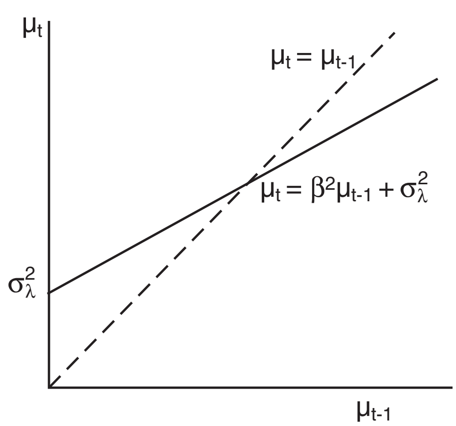

Fig. 2. Steady-state wealth distribution. The dashed line is the steady-state condition requiring wealth inequality to be unchanging from one period to the next. The solid line (Eq. 2) is the combined effect of this period's variance of shocks (the constant) augmented by the inequalities in wealth transmitted from the previous period (the slope).

Table 2. Summary statistics: Intergenerational transmission of wealth (β), by economic system and wealth class. Cell-means were estimated in a regression against a full set of dummy variables for each cell, with conventional standard errors. See (*4*), section 1, for a discussion of alternative approaches to estimating these cell-means and their standard errors, and tables S11 and S12 for the alternative results. Reported *P* values correspond to two-tailed tests of the hypothesis that the true β or Gini coefficient is zero for that cell. Averages across wealth classes (final two columns) are calculated after weighting the cell-mean β values and Ginis by the values of α shown. NA, data not available.

Economic systems		Wealth classes			α-weighted average of β values	α-weighted average of Ginis
		Embodied	Relational	Material		
Hunter-gatherer	α	0.46	0.39	0.15		
	β	0.16 ± 0.06	0.23 ± 0.11	0.17 ± 0.011	0.19 ± 0.05	0.25 ± 0.04
	P	0.01	0.04	0.12	0.00	0.00
Horticultural	α	0.53	0.26	0.21		
	β	0.17 ± 0.05	0.26 ± 0.11	0.09 ± 0.09	0.18 ± 0.04	0.27 ± 0.03
	P	0.00	0.02	0.31	0.00	0.00
Pastoral	α	0.26	0.14	0.61		
	β	0.07 ± 0.15	NA†	0.67 ± 0.07	0.43 ± 0.06†	0.42 ± 0.05†
	P	0.66		0.00	0.00	0.00
Agricultural	α	0.27	0.14	0.59		
	β	0.10 ± 0.07	0.08 ± 0.11	0.55 ± 0.07	0.36 ± 0.05	0.48 ± 0.04
	P	0.16	0.47	0.00	0.00	0.00
Average across all economic systems	α	0.38	0.23	0.39		
	β	0.12 ± 0.05	0.19 ± 0.06	0.37 ± 0.04	0.29 ± 0.03	0.35 ± 0.02
	P	0.01	0.00	0.00	0.00	0.00

†The β and Gini for Kipsigis cattle partners (see Table 1 and table S4) are used in the pastoral/relational cell for the calculation of the α-weighted average across wealth classes.

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the three classes of wealth. A successful hunter-gatherer or horticulturalist depends heavily on his or her strength, practical knowledge, and social networks, while making little use of material resources that are not in the public domain. By contrast, the well-being of a herder or farmer is closely tied to the amount of stock or land under his or her command, which makes material wealth a more important influence on livelihoods in these economic systems.

Estimating the intergenerational transmission of wealth. To estimate our model of wealth transmission, we need two pieces of information: the degree of intergenerational transmission (β) for each wealth type and the importance of each wealth class in a given economic system ($\alpha \equiv \{e, m, r\}$). Note that we do not require identification of the causal paths by which transmission takes place, as might be represented in a multiequation structural model (*15*). Our model instead requires a single estimate of the magnitude of the statistical association between parental and offspring wealth (β) for each data set. This requirement, along with the absence of robust evidence of nonlinearities, motivated our consistent use of linear models. Functional forms, estimation procedures, robustness checks, weighting procedures, and other aspects of our statistical techniques and results are described in (*4*), section 1. Note that the populations studied were not selected at random; instead, we included all populations we were aware of for which intergenerational wealth transmission estimates are feasible and the researchers agreed to share data. Table 1 presents our individual estimates of β; Table 2 presents the summary statistics for both the intergenerational transmission (β) and the importance (α) of the three wealth classes in the four economic systems.

Across the four economic systems, the estimated β for 14 measures of material wealth, including agricultural and horticultural land, livestock, shares in sea mammal–hunting boats, quality of housing, and household utensils averages 0.37 (Table 2). For farm land (5 data points), the degree of transmission is substantial, averaging 0.45 (calculated from the data in Table 1), thus equaling or exceeding the intergenerational transmission of most forms of wealth in modern industrial economies (*16*). Livestock are even more highly transmitted across generations (Table 1, β values averaging 0.66).

Our 23 estimates of the transmission of embodied wealth across generations average 0.12. The highest estimates are for body weight (for which β averages 0.37). We also find a very modest level of intergenerational transmission of reproductive success (number of offspring surviving to age 5); it is entirely absent in three societies, has a maximum value of 0.21, and averages 0.09, similar to low correlations between parental and offspring fertility in many pre-demographic transition populations (*17*). Grip strength is weakly transmitted across generations. The transmission of hunting success is highly variable (0.08 for the Ache, 0.38 for the horticultural Tsimane, and 0.05 for hunting and foraging yields in the Hadza), averaging 0.17. Knowledge and skill, such as the production and management of horticultural crops in the Pimbwe or proficiency in subsistence tasks and cultural knowledge in the Tsimane, are only weakly transmitted from parents to offspring.

The six estimates of relational wealth transmission indicate that the extent to which network links are transmitted across generations is modest, averaging β = 0.19.

To measure the importance of each wealth class in the four economic systems (α) we used ethnographers' judgments (for each wealth class in the population they studied) of the percentage difference in household well-being associated with a 1% difference in the amount of a given wealth class, holding other wealth classes constant at the average for that population, and requiring these percentage effects to sum to one. The average values of α by wealth class and economic system also appear in Table 2. Consistent with descriptive ethnographies of these and other populations, embodied and relational wealth are relatively important for hunter-gatherers, whereas material wealth is key in pastoral and agricultural populations.

Statistical estimates of the importance of each class of wealth across the economic systems (α) would have been preferable, but are precluded by the absence for most populations of a single relatively homogeneous measure of well-being. However, we were able to econometrically estimate *m*—the importance of material wealth—from an equation similar to (4) using data (most of it from half a century ago) from populations not represented in our study, including one horticultural, two pastoral, and seven small-scale agricultural economies. These estimates [see (*4*) section 1] are close to our ethnographers' estimates and suggest that, if anything, we have understated the difference in the importance of material wealth between pastoral and agricultural economies, on the one hand, and horticultural economies on the other. Correcting this understatement would only strengthen our main conclusions.

Results. Our first finding is that the α-weighted averages of the β values (the importance-weighted average transmission coefficients) for the four economic systems differ markedly (Table 2). Intergenerational transmission of wealth is modest in hunter-gatherer and horticultural systems and substantial in agricultural and pastoral systems. However, even the smaller β values of the former imply that being born into the top 10% of the wealth distribution confers important advantages. In these societies, a child of parents in the highest wealth decile is on average more than three times as likely to end up in the top decile as is the child of the bottom decile [(*4*), section 3 and table S7]. Although hardly a level playing field, intergenerational transmission in these economic systems is modest when compared with the agricultural systems, where the child of the top decile is on average about 11 times more likely than the child of the poorest decile to end up in the richest decile, or to the pastoral systems, where the ratio exceeds 20.

Our second finding is that economic systems in which wealth is more heritable are indeed more unequal, as predicted by our model. For each population and type of wealth, we estimated the Gini coefficient, which is a measure of inequality ranging from 0 (equal wealth) to approximately 1 [all wealth held by a single household, see table S4 and discussion in (*4*), section 1]. To calculate an overall measure of wealth inequality for a given economic system we again weight the results for each wealth class in that system by its importance (α). These estimates of overall wealth inequality appear in the last column of Table 2, and in more detail in table S5. They exhibit the same pattern as the transmission coefficients (β values): hunter-gatherer and horticultural populations are both relatively egalitarian; pastoral and agricultural societies are characterized by substantial wealth inequality (see also fig. S2).

A third finding is that neither the overall intergenerational transmission of wealth nor the level of inequality is greater in horticultural than in hunter-gatherer populations. This result challenges a long-standing view (*18*) that foragers are uniquely egalitarian among human societies. Thus, it may be ownership rights in land and livestock, rather than the use of domesticated plants and animals per se, that are key to sustaining high levels of inequality. Our finding that pastoralists transmit wealth across generations to an extent equal to if not greater than farmers, and likewise display similar Gini coefficients, will also challenge widely held views that herders are relatively egalitarian (*19*).

Are the relative intergenerational mobility of the hunter-gatherer and horticultural systems and the high levels of intergenerational wealth transmission of the pastoral and agricultural systems due primarily to technology (the differing importance of the distinct classes of wealth across economic systems) or to institutions (differences in intergenerational transmission, independent of differences in the importance of the wealth classes)? To answer this question, we take advantage of the fact that both the importance of the wealth classes and degree of intergenerational transmission of wealth are similar in the hunter-gatherer and horticultural populations, on the one hand, and the pastoral and agricultural populations on the other. This allows us to reduce the four systems to two. Forty-five percent of the large (namely 0.21) and statistically significant difference ($P < 0.001$) between the average α-weighted β values of these two groups of economic systems is accounted for by differences in technology, reflected primarily in the greater importance of material wealth in producing the herders' and farmers' livelihoods [for the decomposition formula, see (*4*) section 1; for the paired economic systems results, see table S3]. The remaining 55% is due to differences in institutions, reflected primarily in the lesser degree of transmission of material wealth in the

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horticultural and hunter-gatherer populations. Thus, although differences across economic systems in both the importance of the wealth classes and in the heritability of a given class of wealth matter, the latter is somewhat more strongly associated with differences in the extent of wealth transmission across generations, and hence the generation of inequality. This is our fourth finding.

Note that for the intergenerational transmission of wealth, the effects of technology and institutions are complementary rather than simply additive. Econometric analysis (table S13, column 2) shows that this joint (superadditive) effect of material wealth and agricultural or pastoral economic systems in the intergenerational transmission of wealth is statistically robust, even when a fixed-effects regression is used to control for all unobserved population-level characteristics (such as the distinct inheritance and marital systems and other institutional structures of the populations).

Not surprisingly in light of our fourth finding, additional econometric analysis [described in section 5 of (*4*)] shows that both wealth class and economic system significantly and independently predict the level of wealth inequality: material wealth types, and pastoral and agricultural societies, display higher Gini coefficients (table S13, column 3). Moreover, the greater inequality in material wealth is robust to the inclusion of fixed effects to control for unobservable population-level variation (table S13, column 4).

A final finding is that, in the populations studied, the more important forms of wealth are more highly transmitted across generations: The simple correlation between the 43 β values listed in Table 1 and the corresponding population and wealth-class specific α values listed in table S1 is 0.48 ($P = 0.001$). This is consistent with the view that parents differentially transmit to their offspring the forms of wealth that are most important in that society (*20*). This is most striking in the case of material wealth. In pastoral and agricultural societies, its average importance (α) is 0.60 and the average transmission coefficient (β) is 0.61; in hunter-gatherer and horticultural populations, the values, respectively, are 0.18 and 0.13 (calculated from Table 2, and see tables S2 and S4). Similarly, the less important forms of wealth in agricultural and pastoral systems (embodied and relational wealth) display significantly lower β values.

We implemented two robustness checks to make sure, first, that our results are not driven merely by the qualitative estimates of α provided by the ethnographers and, second, that these estimates are themselves plausible. The first is the above decomposition of the effects of economic system and wealth class, which shows that a substantial difference (more than half of that estimated) between economic systems in aggregate wealth transmission across generations would exist even under the unrealistic assumption that the importance of the wealth classes does not differ across economic systems. The second check is provided by our econometric estimates of the importance of material wealth mentioned above. Note that differences between the estimates of the importance of the two nonmaterial types of wealth (e and r) are modest, and that $e + m + r = 1$, so we may group embodied and relational wealth, whose importance we measure by $1 - m^*$, where m^* is the average of our econometrically estimated coefficients for material wealth in pastoral (0.84), agricultural (0.57), and horticultural (0.23) production. (We use the last-mentioned figure also for hunter-gatherers and in light of their evident similarity with horticulturalists.) Using these weights, rather than those estimated by the ethnographers, gives results similar to Table 2 [(*4*) section 5], but with even greater differences in the intergenerational transmission of wealth between the agricultural and pastoral economies, on the one hand, and the hunter-gatherer and horticultural economies, on the other.

Discussion. Our principal conclusion is that there exist substantial differences among economic systems in the intergenerational transmission of wealth and that these arise because material wealth is more important in agricultural and pastoral societies and because, in these systems, material wealth is substantially more heritable than embodied and relational wealth. By way of comparison, the degree of intergenerational transmission of wealth in hunter-gatherer and horticultural populations is comparable to the intergenerational transmission of earnings in the Nordic social democratic countries (*5*)—the average β for earnings in Denmark, Sweden, and Norway is 0.18—whereas the agricultural and pastoral societies in our data set are comparable to economies in which inequalities are inherited most strongly across generations, the United States and Italy, where the average β for earnings is 0.43. Concerning wealth inequality, the Gini measure in the hunter-gatherer and horticultural populations is almost exactly the average of the Gini measure of disposable income for Denmark, Norway, and Finland (0.24); the pastoral and agricultural populations are substantially more unequal than the most unequal of the high-income nations, the United States, whose Gini coefficient is 0.37 (*21*).

Our model explains some seeming anomalies, such as substantial wealth differences in those hunter-gatherer populations whose rich fishing sites can be defended by families or other corporate groups and transmitted across generations and which constitute an atypically important form of material wealth for those societies (*22*). Our findings also provide evidence for the view—widely held among historians, archaeologists, and other social scientists—that some influences on inequality are not captured simply by differences in technology, as measured by our α values. For example, the marked hierarchies among some Australian foragers may be due to polygyny (*23*), elite possession of ritual knowledge (*24*) that may be transmitted intergenerationally, or even to the dynamics of food sharing (*25*). Similarly, the fact that some agricultural and pastoral societies do not exhibit substantial levels of economic inequality despite their characteristic forms of wealth being in principle heritable (*26*, *27*) suggests the importance of deliberate egalitarianism, as well as other cultural influences and political choices (*28*). Examples include the lavish funeral feasting that redistributes the wealth of the elite among the Tandroy and other cattle pastoralists in Madagascar (*29*) and elsewhere (*26*). Other examples are the Nordic social democratic polities mentioned above.

One may speculate on the basis of these results that the current trend toward a knowledge-based economy that is less reliant on material wealth and more reliant on embodied and relational wealth might in the long run be associated with a concomitant reduction in intergenerational wealth transmission. But the importance in our data set of economic systems per se as a determinant of the dynamics of inequality suggests that the implications for inequality of this shift in how humans make a living will depend critically on our institutions.

References and Notes

1. A. Atkinson, in *Studies in Deprivation and Disadvantage: Parents and Children: Incomes in Two Generations*, A. B. Atkinson, A. K. Maynard, C. G. Trinder, Eds. (Heinemann Educational Books, London, 1983), pp. 94–114.
2. G. S. Becker, N. Tomes, *J. Polit. Econ.* **87**, 1153 (1979).
3. S. Bowles, H. Gintis, *J. Econ. Perspect.* **16**, 3 (2002).
4. Materials and methods and supporting text are available as supporting material on *Science* Online.
5. A. Bjorklund, M. Jantti, in *Oxford Handbook of Economic Inequality*, W. Salverda, B. Nolan, T. Smeeding, Eds. (Oxford Univ. Press, Oxford, 2009), pp. 491–521.
6. T. Hertz *et al.*, *B. E. J. Econ. Anal. Policy* **7**, 10 (2007).
7. D. Nettle, T. Pollet, *Am. Nat.* **172**, 658 (2008).
8. J. E. Pettay, L. E. B. Kruuk, J. Jokela, V. Lummaa, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 2838 (2005).
9. D. F. Roberts, W. Z. Billewicz, I. A. McGregor, *Ann. Hum. Genet.* **42**, 15 (1978).
10. F. Galton, *Natural Inheritance* (Macmillan, London, 1889).
11. J. Coleman, *Foundations of Social Theory* (Harvard Univ. Press, Cambridge, MA, 1990).
12. T. W. Schultz, *Am. Econ. Rev.* **51**, 1 (1961).
13. H. Kaplan, *Yearb. Phys. Anthropol.* **39**, 91 (1996).
14. A. W. Johnson, T. Earle, *The Evolution of Human Societies: From Foraging Group to Agrarian State* (Stanford Univ. Press, Palo Alto, CA, ed. 2, 2000).
15. S. Bowles, *J. Polit. Econ.* **80**, S219 (1972).
16. K. K. Charles, E. Hurst, *J. Polit. Econ.* **111**, 1155 (2003).
17. M. Murphy, *Soc. Biol.* **46**, 122 (2007).
18. J. Woodburn, *Man (Lond)* **17**, 431 (1982).
19. H. K. Schneider, *Livestock and Equality in East Africa: The Economic Basis for Social Structure* (Indiana Univ. Press, Bloomington, IN, 1979).
20. J. Hartung, *Curr. Anthropol.* **23**, 1 (1982).
21. A. Brandolini, T. Smeeding, in *The Oxford Handbook of Economic Inequality*, W. Salverda, B. Nolan, T. Smeeding, Eds. (Oxford Univ. Press, Oxford, 2009), pp. 71–100.
22. B. Hayden, *The Pithouses of Keatley Creek* (Harcourt Brace College Publishers, New York, 1997).
23. H. Kaplan, J. Lancaster, in *Offspring: Human Fertility Behavior in Biodemographic Perspective*, K. W. Wachter, R. Bulatao, Eds. (National Academies Press, Washington, DC, 2003), pp. 170–223.
24. I. Keen, *Curr. Anthropol.* **47**, 7 (2006).
25. K. Hawkes, in *Hierarchies in Action: Cui Bono?* M. W. Diehl, Ed. (Southern Illinois Univ. Center for Archaeological Investigations, Occasional Paper 27, 2000), pp. 59–83.

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26. M. Bollig, *Risk Management in a Hazardous Environment* (Springer, New York, 2006).
27. P. Wiessner, *Curr. Anthropol.* **43**, 233 (2002).
28. C. Boehm, *Hierarchy in the Forest* (Harvard Univ. Press, Cambridge, MA, 2000).
29. M. Parker Pearson, *The Archaeology of Death and Burial* (Sutton, Stroud, UK, 1999).
30. K. Hill, A. M. Hurtado, *Ache Life History: The Ecology and Demography of a Foraging People* (Aldine de Gruyter, Berlin, 1996).
31. F. W. Marlowe, *The Hadza* (Univ. of California Press, Berkeley, CA, in press).
32. P. Wiessner, in *Politics and History in Band Societies*, E. Leacock, R. Lee, Eds. (Cambridge Univ. Press, Cambridge, 1982), pp. 61–84.
33. M. Alvard, D. Nolin, *Curr. Anthropol.* **43**, 533 (2002).
34. E. A. Smith, R. B. Bird, D. W. Bird, *Behav. Ecol.* **14**, 116 (2003).
35. R. Quinlan, *Am. Anthropol.* **108**, 464 (2006).
36. R. Sear, F. Steele, I. A. McGregor, R. Mace, *Demography* **39**, 43 (2002).
37. M. Borgerhoff Mulder, *Hum. Nat.* **20**, 130 (2009).
38. M. Gurven, H. Kaplan, A. Zelada Supa, *Am. J. Hum. Biol.* **19**, 376 (2007).
39. M. Borgerhoff Mulder, *Hum. Ecol.* **20**, 383 (1992).
40. I. Fazzio, *Parental Investment Among Arab and Dazagada Herding Societies of West Chad* (VDM Verlag Dr Müller, Berlin, 2008).
41. R. McElreath, *Am. Anthropol.* **106**, 308 (2004).
42. W. Irons, *The Yomut Turkmen: A Study of Social Organization Among a Central Asian Turkic-Speaking Population* (Univ. of Michigan Museum of Anthropology, Ann Arbor, MI, 1975).
43. D. L. Leonetti, D. C. Nath, N. S. Heman, D. B. Neill, in *Grandmotherhood: The Evolutionary Significance of the Second Half of the Female Life*, E. Voland, A. Chasiotis, W. Schiefenhoevel, Eds. (Rutgers Univ. Press, New Brunswick, NJ, 2005), pp. 194–214.
44. M. K. Shenk, *Hum. Nat.* **16**, 81 (2005).
45. G. Clark, *A Farewell to Alms: A Brief Economic History of the World* (Princeton Univ. Press, Princeton, NJ, 2007).
46. M. Borgerhoff Mulder, *Curr. Anthropol.* **36**, 573 (1995).
47. E. Voland, *Behav. Ecol. Sociobiol.* **26**, 65 (1990).
48. B. S. Low, A. L. Clarke, *J. Fam. Hist.* **16**, 117 (1990).
49. The authors declare no competing interests. Financial support for this research was provided by the Behavioral Sciences Program of the Santa Fe Institute, the Russell Sage Foundation, and the NSF. We would like to thank the participating members of the populations we studied for their cooperation and M. Alexander, W. Cote, P. Lindert, C. Resnicke, T. Taylor, D. Ulibarri, and H. Wright for their contributions to this research.

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29 June 2009; accepted 29 September 2009
10.1126/science.1178336

The Crystal Structure of the Ribosome Bound to EF-Tu and Aminoacyl-tRNA

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The ribosome selects a correct transfer RNA (tRNA) for each amino acid added to the polypeptide chain, as directed by messenger RNA. Aminoacyl-tRNA is delivered to the ribosome by elongation factor Tu (EF-Tu), which hydrolyzes guanosine triphosphate (GTP) and releases tRNA in response to codon recognition. The signaling pathway that leads to GTP hydrolysis upon codon recognition is critical to accurate decoding. Here we present the crystal structure of the ribosome complexed with EF-Tu and aminoacyl-tRNA, refined to 3.6 angstrom resolution. The structure reveals details of the tRNA distortion that allows aminoacyl-tRNA to interact simultaneously with the decoding center of the 30*S* subunit and EF-Tu at the factor binding site. A series of conformational changes in EF-Tu and aminoacyl-tRNA suggests a communication pathway between the decoding center and the guanosine triphosphatase center of EF-Tu.

The ribosome is the macromolecular enzyme that synthesizes proteins using aminoacyl-tRNA substrates, as directed by an mRNA template. To faithfully translate the genetic information contained in mRNA, the ribosome must select cognate tRNA by its ability to base pair with the mRNA codon, a process termed "decoding." Elongation factor Tu (EF-Tu), a translation factor with ribosome-dependent guanosine triphosphatase (GTPase) activity, delivers aminoacyl-tRNAs to the ribosome in a ternary complex (TC) of aminoacyl-tRNA•GTP•EF-Tu (where GTP is guanosine triphosphate) and plays an active role in ensuring the fidelity of decoding. Understanding the interplay between the TC and the ribosome that leads to the accurate translation of the mRNA message has been an active area of research for more than three decades.

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Biochemical experiments have provided a wealth of information about the multistep process of tRNA discrimination by the ribosome. Initial binding of TC occurs independently of mRNA (*1*), after which codon-anticodon pairs are sampled at the decoding center of the 30*S* subunit. Correct codon-anticodon matching induces conformational changes in three 16*S* nucleotides—A1492, A1493, and G530 (*Escherichia coli* numbering, see table S1)—that monitor the geometry of the minor groove in the codon-anticodon helix (*2*) and accelerate the forward rate of selection (*3*). Binding of a near-cognate tRNA does not induce these changes (*4*), explaining why initial tRNA selection is more accurate than can be accounted for by the energetic differences between matched and mismatched anticodons alone (*5*). In addition to simple codon-anticodon base pairing, physical properties of the tRNA body are also important for faithful decoding (*6*–*11*). Finally, the binding energy of a cognate tRNA is used to make an important domain closure of the 30*S* subunit (*4*), moving the "shoulder" domain closer to the TC (*12*).

The signal that codon recognition has occurred must then be transmitted to the GTPase center of EF-Tu. The ribosome could stimulate GTP hydrolysis using two strategies: (i) by positioning catalytic residues in EF-Tu for GTP hydrolysis and (ii) by providing ribosomal components that function directly in catalysis. Domain 1 of EF-Tu is responsible for nucleotide binding, and rearrangements in this domain result in the opening of the hydrophobic gate, composed of residues Val^{20} in the P loop and Ile^{60} in switch I, which before activation prevents access of the catalytic His^{84} to GTP (*13*). Mutation of His^{84} results in a 10^5 decrease in the rate of GTP hydrolysis by EF-Tu, and this residue is thought to position and activate a water molecule to hydrolyze GTP (*14*). Ribosomal components implicated in GTPase activity include the sarcin-ricin loop (SRL) of 23*S* ribosomal RNA (rRNA), located adjacent to the nucleotide binding pocket of EF-Tu (*15*), ribosomal protein L7/L12, which stimulates hydrolysis 2500-fold (*16*), and the L11 protein and proximal rRNA (*17*).

Hydrolysis of GTP and release of inorganic phosphate (P_i) by EF-Tu leads to lowered affinity for aminoacyl-tRNA and release from the ribosome. tRNA is then either accommodated into the peptidyl transferase center or rejected via a "proofreading" mechanism (*18*, *19*). Proofreading and initial selection are separated by irreversible GTP hydrolysis, and their multiplicative effect accounts for the high accuracy of decoding (*3*, *20*). Despite the wealth of biochemical data, the transmission of codon recognition to the GTPase center and the activation of GTP hydrolysis is not well understood.

Crystal structures of EF-Tu and TC have been determined for complexes with guanosine diphosphate (GDP) and GTP analogs, as well as a variety of antibiotics [(Protein Data Bank identification code 1OB2) (*13*, *21*, *22*) and references therein]. Isolated structures of EF-Tu revealed the global conformational change of domain 1 that occurs upon transition between the active (GTP) and inactive (GDP) states of the protein (*13*). The

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