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Author for correspondence:
Alexandra Alvergne
e-mail: alexandra.alvergne@anthro.ox.ac.uk

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Ecological variation in wealth–fertility relationships in Mongolia: the 'central theoretical problem of sociobiology' not a problem after all?

Alexandra Alvergne[1,2,3] and Virpi Lummaa[2]

[1]School of Anthropology and Museum Ethnography, Oxford University, Oxford OX2 6PE, UK
[2]Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK
[3]Harris Manchester College, Oxford OX1 3TD, UK

The negative wealth–fertility relationship brought about by market integration remains a puzzle to classic evolutionary models. Evolutionary ecologists have argued that this phenomenon results from both stronger trade-offs between reproductive and socioeconomic success in the highest social classes and the comparison of groups rather than individuals. Indeed, studies in contemporary low fertility settings have typically used aggregated samples that may mask positive wealth–fertility relationships. Furthermore, while much evidence attests to trade-offs between reproductive and socioeconomic success, few studies have explicitly tested the idea that such constraints are intensified by market integration. Using data from Mongolia, a post-socialist nation that underwent mass privatization, we examine wealth–fertility relationships over time and across a rural–urban gradient. Among post-reproductive women, reproductive fitness is the lowest in urban areas, but increases with wealth in all regions. After liberalization, a demographic–economic paradox emerges in urban areas: while educational attainment negatively impacts female fertility in all regions, education uniquely provides socioeconomic benefits in urban contexts. As market integration progresses, socio-economic returns to education increase and women who limit their reproduction to pursue education get wealthier. The results support the view that selection favoured mechanisms that respond to opportunities for status enhancement rather than fertility maximization.

1. Introduction

The effect of resource availability on human reproduction presents a major empirical challenge to evolutionary ecology theory. Classical evolutionary models predict that fertility trade-offs are alleviated by resource availability, and this is supported by fertility increasing with status and economic wealth in men within pre-industrial human populations (reviewed in [1–4]; but see [5] for a more nuanced conclusion on income–fertility relationships) and by maternal energy availability being strongly associated with ovarian function and the duration of lactational amenorrhoea [6,7]. However, the relationship between resource availability and fertility appears negative both between contemporary populations as well as within post-industrial populations [1,8–14] (but see [15] for a positive relationship using a sample of university employees; see [16,17] for a positive relationship when childless individuals are excluded; and for a complex relationship between wealth and the transition to first, second and third births, see [18]). In addition, in most post-transitional populations, high-status groups have reduced their fertility first [4]. Despite such contradictions, evolutionary ecologists argue that optimality models are still valid for understanding this 'central theoretical problem of [human] sociobiology' [9,19] (i.e. that resource availability or wealth does not translate into higher fertility in post-industrial populations). Broadly, they propose a framework within which wealth–fertility relationships result from an evolved flexible cognitive response to the strength of life-history trade-offs between fertility and investment in own and offspring capital (i.e. including somatic, cultural, economic and social) [1,10,20,21]. This framework leads to several hypotheses as to why a 'demographic–economic paradox' may emerge, which have implications for predicting the type of cues (cost of rising children, women socio-economic mobility) individuals respond to when adjusting their reproductive decisions.

A main prediction from the evolutionary framework is that the negative relationship between wealth and fertility results from a covariation between the wealth of a group and the perceived returns to parental investment in that group [22–24]. In this line, the negative effect of family size for educational attainment is stronger among the highest social classes in both developing and developed populations [23,25–27]. It follows that if one compares individuals within groups that are homogeneous for the strength of fertility trade-offs (i.e. individuals within rather than between socio-ecologies), a positive relationship between wealth and fertility will be unmasked [14,22]. However, the empirical investigation of this theoretical framework is incomplete, as only a few studies have considered a multi-level perspective for understanding how market integration shapes the relationship between resource access and reproductive decision-making (but see [18]). Moreover, this approach may become insufficient if the variance in wealth increases so much as to prevent any meaningful grouping.

Most recent studies have focused on the strength of the trade-off between offspring number and offspring fitness (the quantity–quality trade-off, following [28]) across various socio-ecologies [23,27,29–33]. Yet concentrating on total family size may limit uncovering how decision-making relates to fertility transitions if fertility drivers and outcomes are disconnected: individuals may not typically target a specific fertility early in life and then achieve it, but rather make multiple and sequential decisions across the life course that lead to the observed fertility outcomes [18]. The quantity–quality trade-off is thus best understood as the sum of all time-dependent trade-offs between current and future reproduction experienced across life [1,12,34]. By focusing on age-specific decisions and the pay-offs of delayed (rather than total) investment in reproduction, this perspective allows exploring the possibility that a paradox emerges not because rich parents reduce their fertility to invest more in each offspring but because individuals who delay fertility become wealthier.

Later childbearing has long been associated with increased educational participation [35–38]. Studies in various contexts show that women trade off education with the onset of motherhood: increase in the time spent at school, either due to a change in schooling laws (e.g. in the UK [39]) or a reduction in the cost of education (e.g. in Kenya [40]), is associated with reduced teenage fertility and later age at first birth (see also [41]). This trade-off will generate a negative relationship between wealth and fertility if, as the society transits from a subsistence to a skills-based society, wage differentials by educational levels increase [10,42] and individuals with high levels of education become more likely to be employed and to earn more [10]. In this ecology, women who delay their first birth to invest in their own capital may become richer, either directly through their eligibility for higher wages [1,34] and/or indirectly, through educational homogamy [43].

We use evolutionary ecological theory to investigate variation in wealth–fertility relationships among women living in Mongolia, using data from the 2003 national reproductive health survey, which covers all regions of the country. We first use a multi-level framework to investigate wealth–fertility relationships. Specifically, we compare the relevance of this approach for understanding variation in (i) lifetime reproductive success (LRS) among post-reproductive women and (ii) the adoption of contraceptive methods among women of reproductive age. In doing so, we compare individuals within and between regions along a rural–urban gradient. Urban development is here taken as a proxy for market integration as cities tend to operate as the 'wheels' of capitalism [44]. Second, to better understand how market integration may eventually create a 'demographic–economic paradox', we investigate the possibility that a negative wealth–fertility relationship emerges in urban areas as a result of increased returns to educational level in women (i.e. increased trade-offs between fertility and women's socio-economic success), in terms of educational assortative mating and/or household wealth after marriage.

There are several reasons why Mongolia is a particularly suitable context for undertaking this study. First, Mongolia has recently rapidly undergone a drastic economic transition after 70 years of socialism. After the election of the first democratic government in March 1990 and the subsequent pressure from international donors and market economists to administer a 'shock therapy' (1990–1992), the liberalization of prices and the large-scale privatization of publicly owned enterprises took place rapidly: 'by the mid-1990s, the wealthiest 20 percent of the population were having eighteen times the income of the poorest 20 percent' [45, p. 59]. Second, the role of differential access to services in explaining regional variation in fertility is minimized (see Material and methods for changes across time). As the sovereignty of Mongolia was recognized by the United Nations in 1961, standards of living were improved, leading to an efficient delivery of social and health services [46]. Finally, women's contraceptive behaviour is likely to represent women's decision-making as Mongolian women have experienced a significant degree of autonomy for some time. One invoked reason is the gender imbalance that resulted from the success of Lamaism, introduced in the mid-sixteenth century. By the end of the nineteenth century, this Tibetan form of Buddhism had enrolled one-third of the entire male population. It followed that 'The rampant sexual promiscuity of turn-of-the-century Mongolia produced a large number of households headed by single mothers whose children had no clear patrilineal identification, the flip side of which was that Mongolian women enjoyed a significant degree of economic independence and sexual freedom' [46, p. 6] (see also [47]). This independence is likely to have been relatively unchallenged during communist times due to the promotion of gender equality in socio-economic status [46].

2. Material and methods

(a) The ecology of Mongolia

Mongolia is located in central Asia and borders the Russian Federation to the north and the People's Republic of China to the south. According to the 2000 population and housing census, it has a population of 2.4 million people; of which 95.7% are Mongols and 4.3% are Kazakhs. Mongolia is one of the least densely populated countries (1.8 people km^{-2} in 2010) and, in 2004, 35% of Mongolian families were nomadic herders and 45% were working in the animal husbandry sector [48]. Animal husbandry has been the dominant economic pursuit of the Mongols for centuries, although its form (type of animals, size of herd) was influenced by the demands of political regimes [48].

Since the establishment of the 'Mongolian People's Republic' in 1924 and for approximately 70 years, the USSR was the patron and protector of Mongolia and socialism was the dominant political influence [45]. Following the collapse of USSR, the authoritarian communist government stepped down in 1990. In 1992, a new constitution established freedom of speech, assembly, separation between the state and religion, among other things [45]. This democratization was associated with processes of intense privatization and commercialization. If there was an increase in industrial production owing to natural and mineral resource extraction, it did not compensate for closing the industries of the communist era, and unemployment and poverty rose [45]. With the cessation of Russian subsidies, prices increased while salaries remained low. Unemployment combined with the rise of vodka industries led to sharp increases in alcoholism, domestic abuse and divorce [45]. By the mid-1990s, more than 6000 street children appeared in Ulaanbaatar [45].

Over the last century, the demography of Mongolia has been characterized by a slow growth rate until the 1950s, followed by a rise until the 1970s (total fertility rate, TFR = 7.5) and then a gradual decline. It has been argued that changes in fertility and mortality were mostly influenced by ecological constraints, such as the availability of maternal services, rather than pronatalist policies [47]. The slow growth rate of the early twentieth century has been attributed to the high occurrence of venereal diseases promoting infertility and high mortality. After the Second World War, the construction of venereal hospitals and the availability of antibiotics have coincided with a rise in fertility and declines in maternal and infant mortality [47]. This was before pronatalist policies were in place. From the 1970s on, although after their introduction, fertility declined. The incentive to reduce fertility might have resulted from the emergence of compulsory education, which increased the cost of children (less help for labour at home) [47]. By the onset of the economic transition towards capitalism, TFR was less than 5 in most parts of the country. Bans on contraception and abortion were relaxed, and TFR declined from 4.3 children per woman in 1990 to 2.1 in 2006 [47].

The impact of market integration on women's health and education was mixed. On the one hand, the pronatal policy implemented from 1970 to 1990 (with abortion illegal until 1989) led to high rates of maternal mortality. On the other hand, as part of the pronatal policy, women benefited from maternity leave and childcare services. After market integration, the high dependency on international donor agencies led to the privatization of health services and higher education [45]. The introduction of fees for maternal services and the government's reduction in childcare assistance created an important trade-off for women, who had to either quit their job or pay for childcare [45]. Those changes affected population growth: from approximately 1960 to 1990, the annual growth rate was above 2%, but from around 1990 onwards, it fell below 2% [49].

(b) Data

The data have been extracted from the 2003 Reproductive Health Survey (RHS) [50], which was carried out by the National Statistical Office of Mongolia during the cold season to take advantage of immobility. It was funded by the UNFPA, which provided assistance in the field. The RHS is a nationally representative sample of 8399 households (representing 1.47% of all households of the country) and includes data on 9382 women aged 15–49 and 4212 husbands. The survey includes data on household amenities, conditions, income and expenditure, and individual socio-demographic characteristics (age, education, religion, marital status, family planning attitude and use, a partial reproductive history considering the last three children, the total number of children born and the total number of children deceased). The survey was conducted using a two-stage sampling method that gives each household an equal probability of sampling. Two hundred and eighty clusters (sub-districts) were randomly sampled and stratified along a rural–urban gradient: remote rural areas, som centres (i.e. district capitals), aimak centres (province capitals) and the capital, Ulaanbaatar (electronic supplementary material, S1). Within each cluster, 30 households were selected and in each household, all women aged 15–49 were interviewed by one of the 10 teams with seven members. Before the survey, two pilot surveys on 90 and 60 households were conducted to test for understanding and reliability. After data collection, a post-enumeration survey (n = 1192) was conducted to assess the validity of the data collection process, data coverage and content errors.

At the time of the survey, there is evidence of a demographic transition (low fertility and low infant and child mortality): TFR is lower in urban areas (1.9 children per women) than in rural areas (2.9); infant mortality rate is relatively low at 3% of births and child mortality (1–4 years) is 0.5%. Most women want to limit their family size, and among women with three survived children, 85% indicated that they wanted no more children. Knowledge of contraceptive methods is virtually universal among Mongolian women (99%). In 2003, there is a high approval of contraception among wives (96%) and their husbands (90%) [50]. Among women who have ever used a birth-control method (75% of all women and 92% of currently married women), 65.5% have used modern methods, preferentially IUD (33%), pill (11%) and injection (10%); 34.5% of women have only ever used traditional methods, periodic calendar abstinence being the most common (reported by 92.6% of women).

As a proxy for economic wealth, we used average income per person in a household, which was estimated from various housing characteristics (household amenities and condition) and by asking the household head about spending, debt and income per person. In the analyses, household wealth is transformed into a binary variable by grouping the first three levels of wealth (the 'poor') and the remaining levels together (the 'rich'). This is because the sample size of some levels is too low in some areas (electronic supplementary material, S1). Similarly for education, data indicating no education and grades 1–3 have been pooled together (electronic supplementary material, S1). To consider generational effects, the median date of birth was used to create two cohorts.

(c) Statistical inference

(i) General procedure

We conducted five analyses (electronic supplementary material, S2). In all the cases, we used multi-level modelling to consider the hierarchical structure of the data and the associated non-independence of observations within geographical clusters. A multi-level model corresponds to a regression in which the regression coefficients are given a probability model [51]. Each level (cluster and individuals) is attributed a variance component. Specifically, we used multi-level models with varying intercepts (random effects), which enable us to consider variation at both the cluster and individual levels. For each analysis, we built models including variables of interest—'Area' (four levels: remote rural, som centre, aimak centre, ulaanbaatar) and 'Wealth' (two levels: rich and poor; see previous section)—and variables found to be influential in other studies, such as 'Cohort', 'Age', 'Marital Status' (six levels: single, married, living together, divorced, separated, widowed) and 'Religion' (five levels: Buddhist, Muslim, Christian, atheist, other). To investigate ecological variation in the relationships investigated, we systematically compared full models with and without interaction effects between the variable of interest and the variable 'Area' and retained the model with the lowest AIC. Influence diagnostics were performed and the normality of the residuals was checked graphically. To infer

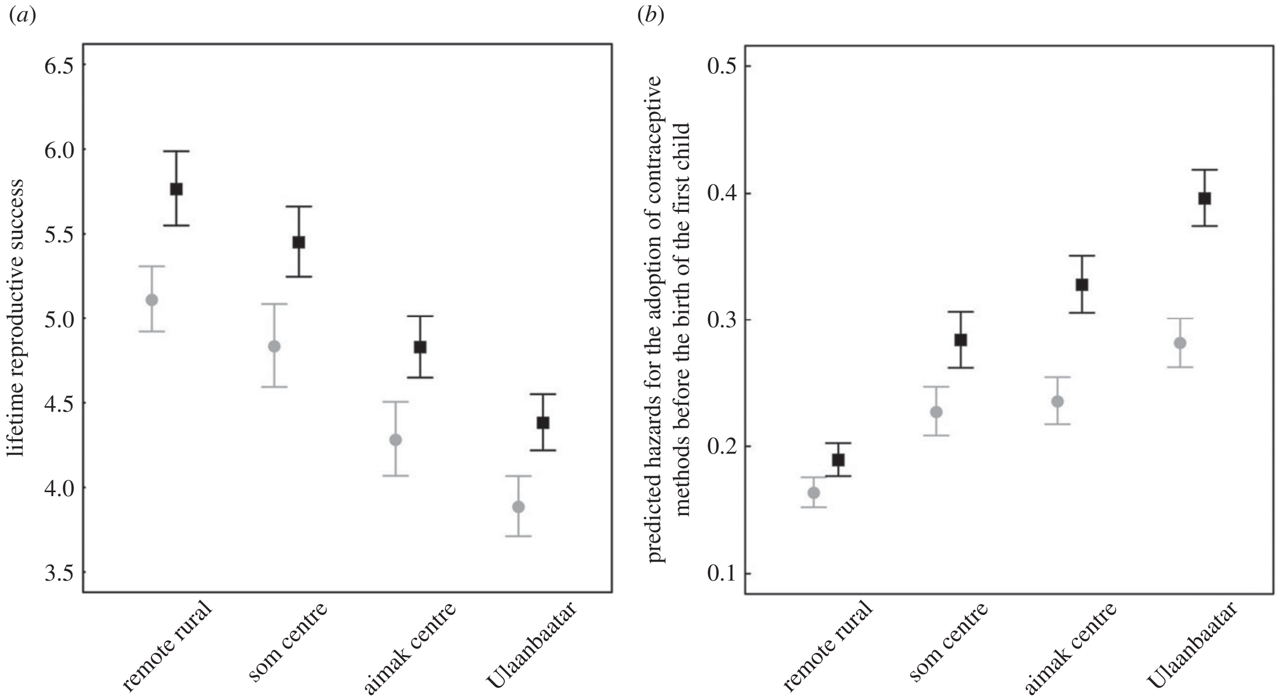

Figure 1. Household wealth and reproductive outcomes along a rural–urban gradient. (*a*) Predicted means (and s.e.) for LRS among post-reproductive women (older than 45 years; $n = 815$). LRS is 12% higher among the wealthiest in all regions. (*b*) Predicted hazards (and s.e.) for the adoption of contraceptive methods before the birth of the first child ($n = 9314$). Wealthy women are more likely to adopt contraceptive methods (either modern or traditional) before the birth of their first, second and third child, and particularly so in urban areas. Values are reported for married women, atheists and born after 1967. Squares represent women living in rich households and circles represent women living in poor households.

the size and uncertainty of the effects of variables of interest, we used likelihood (LL) ratio tests and reported 95% confidence intervals. Analyses were carried out using R software (version 2.11.0) and the package lme4 [52].

(ii) Specific analyses

In analysis (3a), we modelled LRS (the number of children who survived to age 5) as count data using a Poisson error structure; the data were not over-dispersed (observed variance/theoretical variance = 0.86). We restricted our sample to post-reproductive women (older than 45 years) whose last birth occurred before 1998 ($n = 815$). In analysis (3b), we ran a discrete time hazard model to assess the risk of adopting contraceptive methods at a given parity (i.e. number of children alive) conditional of the absence of adoption of any method before that age ($n = 21\,393$ records from 9314 women). We used this approach because our data are right censored (22% of women had never use contraceptive methods by the time of the survey). We used a logistic regression to regress the event indicator (adoption of contraceptive methods) on the time indicator (number of children alive) and included a group level effect for cluster. We considered 0 children to be the start of the risk period. We modelled the time indicator as a categorical variable with multiple intercepts [53]. In analysis (3c(i)), we investigated the negative relationship between education and fertility. Because the relationship is two-ways, we ran two analyses. First, in (3c(i)-1), we modelled age at first birth as a function of educational level. We ran a discrete time hazard model to assess the risk of birth at a given age conditional of no births before that age ($n = 75\,189$ records from 9314 women; 2219 women had not reproduced by the time of the survey). We used a logistic regression to regress the event indicator (first birth) on the time indicator (number of years since 15 years old) and included a group level effect for cluster. Fifteen years was chosen to be the start of the risk period because sex might have occurred before marriage. To model the time indicator variable, we compared a full model including time as a categorical variable with multiple intercepts to models with polynomial specifications for time (of order 2, 3, 4 and 5) [53]. This is because the hazard is expected to be near zero in many time periods and a full model would include too many parameters (greater than 20) for the inclusion of three-way interactions. We retained the model with the lowest AIC, which includes a four-order time specification (electronic supplementary material, S2). In analysis (3c(i)-2), we modelled the probability of currently attending school using a multi-level model with binomial error structure. We limited the sample to women aged 15–24 years (maximum age attending school) and excluded those who reported stopping school because of distance (16%), in order to avoid the confounds of geographic constraint. This left a total sample of 2722 (42.7% currently attending school). In our subsample, 32.4% had reproduced at least once at the time of the survey (mode = 1; max = 5). Our variable of interest was 'reproductive status' (binomial; has reproduced or not). In analysis (3c(ii)), we investigated women's socio-economic success by modelling household wealth using a binomial error structure ('rich' and 'poor'). To measure success by household wealth, we restricted our sample to married women living in households headed by their husbands ($n = 5428$) as it indicates that women have moved to live with their husband after marriage.

3. Results

(a) Does household wealth predict lifetime reproductive success among post-reproductive women?

Among post-reproductive women who started off their reproductive career during the socialist era, the total number of living offspring or LRS is 4.16 ($\pm$s.d. = 1.82). In both rural and urban areas, LRS is 13% higher among the wealthiest (OR[95CI] = 1.13[1.05;1.21]; LL ratio test, $\chi^2 = 10.5$, d.f. = 1, $p < 0.01$; figure 1*a*; electronic supplementary material, S2; $n = 815$). However, as compared with remote rural areas, LRS is 24% (OR[95CI] = 0.76[0.69;0.83]) lower in urban areas. Thus, in line with the prediction from evolutionary ecological theory [1,14,22], if fertility is lower in urban areas, household wealth positively predicts fertility within all areas. The analysis included marital status, religion and age. *Post hoc* analyses revealed that the effect of wealth on LRS is not driven by differences in child mortality but differences in fertility: the effect of wealth remains unchanged when the number of deceased children is entered in the model (OR[95CI] = 1.13[1.05;1.21]), but disappears when the number of births is entered (OR[95CI] = 1.02[0.94;1.10]).

(b) Does household wealth predict contraceptive behaviour among women of reproductive age?

The analysis of the relationship between household wealth and the number of children after which women first use contraception considers both traditional and modern methods of contraception among reproductive-aged women. The results show that women start using birth-control methods at a lower parity in privileged households as compared with poorer households (LL ratio test; $\chi^2 = 15.4$, d.f. = 6, $p = 0.02$; $n = 9314$). The effect of wealth on contraceptive behaviour is observed in all areas but is stronger in cities (LL ratio test; $\chi^2 = 14.7$, d.f. = 3, $p < 0.01$; figure 1*b*; electronic supplementary material, S2): in remote rural areas, poor women are roughly 16% less likely to use contraceptive methods before the birth of their first child (OR[95CI] = 0.84[0.71;0.99]; approx. 20% less likely before their second (OR[95CI] = 0.79[0.67;0.93]) and third child (OR[95CI] = 0.80[0.66;0.98])). In the capital, poor women are 29% less likely to use contraceptive methods before the birth of their first, second or third child (OR[95CI] = 0.71[0.59; 0.86]). The results deviate from classical evolutionary ecological models, as the demographic–economic paradox is not only observed between areas but also within areas.

(c) Is market integration associated with increased trade-off between fertility and socio-economic success?

Women started to limit their fertility earlier in their reproductive careers in cities and this was more pronounced among women living in the wealthiest households. We thus investigated the possibility that it resulted from market integration increasing the trade-off between fertility and socio-economic status. We first explored the two-way negative relationship between fertility and investment in own education among women of reproductive age. We then examined if delaying and/or reducing fertility to devote more time to educational level returns better success in terms of economic wealth among married women. Note that educational resources have been accessible in all regions for approximately 40 years at the time of the survey, leading to an extremely high literacy rate for a developing country (96.9%). In 1985, 63.1% of the students in higher educational institutions were women (70.7% in 1998 [46]).

(i) Fertility and educational level

Age at first birth was found to increase with educational level in all areas (analysis 3c(i)-1; $n = 9314$; figure 2*a*; electronic supplementary material, S2). When women are aged 15–24 years old (the maximum age at which women attend school in the data), those with the highest level of education are less likely to give birth to their first child than highly educated women (all odds < 1). After 25 years of age, the relationship inverses (all odds > 1). The role of education in modulating the speed at which women give birth to their first child does not vary across the urban–rural gradient. Rather, whatever the level of education, the odds of starting to reproduce is 17% (OR[95CI] = 0.83[0.76;0.90]) lower in urban as compared with rural areas, which suggests that those women who remain childless by the time of the survey are concentrated in cities ($n = 923$ in Ulaanbaatar, $n < 489$ in other areas).

Second, we focused on the probability of currently attending school and its relationship to the reproductive status of women at the time of the survey (analysis 3c(i)-2; $n = 2722$; women aged 15–24). Women who have already reproduced by the time of the survey were 63% less likely to currently attend school than those who had not (OR[95CI] = 0.37[0.23;0.58]; figure 2*b*; electronic supplementary material, S2) and the strength of this negative relationship does not vary with the level of urbanization (LL ratio test greater than 0.1). The results may indicate that fertility bears a cost for investment in one's own education (causation) or that women who get pregnant relatively early are also more likely to drop out of school due to, for example, difficult socio-economic situation (correlation). Note that the analysis is controlled for wealth and marital status. Overall, those results demonstrate that negative relationships between fertility and educational level are of similar strength across regions.

(ii) Socio-economic returns to education

The role of educational level for predicting wealth varies with area ($n = 5428$; LL ratio test; $\chi^2 = 43.55$, d.f. = 15; $p < 0.001$). The relationship between women's educational and household wealth is three times stronger in urban areas: as compared with women with no education, women with the highest level of education are around four times more likely to live in the wealthiest households in remote rural areas (OR[95CI] = 4.69[2.52;8.73]), and 12 times more likely in Ulaanbaatar (OR[95CI] = 12.31[1.29;117.91], figure 3; electronic supplementary material, S2). The effect of this interaction decreases when the husband's level of education is included in the model (LL ratio test; $\chi^2 = 32.80$, d.f. = 15; $p < 0.01$), which suggests that the link between women's education and household wealth is partly driven by assortative mating for education. *Post hoc* tests revealed that there is indeed educational assortative mating ($\chi^2 = 2951.9$, d.f. = 16, $p < 0.001$). One may argue that educated women are coming from wealthy families who invested more in their 'quality' in the first place. This effect is likely to be reduced in Mongolia as compared with other ecological settings as most women of reproductive age in 2003 were attending school during the socialist era when wealth inequality was minimal. Yet that wealthy individuals are more likely to receive education may partially account for participation in higher education as fees were introduced in 1993, and 33% of higher education students are enrolled in private institutions. However, it can only be a partial account and does not concern participation to primary and secondary education, for which there are no fees [54]. Overall, the results suggest that market integration increases the positive relationship between the level of education and resource acquisition. This is in line with people's perception:

> Sweeping? I started this job two months ago. [. . .] Before I was a cleaning lady in a hospital. You know, with no higher education

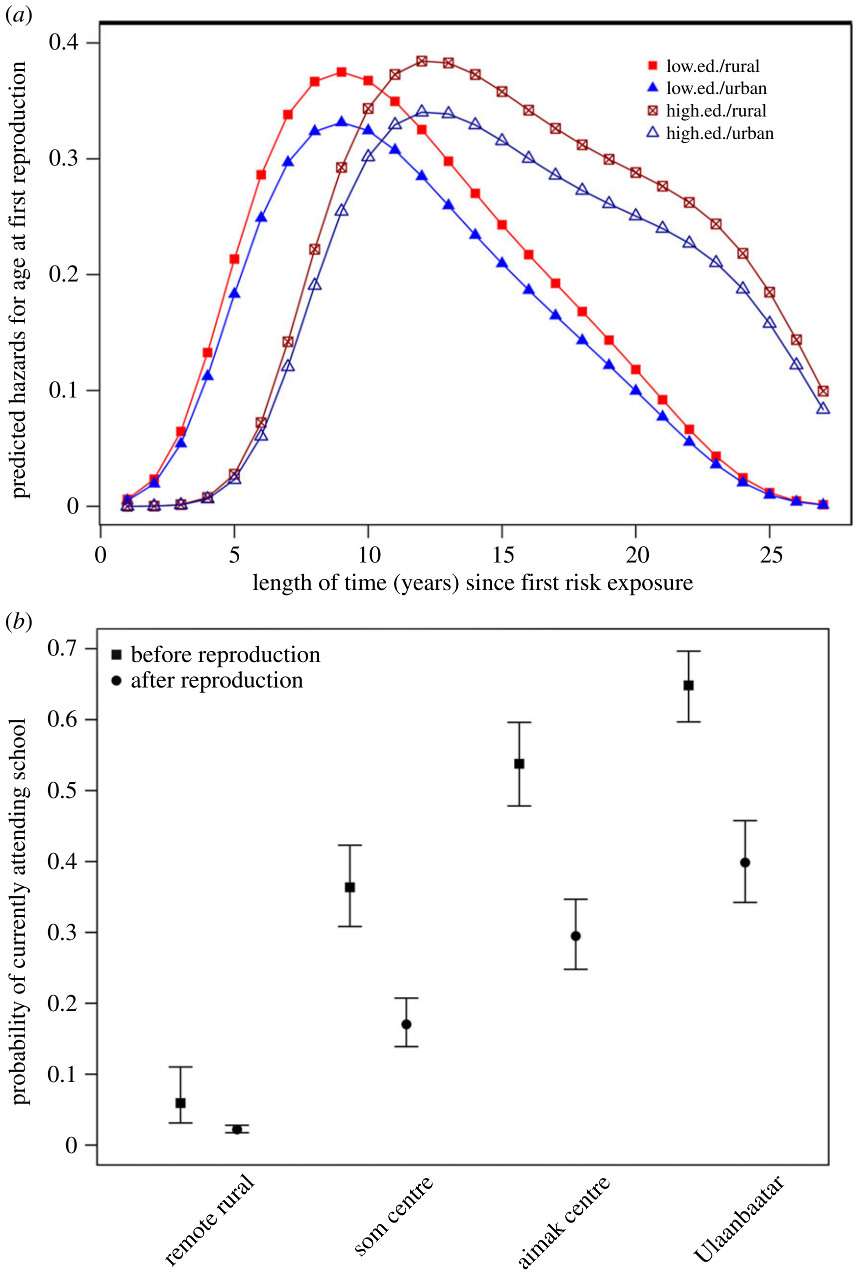

Figure 2. The relationship between educational level and fertility. (*a*) Predicted hazards (and s.e.) for age at first birth ($n = 9314$). The time to the first birth increases with educational level. Time 0 corresponds to age 15, the beginning of the period of risk exposure. As compared with women with lowest level of education, women with the highest level are less likely to have reproduced before the age of 25 years (time = 10; odds = 0.93), but more likely to have given birth to their first child after that time (time = 11, odds = 1.06). (*b*) Probability of school attendance (women aged 15–24, $n = 2722$). Predicted means (and s.e.). Women are approximately 63% less likely to be currently attending school once they have reproduced. Values are reported for women aged 20, married and atheists. (Online version in colour.)

> I couldn't hope to get a better job. [...] I live [...] in the gertown on the edge of Ulaanbaatar. [...] Before the market economy started, four years ago, my salary was enough to get by on. The main reason was that food prices were lower. [...] I'm not well educated—I can't do any of these small enterprises jobs they talk about on my own [...] My daughters will do better, that is my hope. [55, pp. 16–19].

4. Discussion

Evolutionary life-history models posit that fertility is constrained by ecological trade-offs between investments in life-history components, of which strength is alleviated by resource availability. While this framework is insightful for understanding how reproductive physiology responds to resource availability [7], the extent to which existing models account for how reproductive decision-making responds to change of economic mode of production remains unclear. We used data from Mongolia, where liberalization started roughly 24 years ago, to examine variation in the relationship between household wealth and fertility across time and along an urban–rural gradient. The evolutionary ecological perspective was found to have two main insights in accounting for the observed patterns. The first lies in the multi-level perspective to consider that the cost of fertility for investment in offspring capital increases with level of development [14,22]. This revealed that among post-reproductive women, while absolute fitness is the lowest in richest areas (i.e. the cities), within areas, fitness increases with household wealth. The second insight resides in the life-history framework that underpins evolutionary ecological models. By focusing on sequential decision-

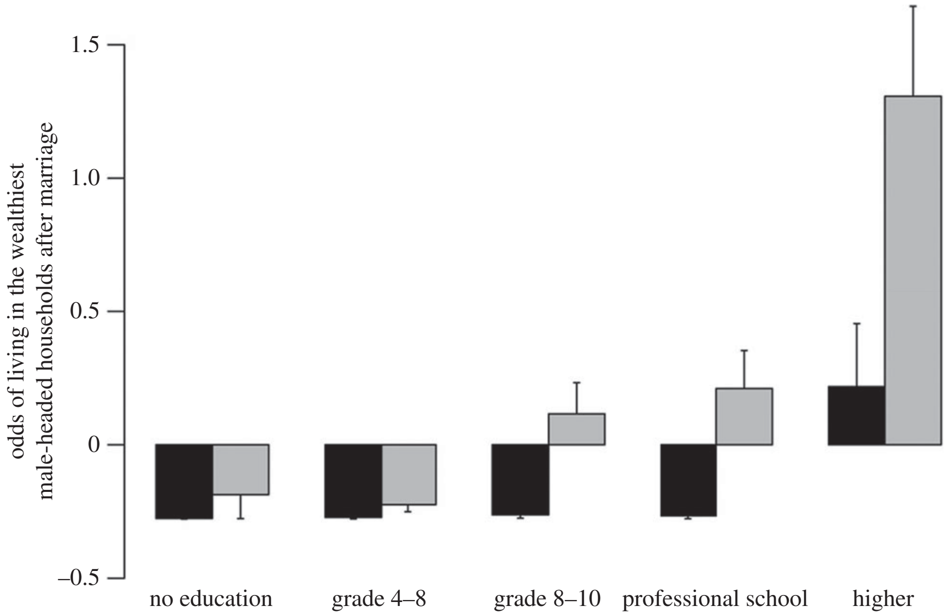

Figure 3. Ecological variation in the socio-economic returns to educational level among married women ($n = 5428$). Predicted odds (and s.e.). The average wealth of household headed by husbands is used as a proxy for how education translates into socio-economic returns. In Ulaanbaatar (grey bars), educational level is positively correlated with household wealth, and women with the highest level of education are 12 times more likely to live in wealthy households as compared with women with no education. In rural areas (black bars), women with the highest level of education are four times more likely to live in rich households. The 'returns' of education are partly mediated by educational assortative mating.

making as opposed to the sum total of decisions (i.e. total family size), one can decipher what motivates reproductive decisions across an individual lifetime. We found that increased capital returns to delaying reproduction for investment in education best explain why a demographic–economic paradox emerges in cities after liberalization.

The multi-level perspective reveals a positive relationship between wealth and LRS among women who had terminated their reproductive career by the time of the survey, but among women of reproductive age living in urban areas, the wealthiest were more likely to start using contraception at a low parity. Given that post-reproductive women mostly reproduced before market integration while women of reproductive age reproduced during and after market integration, the results suggest that the direction of the wealth–fertility relationship reversed during the transition to a capitalist economy. In other parts of the world where such reversal is observed, it is generally interpreted as a response to increased trade-offs between offspring number and offspring capital. Here we argue that such reversal results from an increase in the opportunity cost of fertility for investment in own capital. As the privatization of maternal and educational services created a trade-off between investment in education and child care, a concomitant increase in the value of education to acquire wealth increased the opportunity cost of fertility. Stated otherwise, a negative wealth–fertility relationship is observed if those delaying reproduction to get educated are more likely to achieve wealth. This is supported by a negative wealth–fertility relationship only emerging in areas where education yields socio-economic 'returns' to women (i.e. urban areas). It echoes the fertility limitation–social capillarity hypothesis of French demographer Dumont, according to which having too many children impedes the 'ambitious' and constitutes 'burdensome luggage' for climbing the social ladder [56].

The results show that investment in education is traded off with reproduction in all areas but yields further capital only in urban environments. Capital returns to female education can be direct, if education leads to employment prospects, and/or indirect, through better marriage expectation and social mobility [57]. The emergence of socio-economic returns to education reflects both the rise of inequality in human capital and an increase in the role of education for promoting wealth differentials. Education is central for competing in the market economy, and by 1998, one-third of the 'poor' had not terminated their secondary education, while among the 'rich', only 18% had not completed a secondary education [58]. The extent to which education increases status may differ across socio-political settings, depending on the economic cost of education enrolment, the wage differentials brought about by educational level and the opportunity for educated individuals to achieve upward mobility. Variation in the relationship between education and status returns may explain discrepancy across studies conducted in different urban environments. For instance, while household wealth predicts a higher incentive to regulate fertility in urban areas of Mongolia, it differs from the context of Addis Ababa, where better-off women were found to have shorter birth intervals [59]. Thus, in some parts of sub-Saharan Africa, capital returns to investment in education may not outweigh the cost of low fertility in terms of loss of status for women. Most developing programmes focus on education enrolment to promote lower fertility and economic growth. Rather, our findings suggest that one should favour the socio-economic returns to education for promoting upward mobility and lower fertility.

The pursuit of education at the expense of fertility raises the question as to whether natural selection has favoured predispositions that maximize wealth rather than fertility [27,60]. There have been several accounts as to why predispositions for resource acquisition or status quest [61] may have been favoured. Boone & Kessler [60], for instance, propose that the maximization of wealth through fertility reduction can be explained as part of an evolved strategy that maximizes the long-term survival of lineages, as the wealthier families are less likely to face lineage extinction during demographic crashes. In this line, low fertility in transitional Sweden did not maximize the number of great grand-offspring but rather increased lineage wealth [27]. The conditions under which delayed fertility results in larger lineage persistence are limited [1], however, and low fertility is most probably maladaptive [1,11,27]. Yet, status-seeking strategies may have been favoured by natural selection if status translated into reproductive success across evolutionary times [62]. One must then consider how economic transitions influence the type of resource (physiological, cultural, economic) that yields the highest competitive advantage in the local environment [20]. In pre-industrial economies, cultural norms such as socially imposed monogamy and primogeniture have allowed wealthy groups to secure both long-term resources and fertility. Conversely, in skills-based societies where status is best achieved at the expense of fertility through time investment in the accumulation of cultural capital, a 'demographic–economic paradox' may emerge [10,42]. Our results are in line with such suggestions that reproductive decision-making responds to opportunities for status enhancement rather than fertility maximization.

Why is a negative wealth–fertility relationship not a central theoretical problem for evolutionary approaches to human behaviour, as often claimed [9,19]? Whether or not low fertility is adaptive (i.e. increases future lineage persistence) tells us little about the evolved mechanisms (i.e. resulting from past selective pressures) underlying reproductive decisions. It is also not surprising that individuals are not perfectly adapted to their environment if ecologies are changing fast. Rather, evolutionary demography provides a framework for deciphering the ecological cues individuals respond to when making reproductive decisions. Note that the hypothesis according to which individuals respond to changing returns to investment in own and offspring capital is not an exclusive explanation as various processes take over along the transition towards low fertility, in particular, the diffusion of ideals from the rich to the poor [5,63] (see also [33,64] for a comparison of evolutionary models).

Our results indicate that the real or perceived increase in the socio-economic returns of education is likely to be a significant driver for the adoption of low fertility practices in women. Low returns of education as a result of poor schooling standards might contribute to explain why populations with access to lower-quality teaching show higher fertility, or why 'the poor' are less likely to use modern contraception, despite increasing access to these technologies [65]. We hope that our study will raise awareness about the role of opportunities brought about by education in triggering the spread of low-fertility norms.

Data accessibility. The data are available in electronic supplementary material, S3.

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