Original Article

Wealth modifies relationships between kin and women's fertility in high-income countries

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Kin are generally expected to behave more cooperatively with their relatives than with unrelated individuals, and this cooperative behavior may result in positive effects on fitness. Such kin effects are likely to be modified by resource availability: in contexts of resource stress, cooperation among kin may disappear or weaken as more energy is required for investment in self. We use the Generations and Gender Survey, a large, multinational demographic survey, to test the following: firstly, how kin availability measures (parental survival status and coresidence with parents) affect measures of women's fitness (timing of first birth, total fertility, and probability of childlessness); and, secondly, whether wealth (an indicator of resource stress or abundance) modifies kin effects in a high-income, low-fertility setting. We find differing effects of survival status of, and coresidence with, parents on fertility outcomes. Having a living mother tends to be correlated with higher fitness: women with living mothers have earlier first births, and mothers' death in early life is correlated with a higher probability of childlessness. Fathers' survival has no effect on any outcome. Coresidence with parents, on the other hand, delays first births and results in lower total fertility and higher probability of childlessness. We additionally find that the negative effects of coresidence on reproductive outcomes are exaggerated for poor women. Our results speak of the role of environment in modifying the relationship between kin and fertility.

Key words: **fertility, kin, low fertility, resource availability.**

INTRODUCTION

Helping behavior between kin is both expected, since the development of Hamilton's Rule in the 1960s (Hamilton 1964), and commonly observed. In some species, this cooperation takes the form of help during reproduction, that is, cooperative breeding (see Cockburn 1998 on birds; Solomon and French 1997 on mammals), which can be partly explained by the indirect fitness benefits helpers gain by raising related young (Clutton-Brock et al. 2001; Griffin and West 2003; Russell et al. 2007; Salomon and Lubin 2007). Though obligate cooperative breeding is rare among mammals, the order our own species belongs to is a relatively social order, and kin cooperation has been observed in a number of primate species (Paul 2005; Silk 2006). Further, help from kin has been shown to enhance the fitness of the helped individual across primate species, for example, by allowing higher reproductive rates (Hasegawa and Hiraiwa 1980; Ross and MacLarnon 2000; Pavelka et al. 2002). In humans, the availability of kin is positively correlated with fitness outcomes, including child survival and female fertility (see reviews in Sear and Mace 2008; Sear and Coall 2011), leading some to classify our species as cooperative breeders (Hrdy 2009). Variation in ecological context, however, may modify the effects of kin availability on reproductive outcomes (e.g., Borgerhoff Mulder 2007, in humans). Indeed, kin are not always expected to be cooperative. They may engage in competition, particularly where kin share the same resource base (Clark 1978; Silk 2006), thus diminishing fitness-enhancing effects. Empirically, the effects of kin on women's fitness are not universally positive (Voland and Beise 2005; Sear 2008; Sear and Coall 2011; Strassmann 2011; Strassmann and Garrard 2011).

In this study, we use a large demographic database to test the hypothesis that kin availability will increase women's fertility in a high-income, low-fertility (HILF) context (see also Hank and Kreyenfeld 2003; Kaptijn et al. 2010; Aassve et al. 2012; Waynforth 2012; Mathews and Sear 2013a, 2013b). We also test if and how individual variation in resource availability modifies the effect of kin on fitness outcomes, something not often done in HILF settings. We address 2 main questions:

1) (How) does maternal kin availability—measured by parental survival and coresidence—affect women's fitness in terms of timing of first birth, total fertility, and probability of childlessness?

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2) (How) does individual-level resource availability modify the effects of kin on women's fitness?

We first discuss the previous literature on ecological variation in kin effects, considering contexts in which kin cooperation or competition may occur. Second, we discuss briefly how kin availability is measured and the confounding factors that may muddle the interpretation of results gained from such measures.

Ecological variation in kin effects

Between species, the frequency of cooperation, including cooperative breeding, varies ecologically: one of the factors that influences whether species adopt this relatively rare breeding system is whether ecological conditions are such that the costs of helping are outweighed by the benefits (Stacey and Ligon 1991; Arnold and Owens 1999; Hatchwell and Komdeur 2000). Within species, ecological conditions also relate to patterns of cooperative behavior (Brown and Brown 1993a; Roberts et al. 1998; Canestrari et al. 2008; Eikenaar et al. 2010; Hatchwell et al. 2013): for example, carrion crows respond to enhanced territory resources by increasing their helping behavior at the nest (Canestrari et al. 2008). Behavioral ecologists working on our own species are very fortunate in both the amount of data available on human reproductive behavior and in the broad range of ecologies that humans inhabit; ecological variation in kin cooperation in humans is, therefore, becoming well documented. Although kin availability in both high- and low-fertility settings is often correlated with women's reproductive success (birth timings, child survival and health, total completed fertility, etc.: see summaries in Sear and Mace 2008; Sear and Coall 2011), the exact relationships show some variation among populations. The effects of kin are often positive on women's fitness, as expected due to shared fitness goals between women and their kin, but variation in environment may modify either the costs or the benefits of helping for kin such that kin presence may not result in increased fitness for an individual woman. Resource availability is one factor that may modify the effects of kin due to changing costs and benefits of helping (Clark 1978; Brown and Brown 1993a).

Theoretically, resource availability should enhance potential cooperation between kin, whereas scarcity should magnify competitive outcomes and diminish cooperative behavior (Brown and Brown 1993a, 1993b) as individuals find it harder to address their own needs and fitness interests (Wilson 2000). Empirically, this has been demonstrated in several species (e.g., rainbow trout: Brown and Brown 1993a; pathogenic bacteria: Griffin et al. 2004; and fig wasps: West et al. 2001). In humans, evidence of resource availability modifying the effects of kin on women's fitness measures comes from natural fertility settings: in a Kenyan patrilocal group (i.e., married women live with husbands' kin), paternal kin increase the survival of children more effectively in wealthy families than in poor families (Borgerhoff Mulder 2007). However, in a Tanzanian population, an interaction was found between the effects of socioeconomic status and kin availability on children's weight-for-age status, such that kin availability benefited children from poorer households more than those from wealthy households (Hadley 2004), suggesting that kin are not always detrimental in resource-stressed environments and may be able to buffer the effects of low socioeconomic status in certain contexts. This points to a need for additional studies of the interaction between wealth and kin availability, to clarify under what conditions kin may help and when they may hinder the reproductive output of their relatives. Further, although there is a large body of literature demonstrating that even

in HILF environments, there is competition within families for resources (Lawson and Mace 2011), modification of kin effects on women's reproductive outcomes by wealth in these settings is not well documented.

A potential complication with studying fertility in a HILF setting is that individuals do not seem to be optimizing their fitness; despite high country-level wealth, total fertility rates are extraordinarily low (Lesthaeghe and Willems 1999). However, reproductive decision making is still likely to be influenced by evolved mechanisms, even if total fertility levels are lower than what would be expected under the assumption of fitness maximization. Low fertility is frequently assumed by evolutionary anthropologists to partly result from the misfiring of evolved mechanisms in a novel environment, rather than to be entirely decoupled from fitness considerations (Borgerhoff Mulder 1998; Smith et al. 2001). Testing evolutionary hypotheses in low-fertility contexts is still a worthwhile endeavor, and evidence supports the suggestion that human behavior is still informed by evolved mechanisms even in such contexts (Lawson and Mace 2010), including empirical support for the hypothesis that kin availability increases fertility (Kaptijn et al. 2010; Mathews and Sear 2013a, 2013b). We, therefore, still expect to see women responding to previously fitness-enhancing cues such as kin availability when making reproductive decisions, even if they ultimately do not end up maximizing their fitness. A lack of kin support may even be part of the explanation for very low fertility (Barkow and Burley 1980; Turke 1989; Newson et al. 2005). Individuals may perceive that there is a lack of suitable support for raising children given the loosening of kin ties in industrialized societies and may therefore restrict their fertility even if they are relatively economically secure.

Measures of kin availability

Both parental survival and coresidence with kin are commonly used measures of kin availability in studies of human reproductive behavior (parental survival: Sear et al. 2000, 2003a; Voland and Beise 2002; Gibson and Mace 2005; Sear 2008; Mace and Colleran 2009; Sear and Mace 2009; coresidence: Morgan and Rindfuss 1984; Jamison et al. 2002; Tsay and Chu 2005; Snopkowski and Sear 2013), and we use these measures here. Both measures are generally assumed to indicate the presence of cooperative kin, but there are confounding factors that may mean that the interpretation of such measures is not straightforward, particularly for coresidence.

The availability of kin measured by parental survival may be indicative of kin cooperation but may also capture a healthy family effect because individuals within the same family share similar healthy genes and/or a healthy environment. Comparing correlations across different parents (mothers vs. fathers, as done here, or across maternal vs. paternal kin, as done by Sear et al. 2000, 2003a; Jamison et al. 2002; Voland and Beise 2002) and different outcomes, in addition to examining the timing of parental effects, is often done to try and exclude the possibility that such correlations are spurious. But even where alternative explanations can be excluded, parental survival does not indicate how kin may be supporting women—with allomaternal care, resource transfers, or emotional support.

Coresidence between kin may be a more reliable measure of kin availability than parental survival status as interactions between kin are essentially guaranteed. This measure has been frequently used as a proxy for kin cooperation (Morgan and Rindfuss 1984; Jamison et al. 2002; Tsay and Chu 2005; Snopkowski and Sear 2013). Coresidence has been shown to positively relate to cooperative behavior between parents and their adult children as measured

by providing childcare to grandchildren (Hank and Buber 2009; Smits et al. 2010; Heylen et al. 2012), and such childcare independently has been shown to positively affect women's fertility (Kaptijn et al. 2010; Aassve et al. 2012; Mathews and Sear 2013b). Extended coresidence with kin may, however, indicate poverty (particularly in contexts where adults are expected to maintain households separate from their parents, as has been typical in Western Europe for several centuries: Hanjnal 1982) and/or the need to support either a parent or child incapable of independent living (Choi 2003; Robila 2004), although, empirically, most supportive investments are from older to younger generations as predicted evolutionarily (White 1994; Choi 2003; Pollet and Dunbar 2008; Fingerman et al. 2011; Dykstra and Komter 2012).

METHODS

Data

To address our objectives, we use data collected between 2004 and 2010 by the Generations and Gender Program (GGP; http://www.ggp-i.org/), a collaboration between 11 European institutes with the purpose of improving policy in Europe (United Nations 2005). The data come from 19 high-income countries and include around 10 000 randomly selected participants per country. Sampling methods varied between countries, but effort was made to produce nationally representative samples. Though the purpose of the GGP is policy oriented, the data, collected through face-to-face surveys, include women's birth schedules and provide an excellent opportunity to test evolutionary hypotheses with larger sample sizes than usually available to behavioral ecological researchers. For this study, we use data for 26 787 women between the ages of 17 and 83 from 8 countries—Austria, Belgium, Bulgaria, France, Georgia, Lithuania, Norway, and Russia. Countries and individuals were included in our analyses based on the availability of our variables of interest (outlined below). Austrian data were only included in the timing of first birth model because women aged older than 46 were not surveyed in the country (only 6 women aged 46 years were surveyed, and all other participants were aged 45 years or younger). The total fertility and probability of childlessness models include all 7 other countries. Participants experienced 20 675 births, with parities ranging from 0 to 13. For those older than the age of 45 (assumed to be postreproductive), the average fertility was 1.83, which is in line with recent measures of completed family size in Europe (Myrskylä et al. 2013), and 14.09% of these women remained childless. Fertility varied between the countries we included; it is generally lower in eastern, and higher in northern, Europe. To account for the nonindependence of individuals' fertility outcomes within each country, all analyses outlined in the following section control for country with a random-effects term. All analyses were completed using STATA 12.

Fitness measures

Our study consists of 3 outcomes related to women's fertility—timing of first birth, total fertility, and probability of lifetime childlessness—which we use as proxies for fitness. Each outcome allows us to understand how kin affect different aspects of a woman's reproductive behavior at different points in her life.

Timing of first birth

The relationship between timing of first birth and kin availability was analyzed using random-effects discrete-time event-history analysis, which models the probability of a birth per unit time. Using discrete-time event-history analysis to analyze the timing of first birth offers 2 main benefits relative to using a linear regression with age at first birth as the outcome: 1) the model allows the inclusion of women who have not yet had a child (i.e., censored cases), which avoids biasing the analysis toward those women who have early births and 2) effects of predictors are allowed to vary over time (relevant for predictors such as kin availability because parental survival status and coresidence status both often change across the time period over which women are at risk of having a first birth) (Singer and Willett 1993). All women without missing data for our variables of interest were included in the analysis ($n = 26\ 787$). The dependent variable was a binary indicator of whether a first birth occurred for a participant in a given time interval (i.e., the analysis is based not on an individual-level data file, but a file in which each row represents a unit of time within a woman's life). Time was measured in years, and women were entered into the analysis at 15 years of age because few births occurred before this age. Time and time square were included in the model to control for the nonlinear relationship between age and probability of first birth. Interactions between time/time square and all predictors were included in initial models to test the proportional-hazards assumption of these models, and significant interactions were retained in the model.

Dates of both the first transition out of the parental home and parental deaths were available, so the independent variables coding for kin availability were time-dependent binary indicators of whether, at a given time point, 1) a woman's mother and 2) father were still alive and 3) she still lived with her mother and/or father. The time-varying coresidence variable captures only women's first transition from the parental home (i.e., women are considered noncoresident once they have left the parental home for the first time even if they later move back in) because later transitions tend to be related to hardships such as illness or change in either partnership or employment status (Grundy and Harrop 1992; Smits et al. 2010; Berrington and Stone 2013), the effects of which we do not wish to capture. The number of siblings was included to control for heritable fertility and/or fecundity, and this was modeled using a quadratic function because the correlation between number of siblings and probability of birth was not linear.

Resource availability is approximated by a wealth score created using factor analysis from a set of variables regarding women's possessions (whether she owned a second home, washing machine, digital video disk player, home computer, dish washer, and second car), whether the household can make ends meet, and whether the respondent had accrued savings. Due to the binary and categorical nature of these variables, a Pearson correlation matrix, from which factor analyses are generally run, was not appropriate (Child 2006). Rather, a polychoric correlation matrix was created under the assumption that the variables included herein represent a trait (wealth) that is continuously distributed among the people in the study population (Kolenikov and Angeles 2004; Howe et al. 2008; Kolenikov and Angeles 2009). A factor score was then created from the polychoric correlation matrix by country. Higher wealth scores represent higher wealth relative to fellow country residents. This single variable coding for wealth was then entered in the model, as were interactions between wealth and the kin availability variables.

In addition, several control variables were included in the model. At the participant level, these included a binary, time-varying indicator of partnership status (partnership was defined as coresiding with an unmarried or married partner), a categorical measure of

the highest level of completed education (1 = no school or primary only; 2 = secondary school; and 3 = postsecondary/tertiary), respondent age group, and a binary indicator of whether the respondent was in education at the time of interview. Country-level wealth was also included. An interaction term between living with parents and partnership status was included in the model because we expect partnership status to modify the effects of parents: women may need more help from parents if they lack help from a partner, for example.

The wealth and control variables were all collected as current status data, that is, women's wealth at the time of interview (not necessarily at the time of first birth) was included in the model (as is commonly done in the literature on socioeconomic status and fertility; see Weeden et al. 2006; Fieder and Huber 2007; Huber et al. 2010; Fieder et al. 2011; Barthold et al. 2012). In an attempt to account for any potential social mobility among women between their first births and their current status, we included a social mobility score. This was created by measuring the difference between women's educational achievement and that of their fathers. We calculated the mean for educational attainment for different age groups and then, for both women and their fathers, we calculated the standard deviation from the mean for educational attainment for their age group. The fathers' values were subtracted from those of their daughters to obtain the social mobility score.

Total fertility

Total fertility at the time of the survey was modeled using a random-effects Poisson regression, as the outcome is a count variable. Women aged older than 45 years, presumed to be postreproductive, were included in the model if data for key variables were not missing (n = 12 910). Mother's survival status was measured with a categorical variable, coded for the age of the woman when her mother died. Women who were older than the age of 45 when their mother died or whose mothers were still alive at the survey date were used as a reference category. A variable for father's survival status was created similarly. The age at which women left their natal home was included as a categorical variable. Those who exited the natal

home prior to the age of 15 years were the reference category. The oldest category, women who exited the natal home after the age of 30 years, included the very small number of women who still lived with their parents at the time of interview (n = 161). Women's age and age square were included in the model, as was a binary variable indicating whether the respondent had ever had a partner. As in the first birth models, number of siblings and number of siblings square, education, wealth, country wealth, and social mobility were also controlled for. An interaction between wealth and the age at which women left their natal home was included to address our second objective.

Probability of childlessness after age 45

Probability of childlessness was analyzed using a random-effects logistic regression. The binary dependent variable indicated whether respondents were childless at the age of 45 years. The sample included only women older than 45 years at the time of interview for whom we had all variables of interest (n = 12 910). The predictors in this model were identical to those in the total fertility Poisson regression model (above).

RESULTS

Women typically followed a predictable sequence of life events, starting with exiting the parental home (median age: 20 years), gaining a cohabiting partner (median age: 22 years), and then reproducing (median age: 24 years) (Table 1). There is some variation among countries in the timing of this sequence, but in all countries, the median of these transitions occurs within 2–6 years of one another, and the transitions are always in the order described. Median ages at the time of death of mothers and fathers differed by 9 years between countries; the medians for all countries combined was 45 years at mother's death and 36 years at father's death. The median education of respondents was 2, indicating secondary school, across wealth quartiles and countries. Average number of siblings ranged from 1.6 in Bulgaria to 2.9 in France, with total mean of 2.3.

Table 1

Descriptive data for key variables used in the analysis by wealth quartiles

	Wealth quartile				
	Lowest	Low	High	Highest	Total
Median age (in years)[a] at					
Leaving natal home	20	20	20	20	20
First partnership	21	21	22	22	22
First birth	23	23	24	25	24
Mother's death	46	44	44	44	45
Father's death	37	36	35	38	36
Education (%)					
No education/primary education	17.7	8.6	8.8	9.8	11.1
Secondary education	58.3	55.8	45.8	48.2	51.5
Postsecondary/tertiary education	24.0	35.6	45.3	42.0	37.4
Number of siblings (%)					
1	26.9	38.8	42.0	33.4	35.0
2	24.5	24.0	24.8	27.6	25.5
3	17.0	14.2	12.2	16.0	15.0
4	11.0	8.5	7.4	8.1	8.7
5	7.7	5.2	4.6	4.4	5.4
6+	12.9	9.4	9.1	10.5	10.5
Social mobility (mean)	0.05	0.08	0.14	0.16	0.12

[a]Calculated using censored cases.

Fertility outcomes

The results of all 3 fertility models are presented in Table 2, as either odds ratios (ORs, for the analysis of the timing of first birth and the probability of childlessness) or incidence rate ratios (IRRs, for the Poisson model of number of children). Values greater than 1 represent a higher likelihood of the outcome (i.e., earlier first births, more children, or higher probability of childlessness), and values less than 1 represent lower likelihood of the outcome. The table includes a measure of intraclass correlation (ρ or α in Table 2) for each model. In all cases, this value is very small, indicating that the variation in each fertility outcome within countries is rather small. We tested for differences between countries in the effects of our predictors and found no

evidence to suggest that predictor variables behaved differently in different countries.

Coresidence with parents was correlated with delayed first births: in the analysis of first births, women who were still resident with their parents had much lower odds of a birth per unit time than did those who had left the parental home (OR = 0.11; $P < 0.001$). Women who remained coresident with parents longer also had lower completed fertility and higher probability of childlessness after age 45 years than those who left the parental home early. The results of both the total fertility and probability of childlessness models suggested a roughly linear relationship between coresidence and the fertility outcomes, in that the longer the woman remained resident with her parents, the lower was her completed fertility

Table 2

Results from random-effects models for timing of first birth (discrete-time event history analysis), total fertility (Poisson regression), and childlessness (logistic regression)

Variable	Timing of first birth[a]			Total fertility[b]			Probability of childlessness[b]		
	OR	95% CI		IRR	95% CI		OR	95% CI	
Resources									
Wealth	0.46**	0.41	0.51	1.06	0.97	1.15	0.74	0.49	1.10
Kin and partners									
Has partner	18.87**	16.50	21.58						
Has had partner				1.98**	1.84	2.13	0.07**	0.06	0.08
Ref.: Ended coresidence before age 15									
16–20				1.07	0.96	1.19	0.74	0.44	1.24
21–25				0.99	0.89	1.11	0.88	0.51	1.50
26–30				0.91	0.79	1.05	1.30	0.69	2.43
>30				0.69**	0.59	0.80	4.64**	2.64	8.18
Ref.: Not coresiding with parents									
Coresiding with parents	0.11**	0.09	0.12						
Ref.: Mother dead									
Mother alive	1.14**	1.06	1.23						
Ref.: Age at mother's death >45 years									
<10				0.98	0.87	1.09	1.29	0.80	2.09
10–19				0.96	0.88	1.05	1.56*	1.09	2.25
20–24				1.01	0.92	1.10	0.99	0.65	1.50
25–29				0.97	0.90	1.05	1.07	0.75	1.54
30–34				1.03	0.97	1.10	0.97	0.71	1.32
35–39				1.00	0.95	1.05	1.16	0.91	1.48
40–44				0.99	0.95	1.04	0.99	0.80	1.22
Ref.: Father dead									
Father alive	1.02	0.97	1.07						
Ref.: Age at father's death >45 years									
<10				1.05	0.94	1.16	0.98	0.61	1.55
10–19				0.96	0.91	1.02	1.24	0.97	1.58
20–24				1.00	0.94	1.06	1.20	0.92	1.58
25–29				1.00	0.95	1.05	1.10	0.86	1.40
30–34				1.03	0.98	1.08	0.91	0.73	1.14
35–39				0.99	0.94	1.03	1.04	0.85	1.27
40–44				1.03	0.99	1.07	0.87	0.71	1.05
Interactions									
Wealth × coresidence	1.24**	1.16	1.32						
Coresidence × partner status	2.43**	2.25	2.62						
Ref.: Wealth × ended coresidence before age 15									
Wealth × coresidence 16–20				0.95	0.88	1.04	1.07	0.71	1.60
Wealth × coresidence 21–25				1.00	0.92	1.09	0.96	0.64	1.46
Wealth × coresidence 26–30				0.99	0.88	1.11	0.90	0.54	1.49
Wealth × coresidence >30				1.14*	1.00	1.31	0.57*	0.34	0.94
ρ (α for total fertility)	0.01			0.01			0.04		
n	26 787			12 910			12 910		

CI = confidence interval.

[a]Model controls for woman's age, time, and time square; number of siblings, number of siblings square; highest level of education, present education; country wealth; social mobility; and interactions between time, time square, partnership status, coresidence with parents, and wealth.

[b]Models control for woman's age, age square, country wealth, highest level of education, social mobility, number of siblings, and number of siblings square.

*$P \leq 0.05$; **$P < 0.001$.

and the higher was her probability of childlessness. The only significant differences, however, were for the woman who remained coresident with her parents after the age of 30 years (for total fertility, IRR = 0.69 for women who remained coresident with parents after age 30 compared with those who moved out before age 15; $P < 0.001$; for the probability of childlessness, OR = 4.64 for women who were coresident with parents until older than age 30 compared with those who moved before age 15; $P < 0.001$). The timing of first birth analysis included an interaction between coresidence and partner status. This interaction was statistically significant and demonstrated that having a partner slightly mitigated the negative effects of coresidence: partnered women, whether coresident or not, were more likely to have a first birth per unit time than unpartnered women, but unpartnered women who were still coresident with parents were much less likely than unpartnered women who were no longer coresident. This suggests having a coresident partner may be more important than coresidence with parents for predicting the timing of first birth.

Parental survival had more mixed effects than coresidence. Having a living mother was associated with earlier first births (OR = 1.14; $P < 0.001$), but having a living father had no effect on first birth timing. Examining the ORs for the probability of childlessness model suggests that women who lost their mothers in childhood were more likely to be childless at age 45 than those whose mothers lived longer, and there was a significant difference for women who experienced the death of a mother between the ages of 10 and 20 years compared with those with living mothers (OR = 1.56; $P = 0.02$). Father's survival status had no significant effect on the probability of childlessness. Parental survival, of neither mothers nor fathers, was significantly associated with total fertility. Overall then, having a longer-living mother was associated with pronatal outcomes, a younger age at first birth, and lower probability of childlessness, but father's survival status appeared unimportant for fertility outcomes.

There is a possibility that any kin effects that we found might be confounded by maternal or paternal age effects because women whose parents were still living were likely to have had parents who were younger at the time of their births. To account for this, we ran all models again with a control for women's mothers' ages at the birth of the focal woman (essentially a generation-gap control). This did not change the direction or significance of our results, nor was mothers' age at birth a significant predictor of the outcome in either the probability of childlessness or total fertility models. The timing of first birth was significantly correlated with mothers' age at birth, but the magnitude of the effect was negligible (OR = 0.99; $P = 0.048$).

A wealth score was our main measure of resource availability. Higher wealth was associated with later first births (OR = 0.46; $P < 0.001$) but had no statistically significant relationship with the probability of childlessness or total fertility. For all 3 fertility models, we found a significant interaction between wealth and coresidence between women and their parents. In each case, the interaction suggested that the negative effects of coresidence on fertility were exacerbated for low-wealth women. Figure 1 illustrates the interaction between wealth and coresidence in the first birth model by plotting predicted survival curves for first births by women's wealth and the age at which they leave their natal home for the first time. This figure shows the proportion of women predicted (based on model output) not to have progressed to a first birth at each age (plotted for women who gained a partner at age 22, other variables held at their means). We have plotted out these curves for high- and

low-wealth women (defined as women in the highest and lowest deciles of wealth, respectively) and for women who left home at ages 20 and 29 (ages were chosen to represent women who leave home at a normative age and relatively late). We see that leaving home earlier (plotted for age 20) for both women of high and low wealth leads to earlier first births but that poorer women who leave home early progress more quickly to first births than wealthier women. Women of both high and low wealth who leave home late have later first births, but wealthy women who leave home late do "catch up" by age 35 with those women who leave home early. Low-wealth women who left their homes later, however, did not catch up in terms of progressing to a first birth by the age of 35 years, suggesting that low wealth exacerbates the fertility-inhibiting effect of coresidence. For total fertility, a similar pattern is exposed when we plot predicted fertility from the interaction (Figure 2). Women with lower wealth feel the negative effects of extended coresidence on their fertility more strongly than women
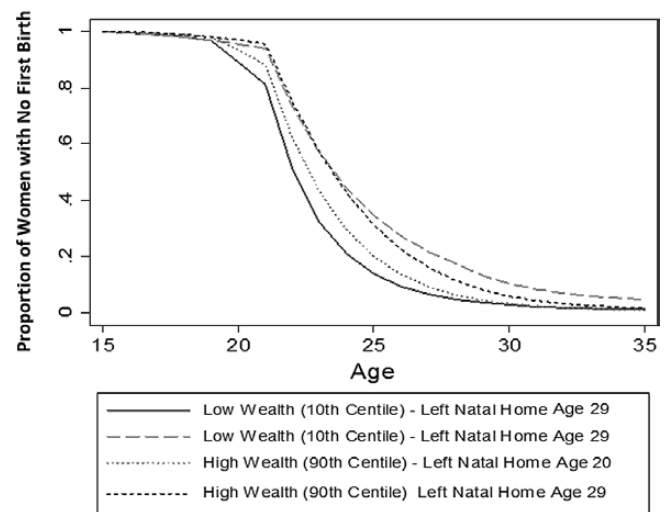
Figure 1
Predicted survival curves (estimated from model output) for timing of first birth by wealth and age of leaving natal home.
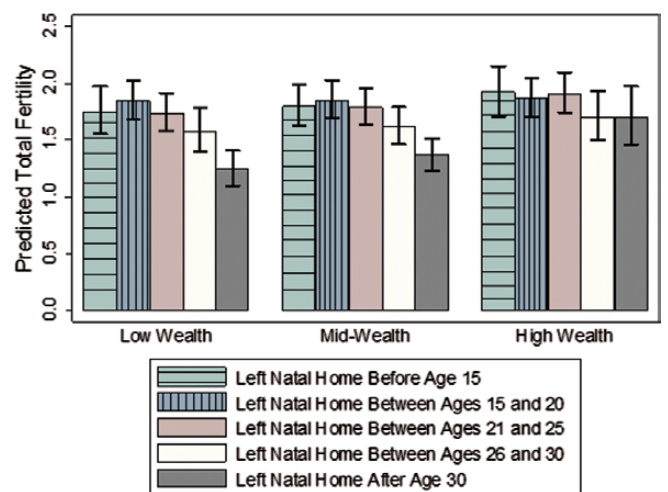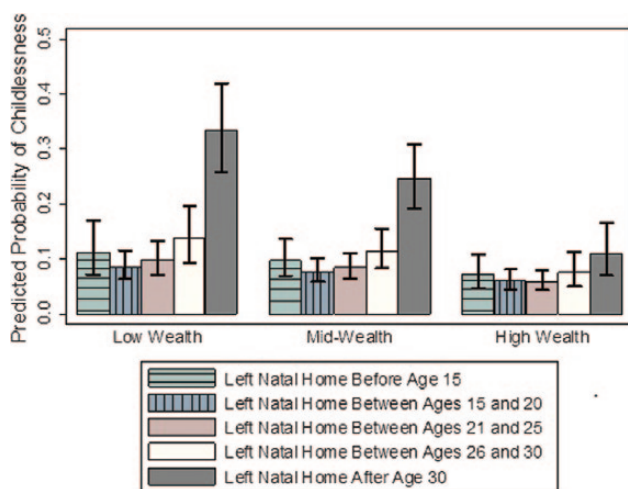

Figure 2
Predicted total fertility (estimated from model output) by wealth (low = 10th percentile; mid = 50th percentile; and high = 90th percentile) and age of leaving natal home, with 95% confidence intervals.

with higher wealth. Low-wealth women who leave home later have significantly lower total fertility than wealthier women who leave their natal home at the same age. Finally, the effect of coresidence on the probability of childlessness is also most strongly felt by low-wealth women (Figure 3): poorer women who leave the natal home later are significantly more likely to remain childless than high-wealth women who leave the natal home at the same age.

DISCUSSION

Our results demonstrate that kin availability is correlated with fertility in our study population. The nature of these correlations, however, depends on the measure of kin availability used. Although maternal survival predicts early first births and maternal absence in early life increases the probability of childlessness, paternal survival has no significant effects on our fitness measures. The positive effects of maternal survival on women's fitness may be due to the benefits of kin helping behavior known to enhance fitness across species (Clutton-Brock et al. 2001; Griffin and West 2003; Salomon and Lubin 2007; Sear and Mace 2008). We cannot entirely exclude the possibility that the positive correlations are due to a healthy family effect, whereby longevity and early reproduction are correlated because some families are simply healthier than others and are therefore good at both surviving and reproducing. Health, however, is not typically the strongest determinant of reproductive behavior in HILF societies, as it is in poorly nourished societies (Sear et al. 2003b). We also see no correlations between fathers' survival and the fertility of their daughters, which we might expect to see if a healthy family effect is influencing our results for mothers. An obvious extension of this research will be to explore more fully the pathways through which mothers may encourage their daughters to reproduce. For example, social pressure, the provision of childcare, emotional support, or financial transfers (or a combination of these) may be means by which mothers affect their daughters' fertility and thus enhance their own inclusive fitness. The first wave of the GGP does not allow us to adequately explore this issue further; however, the second and third waves of the survey will allow an analysis of how different types of kin investments in the first wave affect subsequent fertility outcomes.

Figure 3
Predicted probability of childlessness (estimated from model output) by wealth (low = 10th percentile; mid = 50th percentile; and high = 90th percentile) and age of leaving natal home, with 95% confidence intervals.

In contrast with maternal survival, coresidence is correlated with *lower* fertility across all 3 of our outcome measures: later age at first birth, lower total fertility, and higher probability of childlessness. This is not expected if coresidence is an indicator of the availability of helpful kin, as it is often suggested to be in other parts of the world (Hank and Buber 2009; Smits et al. 2010; Heylen et al. 2012), but it may perhaps be explained by coresidence being an indicator of competition between kin. Our study population is in a resource-abundant context, however, where resources are not limiting women's reproductive ability. Although it is possible that perceptions of resource scarcity relative to other individuals in the population may well be influencing reproductive decisions, we are wary of concluding that competition between kin is the sole explanation for our results. We note that although coresidence implies kin availability, there are some challenges with the interpretation of this variable when considering our own species. For nonhuman animals, kin (or nonkin) sharing a territory will involve sharing a resource base and will allow both competitive and cooperative behavior, whereas once kin have dispersed to a different territory, they tend to be relatively independent of one another. For humans, it can be difficult to define a "territory." Coresidence within the same household certainly implies sharing a "territory" and does allow the opportunity for both competition and cooperation between kin, but non-coresident kin also frequently share resources and are often involved in cooperative and sometimes competitive behaviors. This is particularly likely to be true in the high-income context that we study here because "resources" typically refer to monetary wealth or assets, which are easily transferable between individuals and households. Here, we suggest that self-selection of coresiders may also be a factor in the negative correlations we find between women's fertility outcomes and coresidence. It is normative for adult children to leave the parental home before reproducing, in the context of this study; hence, coresidence with parents beyond a normative age may indicate an inability or lack of desire to set up one's own home and is therefore perhaps an indicator of the "quality" of the individual (in terms of fitness potential).

One potential alternative explanation for our finding that coresidence is correlated with lower fertility is that women who do not wish to have children choose to stay at home longer than those who are keen to have children (i.e., reverse causation), but this begs the question of why certain women would like to have children, whereas others do not. The interaction that we find between wealth and coresidence makes improbable the possibility that women who extend coresidence are simply uninterested in reproduction at all. If this were the case, wealth would not buffer the negative effects of coresidence on fertility. Based on the negative relationship between coresidence and fitness measures, along with the interaction between coresidence and wealth in all 3 fitness models, we suggest that coresidence is indicative of either possessing non-normative characteristics, which may decrease one's mate value, or some other characteristics associated with relatively low fitness potential, including adverse family circumstances (such as the need to care for a family member).

As mentioned above, we do, however, find ecological variation in these correlations between coresidence and fertility: across all 3 of our outcomes, coresidence has fitness-diminishing effects, but these effects are more strongly felt by poorer women than wealthier women. Wealth may mitigate these characteristics, if, for both poor and wealthy women, coresidence delays first births, but on exiting the parental home, being wealthy allows women to more quickly gain a home and partner—both tasks deemed important for entering

adulthood in HILF settings (Furstenberg et al. 2004)—and to ultimately reproduce. This could occur if being wealthier would allow women to 1) purchase or rent a stable home more quickly on exiting coresidence (see Mulder 2013 for evidence of this), 2) be more readily able to enlist paid help for a household help or for childcare, or 3) more easily attract mates. Alternatively, long coresidence may mean something slightly different in poor and wealthy households: whereas in poor households, extended coresidence may be an indicator of relatively low fitness potential, compared with peers, in wealthy households, long coresidence may instead allow women to capitalize on the substantial amounts of parental investment they get from their wealthy parents (extending their education in order to improve their job prospects and subsequent earning power, e.g.: see Ellis 2004).

Our research contributes to a growing body of literature applying evolutionary approaches to human reproductive behavior. We are able to use a large, rich data set on our own species to explore ecological variation in reproductive behavior and find that, as predicted, resource environments modify relationships between indicators of kin availability and reproductive behavior. We find that coresidence, a common measure of kin presence/investments, does not result in enhanced fitness and suggest that the use of coresidence as a measure of kin cooperation or competition (Strassmann and Garrard 2011) may not always be appropriate in human evolutionary studies of kin and fertility, particularly in HILF contexts such as that explored in our study. Maternal survival positively relates to 2 fitness outcomes, suggesting that although fertility behavior is perhaps not optimized in HILF contexts, women still respond to evolved cues.

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