Optimizing Modern Family Size Trade-offs between Fertility and the Economic Costs of Reproduction

David W. Lawson · Ruth Mace

Published online: 9 March 2010 © The Author(s) 2010. This article is published with open access at Springerlink.com

Abstract Modern industrialized populations lack the strong positive correlations between wealth and reproductive success that characterize most traditional societies. While modernization has brought about substantial increases in personal wealth, fertility in many developed countries has plummeted to the lowest levels in recorded human history. These phenomena contradict evolutionary and economic models of the family that assume increasing wealth reduces resource competition between offspring, favoring high fertility norms. Here, we review the hypothesis that cultural modernization may in fact establish unusually intense reproductive trade-offs in wealthy relative to impoverished strata, favoring low fertility. We test this premise with British longitudinal data (the Avon Longitudinal Study of Parents and Children), exploring maternal self-perceptions of economic hardship in relation to increasing family size and actual socioeconomic status. Low-income and loweducation-level mothers perceived the greatest economic costs associated with raising two versus one offspring. However, for all further increases to family size, reproduction appears most expensive for relatively wealthy and well-educated mothers. We discuss our results and review current literature on the long-term consequences of resource dilution in modern families.

Keywords Parental investment · Sibling competition · Demographic transition · ALSPAC

Navigating the human life course from birth through to adulthood and ultimately reproduction is a risky and competitive business closely dependent on individual resource budgets. This, for example, results in robust socioeconomic gradients in

D. W. Lawson (🖂)

Centre for Population Studies, London School of Hygiene & Tropical Medicine, 49-51 Bedford Square, London WC1B 3DP, England e-mail: David.Lawson@lshtm.ac.uk

health and mortality, even in the wealthiest and most egalitarian of societies (De Vogli et al. 2007; Marmot 2005; Petrou et al. 2006). Optimal fertility, in terms of long-term Darwinian fitness, is therefore rarely represented by maximum fertility. All parents must balance the key life history trade-off between quantity of offspring and individual allocations of parental resources (Lack 1947; Mace 1998; Roff 2002; Williams 1966). Research conducted across a wide variety of populations confirms that high fertility often entails negative effects on the health (Desai 1995; Hagen et al. 2001, 2006; Lawson and Mace 2008), survival (Gillespie et al. 2008; Meij et al. 2009; Penn and Smith 2007; Strassmann and Gillespie 2002; Voland and Dunbar 1995), and reproductive success of offspring (Borgerhoff Mulder 1998; Low 1991; Mace 1996; Voland and Dunbar 1995).

Evolutionary ecologists have suggested a number of mechanisms by which the human organism responds to local socioecology to optimize this "quantity-quality trade-off." For example, at the physiological level, lactational amenorrhea can be understood as a mechanism to avoid new pregnancies at a time when investment in current, vulnerable offspring is critical. Similarly, the automatic suppression of ovulation during periods of intense physical stress or nutritional deficit prevents further divisions of parental investment in times of hardship by literally turning off the reproductive system (Bentley 1999; Ellison 2003). At the psychological level, we can expect reproductive decision making to be regulated by equivalent cognitive mechanisms utilizing environmental information on observed or expected relationships between parental investment and offspring development (Kaplan 1996; Kaplan and Gangestad 2005). Experimental studies show that such cognitive mechanisms are important regulators of fertility behavior in many animal taxa. For example, Eggers et al. (2006) have demonstrated that Siberian jays exposed to playbacks of predator calls seek out nests offering more protective covering and reduce current clutch size, even when predation itself is not increased. In humans, behavioral pathways of fertility regulation may often be institutionalized in cultural systems, such as marriage and inheritance practices, contraception, and celibacy rules (Kaplan 1996).

A central assumption of quantity-quality trade-off models is that parental resources are finite (Becker and Lewis 1973; Lack 1947; Stearns 1992; Williams 1966). Increases in personal or societal wealth may therefore relax this assumption and reduce the magnitude of trade-off effects (Tuomi et al. 1983; van Noordwijk and de Jong 1986). Empirical support for this position has been demonstrated in a number of animal studies (e.g., Boyce and Perrins 1987; Risch et al. 1995). In humans, studies of both contemporary African (Borgerhoff Mulder 2000; Meij et al. 2009) and preindustrial European (Gillespie et al. 2008) agriculturalists also confirm that the costs of high parental fertility to individual offspring tend to be less pronounced in the wealthiest strata. From an adaptive perspective, these studies fit neatly with observed strong positive correlations between wealth and family size characteristic of most traditional societies (Borgerhoff Mulder 1987; Cronk 1991; Voland 1990; see Hopcroft 2006 for review); when sibling competition is relaxed, individuals can afford to raise more offspring.

In contrast, modern post-demographic-transition societies appear to contradict evolutionary models of fertility optimization (Borgerhoff Mulder 1998; Kaplan et al. 1995). Firstly, despite substantial increases in personal wealth and the establishment

of the welfare state, which aims to guarantee basic levels of well-being independent of parental care, fertility has fallen in recent decades to the lowest levels in recorded human history. Secondly, fertility decline within societies is generally characterized by markedly larger reductions of fertility in wealthy families compared with the rest of the population (Livi-Bacci 1986). As a consequence, modern fertility not only is dramatically reduced in comparison to traditional populations but also is typified by relative socioeconomic leveling (Nettle and Pollet 2008). Thus, contrary to adaptive predictions, relationships between wealth and fertility are typically recorded as null or negative in demographic surveys (Kaplan et al. 1995; Kaplan et al. 2002). Some studies have suggested that when education is held constant, positive correlations between income and fertility persist, at least for males (Fieder and Huber 2007; Hopcroft 2006; Nettle and Pollet 2008). However, these relationships appear to operate on mating success rather than reproductive decisions per se (i.e., influencing levels of childlessness, rather than family size amongst reproducing individuals) and remain considerably weaker than relationships observed in traditional societies (Nettle and Pollet 2008).

Evolutionary Models of Modern Low Fertility

This "evolutionary puzzle" of modern family size has sparked considerable debate within the human evolutionary behavioral sciences (Borgerhoff Mulder 1998; Mace 2007; Sear et al. 2007). Many researchers stress that adaptive behavior should not always be anticipated when current environments differ from the ancestral conditions under which our physiological and cognitive mechanisms of fertility regulation evolved (Irons 1998). The lack of a clear positive relationship between wealth and fertility may therefore be explained by the interaction of ancestrally formed adaptations and novel socioecological factors. For example, it has been emphasized that the widespread availability of efficient birth control technology in modern environments negates the ancestral association between sexual intercourse and reproduction (Barkow and Burley 1980). In support of this model, Pérrusse (1993) has shown that wealthier men achieve higher copulation rates than their poorer counterparts, proposing that without contraception the wealthy would outreproduce the poor (see also Kanazawa 2003). The importance of contraception in regulating fertility behavior, however, is contested by evolutionary and economic demographers, not least because the European demographic transition was apparently initiated by *coitus interruptus* and because such models fail to explain the demand driving the invention and accessibility of modern contraceptive technology (Borgerhoff Mulder 1998; Lee 2003). Studies demonstrating strong, socially recognized motivations for reproduction and the care of children distinct from sexual activity further dissuade from the simplicity of this hypothesis (Foster 2000; Rotkirch 2007).

Alternatively, it has been suggested that low fertility preferences may result from novel changes in the social context of reproduction (Boyd and Richerson 1985; Newson et al. 2005). Newson et al. (2005), for example, argue that ancestral and traditional societies are characterized by frequent and sustained interaction with kin who, sharing our reproductive interests, place social pressure and rewards on

reproduction. Low fertility may therefore result from the fragmentation of kin networks associated with modernization. In support of this hypothesis, role-playing experiments demonstrate that individuals playing the role of friends, in contrast to relatives, are less likely to offer favorable advice about reproduction (Newson et al. 2007). Related models of social influence and cultural diffusion have recently become popular in the demographic literature (Bongaarts and Watkins 1996; Kohler 2001; Montgomery and Casterline 1996).

Evolutionary ecologists, along with many economic demographers, however, remain resistant to the view that modern reproductive decisions have become uncoupled from observed costs of child rearing (Kaplan et al. 2002; Mace 2007, 2008). For example, while low fertility may not provide obvious survival or reproductive benefits to offspring, there is clear evidence of positive effects on outcomes such as educational achievement and adult wealth ownership (Downey 2001; Kaplan et al. 1995; Keister 2003; Steelman et al. 2002). It is therefore possible that modern low fertility remains adaptive if we take into account that immediate deficits in reproductive success may eventually be offset by acquired benefits to wealth inheritance or other predictors of long-term lineage survival. Such a scenario has been formally modeled as theoretically plausible by a number of researchers (Boone and Kessler 1999; Hill and Reeve 2005; Mace 1998; McNamara and Houston 2006). Alternatively, Kaplan (1996) argues that modern low fertility is maladaptive, but nevertheless the product of an evolved psychology which regulates reproduction in balance with the local effects of parental investment on offspring status. This psychology fails to function adaptively in modern contexts because novel factors, such as the establishment of skill-based wage economies, offer radically extended scope for status competition between individuals at levels which now fail to translate into significant survival or reproductive benefits (Kaplan 1996; Kaplan et al. 2002).

Distinguishing between these two hypotheses at an empirical level is currently limited by a lack of sufficient multigenerational data. However, adaptive or not, parental investment models of fertility decline share a fundamental, but rarely tested, prediction: population relationships between wealth and fertility should remain mapped onto varying intensities of resource competition between offspring. In other words, to explain negative or null relationships between wealth and fertility, cultural modernization must establish a reversal of the traditional life history model of quantity-quality trade-offs, creating unusually intense resource competition effects when resources are relatively abundant rather than scarce.

Cultural Modernization and the Quantity-Quality Trade-off

In traditional human societies, factors such as high infectious disease rates, famine, and warfare lead offspring quality to be significantly determined by external risk factors beyond the grasp of parental control under feasible ranges of investment. As a consequence there may be substantial diminishing returns to parental effort, with a saturation point beyond which "chance" becomes the principal determinant of offspring success (Pennington and Harpending 1988). As the traditional life history model assumes, this pattern leads to reduced levels of resource competition between

offspring at higher wealth, favoring high fertility norms (Quinlan 2007). Cultural modernization, through the relative abolishment of these risk factors, buffers populations from environmental instability and may therefore create a higher degree of reliability in investment returns (Winterhalder and Leslie 2002). As such, higher levels of wealth can lead to a closer association between parental investment and offspring quality, and subsequently increased costs to resource competition between offspring (Kaplan 1996; Kaplan et al. 2002). Supportive of this argument, in a cross-country analysis of the influence of family size on child growth in 15 developing populations, Desai (1995) found that higher levels of access to both safe drinking water and health care facilities were associated with larger negative effects of family size on height. It seems that the improved ability of parents to control the determinants of their children's development increases the intensity of sibling resource competition.

Kaplan and colleagues further emphasize that the establishment of skill-based wage economies in industrialized nations may reinforce exponential returns to parental investment, with high investment strategies bringing about disproportionately large benefits to offspring status and consequently increasing the magnitude of trade-off effects. This is because direct financial allocations to offspring, along with investments in skill acquisition through formal education, may doubly advantage offspring by offering the additional benefit of increased ability to generate new wealth during the life course (Kaplan 1996; Kaplan et al. 2002; Rogers 1990). As Rogers (1990:493) puts it, "the heir of a large estate is likely to earn more than a pauper. Now if, by leaving my child a dollar, I can improve her chances of earning another dollar, then inheritance is worth more than a dollar." Under such conditions the relative benefits of adopting a reproductive strategy focused on child quality over quantity will be increased.

Finally, the construction of the modern welfare state may selectively reduce the costs of resource competition between offspring in impoverished relative to wealthy strata. Downey's (2001) categorization of parental investment into the transfer of "base" and "surplus" resources is useful in understanding this point (Lawson and Mace 2009). Base resources are those necessary for survival and essential social functioning, and poor and wealthy parents alike invest in them. Surplus resources, however, require a qualitatively higher level of parental investment which is exclusively available in relatively rich families. In traditional populations, following a quantity-quality trade-off model, both base and surplus resources will be diluted by large family size. However, under a welfare state, competition for base-level resources may be relatively eliminated by guaranteed provisioning of basic schooling, health care, and social opportunity. As such, family size may hold more influence on the success of offspring in wealthy compared to relatively impoverished families in modern populations in strong welfare states.

In this study, we consider relationships between fertility, socioeconomic status, and maternal self-perceptions of economic hardship in contemporary British families. Following previous studies we predict negative relationships between indicators of socioeconomic status and female fertility. We also predict that, adjusting for the independent effects of socioeconomic status, all mothers will experience increasing levels of economic hardship when raising additional children, representing the trade-off between number of offspring and desired levels of parental investment. We then test to see if low-, middle-, and high -socioeconomic-status families experience different trade-offs between fertility and economic hardship. If negative correlations between fertility and socioeconomic status are to be understood as a response to perceived or real costs of rearing children, then increasing socioeconomic status should intensify, rather than alleviate, trade-offs between fertility and economic hardship.

Methods

Study Sample

All data are sourced from the Avon Longitudinal Study of Parents and Children (ALSPAC), a uniquely detailed, ongoing cohort study designed to examine environmental and genetic influences on the health and development of British children. Study recruitment began in pregnancy, enrolling women who had an expected delivery date between April 1991 and December 1992 from the three main Bristol-based health districts of the former county of Avon. 14,472 pregnant women (14,062 live births) were recruited into the initial sample (an estimated 80–90% of known births from the defined area). Avon has a predominantly white population, a mixture of rural and urban communities, and a socioeconomic mix similar to the rest of the UK (Golding et al. 2001). The analyses presented in this paper are based on available data from the first 10 years of data collection. All data considered were collected by self-completed questionnaires. Further information on the distribution of each independent variable over the study period and descriptive statistics can be found in Lawson and Mace (2008).

A number of exclusion criteria remove rare family configurations from our sample. Mothers who had multiple births, experienced the death of a child, or cohabited with children unrelated to either themselves or their current partner (e.g., foster or adopted children) over the study period were all excluded. Cases where the study child's "mother figure" is ever recorded as other than the biological mother, as absent, or as in a lesbian relationship were also excluded. Cases of biological father absence after birth were included. We also include cases where the mother is recorded as in a new relationship with someone other than the biological father. However, we exclude rare cases where the mother reports unsure paternity of the study child or starts a new relationship during this pregnancy. After implementing these criteria our total study sample contained 13,176 mothers.

Family Size

Family size is defined for the purpose of this study as all maternally related offspring (i.e., including children of different biological fathers, but excluding children from different mothers). Family size data are available at six intervals from recruitment to 10 years after the birth of the study child (Lawson and Mace 2008). At all points of data collection subsequent to the birth of the study child, modal family size was two. At 10 years after the birth of the study child, 27% of mothers had three children and 10% had four or more. In the absence of completed family size data for all mothers

(the mean age of mothers at the end of the study period is 38.0, with a standard deviation of 5.0), we assess the relationship of socioeconomic measures to age-specific fertility (i.e., in the presence of controls for maternal age).

Socioeconomic Status and Additional Covariates

We include mother's educational attainment (coded in pregnancy) as a time-invariant measure of socioeconomic status (educational status rarely changes during motherhood). In addition we use three time-varying measures of wealth: "take home" household income, home ownership, and neighborhood quality. Two measures of social support were also incorporated, both based on questionnaires distributed to the mother in pregnancy. These measures were recorded only once and so could not be entered as time-varying variables. The social network score comprises ten items which ascertain the quality and frequency of social contact with friends and family and ranges from 0 to 30. The social support score measures perceived social support from family, friends, and official agencies using a set of ten items specifically designed for the cohort. The item presents statements relating to emotional, financial, and instrumental support, with a summed overall score also ranging between 0 and 30. This measure shows a strong association with the mother's emotional well-being during pregnancy (Thorpe et al. 1992). Both measures were banded into three groups of equal size, coded as "low," "medium," and "high." Mother's employment status and ethnicity were also included as an additional dichotomous covariate terms in all models. Mother's employment status was measured at four intervals over the study period. A large majority (95%) of the ALSPAC population is recorded as being white.

Fathers are coded as present provided the mother states the study child has a biological father as the live-in "father figure" at the time of the questionnaire. In cases where the father is coded as absent, the mothers are either coded as alone or as with a new live-in partner. These data do not distinguish between different partners of the mother subsequent to the biological father of the study child. Father presence, like family size, was assessed at six intervals, with almost a quarter of mothers (24%) separating from the father of the study child by the end of the current study period. Finally, maternal and paternal age at recruitment are included as additional covariates.

Economic Hardship

Financial difficulty of the mother in affording the key expenditures of food, rent, heat, clothes, and items for the study child was self-rated at four points over the study period between 8 months and 7 years 1 month (Table 1). At each point difficulty was scored as not difficult (0), slightly difficult (1), fairly difficult (2) or very difficult (3). Cases where the respondent indicated that heating or rent was paid by the Department of Social Security were coded as very difficult (3); missing cases were coded as not difficult (0—always the most frequent category) provided a response for at least one other expenditure was present in the same questionnaire. A summed measure, which we refer to as the *economic hardship score*, was then derived ranging from 0 to 15 and treated as a continuous outcome variable in each

		Time since Birth of Study Child					
		0y8m	1y9m	2y9m	7y1m		
Economic Hardsh	ip Score						
Mean		3.17	2.99	3.07	2.05		
SD		3.58	3.49	3.64	2.05		
N		10,510	9,409	9,002	7,741		
Items	Coding	%	%	%	%		
Food	Not Difficult	71	73	76	87		
	Slightly	19	18	16	10		
	Fairly	8	8	7	3		
	Very	2	2	2	1		
Clothing	Not Difficult	34	35	40	58		
	Slightly	33	35	33	29		
	Fairly	18	17	17	9		
	Very	14	13	11	4		
Heating	Not Difficult	65	65	69	85		
	Slightly	21	21	19	11		
	Fairly	10	11	9	3		
	Very (or DSS paid)	4	4	3	1		
Rent	Not Difficult	68	65	63	74		
	Slightly	19	17	17	11		
	Fairly	8	7	8	3		
	Very (or DSS paid)	5	12	15	12		
Items for child	Not Difficult	59	57	59	66		
	Slightly	26	28	27	25		
	Fairly	11	11	10	6		
	Very	4	5	4	2		

Table 1 Economic hardship score

Note that these values refer to the sample available at each study wave. They should not be directly interpreted as evidence of change over time due to selective attrition.

analysis. In total, 36,662 measurements of economic hardship are available for 11,257 individual mothers.

Data Analysis

Two relationships are of interest in this study. First, the relationship of socioeconomic status to family size (age-specific fertility), and second, the independent relationship of family size to economic hardship. Utilizing all relevant data from our longitudinal sample, we examined these relationships with multivariate multilevel models (Singer and Willett 2003). All analyses were carried out using MLwiN 2.02. Individuals were treated as level-two units and the timing of

measures as level-one units. Modeling data in this way requires contemporaneous data on predictor and outcome variables, a feature not strictly met by the temporal distribution of time-varying measures included in this study (Lawson and Mace 2008). To overcome this issue we assumed that time-varying independent variables had equal values to the mid points between each coding, imputing their value at the months where outcome data were recorded for each individual child.

The major advantage of a multivariate multilevel modeling strategy is that it allows us to incorporate all available outcome data rather than restrict analysis to participants who provided complete assessments at a specific subset of time points. However, in order to have unbiased estimates in the presence of missing data, it must be assumed that responses are missing at random (MAR); that is, the probability of any outcome measure being missing can depend on observed, but not unobserved, covariates (Little and Rubin 1987). Although we do not formally investigate this issue, given the large range of relevant independent variables included in our models, it is likely that our analyses conform to the MAR assumption.

We first determined the overall relationship of fertility with years since recruitment by establishing an "unconditional model" (Singer and Willett 2003), containing only a constant and significant effects of time (study child age in years). We then assessed the relationship between socioeconomic measures and age-specific fertility trajectories, constructing a final multivariate model in a series of blocks. For each independent variable, effects were estimated by both a main effect term (effect on initial fertility at the birth of the study child) and an interaction term with time (effect on rate of fertility change per year). Statistical significance of each predictor term was assessed (as in standard linear regression) by dividing the regression coefficient by its standard error and 95% confidence intervals were calculated. Maternal age and all socioeconomic measures (maternal education, family income, home ownership, neighborhood quality) were entered in the first block. This model was then reduced by a backwards procedure removing associations that did not reach significance at the p < 0.05 level. The second block then entered all additional covariates and was reduced in a similar fashion to produce the final model. Predictor terms were maintained if p < 0.05 or their presence effected notable changes on any of the coefficients relating to socioeconomic status.

A parallel set of models was then used to assess the independent relationship of family size to economic hardship. An unconditional model, containing only a constant and significant effects of time, was established and then a final multivariate model constructed in blocks. All variables relating to family configuration (family size, parental age, father presence) were entered in the first block. All additional covariates, including socioeconomic measures, were then entered in a second block. Predictor terms were maintained if p < 0.05 or their presence effected notable changes on any of the family configuration coefficients.

Finally, variation in family size effects by socioeconomic status was explored by running separate versions of the final family size models for low, medium, and high socioeconomic strata. Since previous studies have found different relationships of income and educational achievement to fertility, we consider these components of socioeconomic status separately. Comparison of effect sizes between socioeconomic strata is made incrementally by family size (i.e., effect of increasing family size from one to two children, from two to three children, and so on) to allow for the possibility that interactions with socioeconomic status may vary at different family size thresholds.

Results

Socioeconomic Status and Fertility Trajectories in the ALSPAC Sample

Overall fertility was positively related with time since the birth of the study child; initial status at 0 years is estimated as 1.81 children (CI: 1.79–1.83, p<0.001), increasing at 0.08 per year (CI: 0.08–0.08, p<0.001). Table 2 shows the final multivariate model for fertility after removal of statistically weak (p<0.05)

 Table 2 Final multivariate model predicting family size

Coefficient		Initial Status (at 0y 0 m)		Rate of Change (per year)	
		В	95% CI	В	95% CI
Intercept ^a		0.50 ***	0.35 to 0.65	0.31 ***	0.29 to 0.33
Family Configuration					
Mother's Age at Recruitment (years)	Continuous	0.06 ***	0.05 to 0.07	-0.01 ***	-0.01 to -0.01
Partner's Age at Recruitment (Ref: <25 years)	25-29 years	0.08	0.00 to 0.16	-0.01	-0.02 to -0.01
	30-34 years	0.19 ***	0.11 to 0.27	-0.02 **	-0.03 to -0.01
	35+ years	0.26 ***	0.18 to 0.34	-0.02 ***	-0.03 to -0.01
Father Presence (Ref: Present)	Mother Alone	-	-	-0.03 ***	-0.04 to -0.02
	New Partner	-	-	-0.03 ***	-0.04 to -0.02
Socioeconomic Measures					
Maternal Education (Ref: CSE/Voc)	O-level	-0.21 ***	-0.26 to -0.16	0.01 **	0.00 to 0.02
	A-level	-0.35 ***	-0.41 to -0.29	0.02 ***	0.01 to 0.03
	Degree	-0.49 ***	-0.56 to -0.42	0.05 ***	0.04 to 0.06
Household Weekly Income (Ref: <£200)	£200–299	0.01	-0.02 to 0.04	_	-
	£300–399	0.00	-0.03 to 0.03	_	-
	£400+	-0.03 **	-0.06 to 0.00	_	-
Neighbourhood Quality (Ref: <v. good)<="" td=""><td>V. Good</td><td>_</td><td>_</td><td>_</td><td>_</td></v.>	V. Good	_	_	_	_

<V. Good)

Table 2 (continued)

Coefficient		Initial Status (at 0y 0 m)		Rate of Change (per year)	
		В	95% CI	В	95% CI
Intercept ^a		0.50 ***	0.35 to 0.65	0.31 ***	0.29 to 0.33
Home Ownership (Ref: Rented)	Mortgaged/ Buying	-0.10 ***	-0.07 to -0.13	-	-
	Owned Outright	-0.15 ***	-0.20 to -0.10	_	-
Social Support					
Social Network Score (Ref: Low)	Medium	-0.09 ***	-0.14 to -0.04	0.01 ***	0.00 to 0.02
	High	-0.09 **	-0.14 to -0.04	0.01 ***	0.00 to 0.02
Social Support Score (Ref: Low)	Medium	-0.09 ***	-0.14 to -0.04	0.01 *	0.00 to 0.02
	High	-0.10 ***	-0.15 to -0.05	0.01 **	0.00 to 0.02
Other					
Ethnicity of Child (Ref: White)	Non-White	_	-	_	_
Maternal Employment (Ref: No)	Yes	-0.06	-0.08 to -0.04	-0.02	-0.02 to -0.02

^a The estimated mean value for initial status and rate of change for the group with the baseline values for every factor included in the model

*p<0.05, **p<0.01, ***p<0.001, N=36,028

associations (see Methods). Older mothers had higher initial family size at recruitment, but, as indicated by negative effects on rate of change, were less likely to have further children as the study progressed. The age of the mother's partner at recruitment (i.e., father of the study child) had similar effects, with higher initial fertility in mothers partnered with older men, but a reduced rate of fertility increase. Mothers who subsequently were not partnered with the father of the study child were less likely to continue having offspring.

Controlling for these effects, socioeconomic status was an important predictor of family size across the study period. Levels of maternal education had large negative effects on fertility. This effect is most apparent in the early stages of the study, where mothers holding a university degree had 0.49 fewer children (CI: -0.56 to -0.42, p < 0.001) than mothers with the lowest level of qualifications. This difference is attenuated over time to some extent by a positive effect on rate of change (Table 2). Thus maternal education appears to reduce completed fertility, but its largest effects are on fertility immediately following the birth of the study child (i.e., delayed further reproduction). Household income had a very small negative effect on fertility, with mothers living in households earning £400+/week having 0.03 fewer children (CI: -0.06 to 0.00, p < 0.05) compared with the poorest households across the study

period. Mothers living in owned or mortgaged accommodation had 0.15 (CI: -0.20 to -0.10, p < 0.01) and 0.10 (CI: -0.13 to -0.07, p < 0.01) fewer children, respectively, than those living in rented accommodation. Rerunning the final model without home ownership (not shown) slightly increased the magnitude of income effects on fertility (with mothers living in households earning £400+/week having 0.06 [CI: -0.09 to -0.03, p < 0.01] fewer children compared with the poorest households). Thus, negative income effects on fertility may be partially mediated by home ownership status. There was no statistically significant relationship between neighborhood quality and fertility in the presence of other socioeconomic measures.

Measures of social support also influenced fertility trajectories, with mothers with relatively high levels of social support or large social networks having lower initial fertility at recruitment. However, these mothers were slightly more likely to have children over the study period. Maternal employment had strong negative effects on fertility at recruitment and on the rate of fertility increase over the study period.

In a multilevel model for change total outcome variation is partitioned into within- and between-person variance components. For each of these components a pseudo R^2 statistic can be calculated based on the reduction of this term from unconditional models containing only a constant and an age term (Singer and Willett 2003). In our final model, 47% of within-person variance over time, 16% of between-person variance in initial status, and 29% in rate of change is explained by the predictors.

Family Size and Economic Hardship

A negative linear relationship between time and economic hardship was not significantly improved upon by any higher-order function; overall, mothers perceived a steady decline in economic hardship over time. Initial status at 8 months since study recruitment is estimated as 3.30 (CI: 3.27-3.37, p<0.001), decreasing at -0.17 (CI: -0.18 to -0.16, p<0.001) units per year.

Table 3 shows the final multivariate model after backwards removal of statistically weak associations. As expected, measures of socioeconomic status showed strong negative relationships with perceived economic hardship. Mothers with higher household income, living in better-quality neighborhoods, or with higher home ownership status all reported lower levels of economic hardship. While maternal educational achievement also showed a negative univariate association with economic hardship, this association was not significant in the presence of other socioeconomic measures. Improved social support and network scores were associated with lower economic hardship. Non-white mothers perceived higher economic hardship, even in the presence of other socioeconomic and social support variables. Working mothers perceived lower levels of economic hardship.

Controlling for the effects described above, family size was positively related to economic hardship (Table 3). This effect did not interact with time, indicating that the economic burden of children was relatively constant over the study period. Compared with mothers with only one child, economic hardship increased by 0.28 (CI: 0.18–0.38, p<0.001) for those with two children, by 0.56 (CI: 0.43–0.69, p<0.001) for those with three children, by 0.89 (CI: 0.69–1.09, p<0.001) for those

Rate of Change (per year)	
% CI	
.15 to)3	
.07 to)5	
.01 to 1	
.05 to)7	
.18 to .04	
.02 to 20	
.22 to .12	
.22 to .10	
.17 to .07	
.04 to)6	
31 to 0.4	

Coefficient		Initial Status (at 0y 8 m)		Rate of Change (per year)	
		B 6.07 ***	95% CI 5.74 to 6.40	B -0.09 **	95% CI -0.15 to 0.03
Intercept ^a					
Social Support					
Social Network Score (Ref: Low)	Medium	-0.45 ***	-0.65 to -0.25	_	-
	High	-0.44 ***	-0.63 to -0.25	-	-
Social Support Score (Ref: Low)	Medium	-0.58 ***	-0.76 to -0.40	0.04 *	0.01 to 0.07
	High	-0.92 ***	-1.10 to -0.74	0.07 ***	0.04 to 0.10
Other					
Ethnicity of Child (Ref: White)	Non-White	0.47 *	0.06 to -0.88	-0.10 **	-0.18 to -0.02
Maternal Employment (Ref: No)	Yes	-0.21 ***	-0.33 to -0.09	0.04 **	0.01 to 0.07

Table 3 (continued)

^a The estimated mean value for initial status and rate of change for the group with the baseline values for every factor included in the model

*p<0.05, ** p<0.01, *** p<0.001, N=23,302

with four children, and by 1.30 (CI: 0.98-1.62, p<0.001) for those with five or more children. These effects are illustrated in Fig. 1.

The ages of the mother and her current partner were not significantly associated with economic hardship in the presence of socioeconomic measures. However, they did show negative associations with economic hardship in the first block containing only family configuration variables and so are retained in the final model. Mothers who no longer lived with the biological father of the study child experienced higher levels of economic hardship. However, those mothers who had subsequently partnered with a new male did not differ from those who stayed with the biological father of the study child.

In our final model, 27% of within-person variance over time, 32% of betweenperson variance in initial status, and 20% in rate of change is explained by the predictors.

Socioeconomic Variation in the Fertility-Economic Hardship Trade-off

Rerunning the final model for low, middle, and high socioeconomic strata by income and educational attainment shows clear evidence of socioeconomic variation in the trade-off between fertility and economic hardship. Household income was coded into bands by the ALSPAC questionnaires, with the modal take-home weekly income being £200–299 when first recorded at 2 years, 9 months. In our analysis,

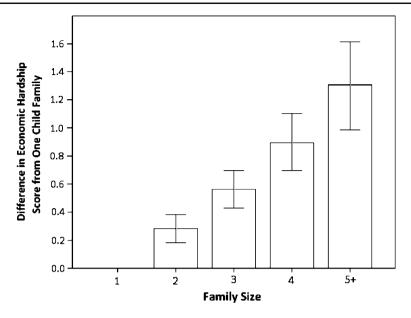


Fig. 1 Family size and maternal perceptions of economic hardship. Increasing family size is associated with higher levels of economic hardship (for all contrasts, p < 0.001). Final model controls for time of measurement, mother's age, partner's age, father presence, household income, neighborhood quality, home ownership, social support score, social network score, ethnicity, and maternal employment (Table 3)

incomes below £200 per week were coded as low (n=4,420), between £200–399 as middle (n=15,428), and £400 and above as high income levels (n=7,377). Maternal education of less than an O-level was coded as low (n=4,955), O-level and A-level qualifiers as middle (n=14,597), and degree-level education as high (n=3,750)levels of education. In the UK, O-level and A-level qualifications correspond to 16 and 18 years of formal education, respectively. Models partitioned by education control for income. Models partitioned by income do not control for education, as education effects fail to reach significance in the final model predicting economic hardship (Table 3). Additional analyses (not shown) confirm that running variations of the income group models with education controls or without home ownership status (which may mediate the effects of household income on fertility) do not notably modify the presented results.

Figure 2a shows the estimated difference in economic hardship when caring for two children relative to one child for each of these groups. Increasing socioeconomic status is associated with decreasing reproductive costs. Economic hardship increases by 0.46 (CI: 0.17–0.75, p<0.01) in the low-income stratum, by 0.30 (CI: 0.18–0.42, p<0.001) in the middle-income stratum, and 0.13 (CI: 0.01–0.25, p<0.05) in the high-income stratum. Similarly, economic hardship increases by 0.28 (CI: 0.03–0.53, p<0.05) for the low education stratum, by 0.32 (CI: 0.20–0.44, p<0.001) for the middle stratum, but is statistically indistinguishable from the economic hardship associated with raising a single child in the high education stratum.

The situation changes when the difference in economic hardship when caring for three relative to two children is considered (Fig. 2b). Here, increased

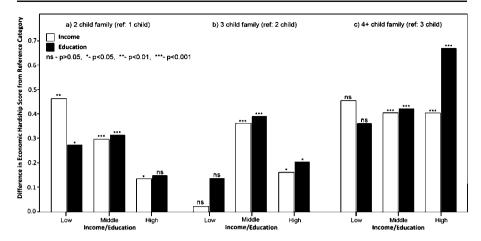


Fig. 2 Incremental differences in economic hardship score as family size increases by socioeconomic strata: a caring for two children relative to one child, b caring for three relative to two children, c caring for four or more relative to three children. Higher socioeconomic status appears to reduce the trade-off between family size and economic hardship in the transition from one to two children. Above this threshold, middle- and high-socioeconomic-status families face the strongest trade-offs between family size and parental care. Final models control for time of measurement, mother's age, partner's age, father figure status, household income (education models only), neighborhood quality, home ownership, social support score, social network score, ethnicity, and maternal employment (Table 3). See text for confidence intervals

socioeconomic status fails to alleviate the perceived costs of further reproduction, with the middle level in particular experiencing the highest increases in economic hardship. In the low-income and low-education strata, differences in economic hardship are statistically indistinguishable between raising three children and raising two. Economic hardship is increased by 0.40 (CI: 0.26-0.54, p<0.001) for the middle-income group and by 0.15 (CI: 0.03-0.27, p<0.05) for the high-income group, while economic hardship is increased by 0.36 (CI: 0.22-0.50, p<0.001) for the middle educational level and 0.20 (CI: 0.00-0.40, p<0.05) for the high educational level.

Finally, Fig. 2c shows the estimated difference in economic hardship when caring for four or more children relative to three children is considered. Once again increased socioeconomic status fails to alleviate the perceived costs of reproduction; in fact the largest increases in economic hardship are experienced by the middle and high levels. In the low income and low education strata, differences in economic hardship are statistically indistinguishable between raising four or more children and raising three. Note that all non-significant contrasts reported are based on comparisons of group samples of at least 373 cases. Non-significance is therefore unlikely to reflect lack of statistical power. Economic hardship is increased by 0.40 (CI: 0.26–0.54, p<0.001) for the middle income stratum, and 0.40 (CI: 0.18–0.62, p<0.001) for the high income stratum, while economic hardship is increased by 0.42 (CI: 0.18–0.66, p<0.001) for the middle and by 0.65 (CI: 0.28–1.02, p<0.001) for the high educational attainment stratum.

Discussion

Quantity-Quality Trade-offs in Modern Populations

Parental investment models of modern fertility argue that current low family size norms are a response to high real or perceived costs of childrearing (Kaplan 1996; Kaplan et al. 2002; Mace 2007, 2008). In support of this model, there is clear evidence that high fertility comes at a significant economic cost in modern populations. In the current study, mothers raising larger families, when the independent effects of socioeconomic status and social support are controlled, report greater difficulty in meeting their economic demands. This suggests that mothers must trade off their own quality of life with the decision to have children, and that children suffer economic deficits in investment with the addition of siblings. These deficits may be reflected in the general quality of the rearing environment, such as relatively cramped housing conditions, low-quality diets (Northstone and Emmett 2005) or poor attendance to health care (Hay et al. 2005) reported in other studies of this cohort.

We are not the first to suggest such a causal relationship between high fertility and economic hardship. A number of social-policy-directed studies have reported that children in large sibships are substantially overrepresented in families coded as experiencing conditions of poverty (reviewed in Bradshaw et al. 2006; Iacovou and Berthoud 2006). "Poverty" in these studies is generally indexed by "hardship" or "deprivation" scores very similar to the dependent variable analysed in this study. This research confirms that while large households are more likely to be of low socioeconomic status, the association between large family size and poverty measures remains after adjustment for a range of factors, including income, education, employment, and ethnicity (Iacovou and Berthoud 2006).

Studies of financial investments in education further indicate a dilution of material resources in large sibships. In large relative to small families, parents are less likely to save for college expenses during their offspring's childhood (Downey 1995), and children receive lower financial assistance and are relatively more dependent on loans and scholarships (Steelman and Powell 1989). Children in large families are also less likely to have computers or educational objects (such as a dictionary or calculator) present in their home (Downey 1995).

Lawson and Mace (2009) also confirm that high fertility can only be maintained at an important cost to time spent with each child. In fact, when the same range of independent variables considered in this study was explored, for both mothers and fathers, family size was the principal determinant of time allocation to care activities over the first decade of the study-child's life (Lawson and Mace 2009). Available evidence demonstrates that a dilution of parental investment, in terms of both time and money, persists well into adulthood. Cooney and Uhlenberg (1992), for example, have reported that, independent of socioeconomic status, number of siblings is negatively related to a range of later investments, including the direct receipt of money or gifts, giving advice in difficult decisions, and direct assistance with childcare. Keister (2003) has also demonstrated that number of siblings is a strong determinant of the likelihood of receiving a trust fund or an inheritance. Low financial and time investments in children of large families represent strong candidate mechanisms behind well-established negative effects of sibship size on cognitive development, educational achievement, and ultimately adult wealth ownership (Bjerkedal et al. 2007; Blake 1989; Conley 2001; Downey 1995, 2001; Kaplan et al. 1995; Keister 2003, 2004; Nettle 2008; Steelman and Powell 1989; Steelman et al. 2002). Family size is also a significant determinant of childhood growth trajectories, with sibship size negatively related to growth rates, particularly for later-born children in this cohort (Lawson and Mace 2008). This suggests that, all else being equal, children in large families suffer costs to physical health (see also Hart and Davey Smith 2003).

Are Quantity-Quality Trade-offs Intensified in High-Socioeconomic-Status Families?

The existence of substantial reproductive costs in modern populations cannot be considered as strong evidence that observed fertility patterns are driven by such relationships. A more convincing test of this hypothesis requires demonstration that fertility within modern populations covaries with the magnitude of trade-off effects. In the current study population, we demonstrate that measures of socioeconomic status are negatively correlated to age-specific fertility. Women with relatively high levels of education, high household income, and living in owned versus mortgaged or rented accommodation had fewer children than their same-age counterpoints of lower socioeconomic status. High-socioeconomic-status mothers are therefore predicted to face the strongest trade-offs between family size, parental investment, and offspring status.

We find partial support for this prediction. When contrasting one- and two-child families, higher income and education reduce the perceived economic costs of reproduction. However, when considering mothers with more than two offspring, relatively high socioeconomic status appears to hold increasing disincentives to further reproduction, while low-income and low-educational-attainment mothers pay no additional penalty. This pattern is particularly clear in the case of maternal education (Fig. 2), which has strong negative effects on female fertility that are recognized here and elsewhere (Fieder and Huber 2007; Hopcroft 2006; Nettle and Pollet 2008). Thus, although it is not clear why low-socioeconomic-status mothers are more likely to bear more than one child, assuming fertility is optimized to a function of the economic costs of reproduction can explain why they are relatively more likely than rich and well-educated mothers to keep reproducing beyond two children. Interestingly, a strong two-child norm characterizes contemporary Western populations (Carey and Lopreato 1995; Kaplan et al. 2002). Alternative social or psychological factors may therefore assure that majority of reproducing females, of any socioeconomic status, reach this threshold.

Our data do not reveal an exact mapping of the magnitude of reproductive tradeoffs and fertility levels across socioeconomic strata; for example, mothers in middleincome households appear to perceive larger economic costs when reproducing beyond the two-child norm compared with low-income households (Fig. 2)—yet age-specific fertility levels are not significantly different between low- and middleincome groups in multivariate models (Table 2). One possible interpretation of this pattern of results is that any increase in the economic costs of reproduction for middle- compared with low-income families is strong enough to dissuade them from channeling higher levels of wealth into additional children, but not strong enough to enact a significant reduction in fertility optima. It is also important to stress that the conclusions of the analyses presented here may rest to some extent on the measures of socioeconomic status considered and the indirect method of assessing the economic costs of reproduction. Contrary to the expectations to some traditional models of life history, our analyses make clear that relatively high socioeconomic status is not associated with a uniform reduction in the economic costs of reproduction in the context of modern families. Further research should consider whether the suggested reverse pattern of increasing economic costs at relatively high fertility levels for wealthy and well-educated households is obtained with alternative data sets and methodologies.

In recent years, economists and sociologists of the family have recognized that negative effects of family size on offspring status may not be uniform within populations (Downey 2001; Steelman et al. 2002). However, being content with establishing population-level trends, few studies have explicitly modeled the source of this variation. Available evidence confirms that high socioeconomic status may indeed carry larger penalties to within-family resource division in modern populations. Grawe (2010), for example, demonstrates that large family size is associated with negative consequences on the income generation of offspring in wealthy US families, but of little consequence to children from poor families. Similarly, Keister (2004) has shown that number of siblings is negatively related to adult wealth ownership in US families from middle and upper socioeconomic strata, but not for those born below the poverty line. Our own study of parental time investments in offspring for this cohort also revealed that, in most cases, middle- and high -socioeconomic-status parents face the strongest trade-offs between number of children and allocations of care time (Lawson and Mace 2009). Downey (2001:499) cites further unpublished work which apparently confirms this pattern for family size effects on investments in education.

Conclusions

Whether or not modern low fertility behavior can be understood as adaptive in the long-term remains difficult to evaluate in the absence of sufficient multigenerational data (Boone and Kessler 1999; Hill and Reeve 2005; Kaplan et al. 1995; Mace 1998; McNamara and Houston 2006). Nevertheless, struck by the unusual lack of strong positive relationships between wealth and fertility, many researchers have argued that novel socioecological factors, such as contraception or changing social networks, have uncoupled reproductive decision-making from the costs and benefits associated with raising children (Barkow and Burley 1980; Newson et al. 2005; Pérrusse 1993). We provide evidence to the contrary. In contemporary Britain, relatively wealthy and well-educated mothers perceive greater economic costs to raising a large family. Evidence from a number of studies supports our interpretation that this reflects increased concerns about the production of socially and economically competitive offspring. This provides some support for parental

investment models of modern fertility (Kaplan 1996; Kaplan et al. 2002; Mace 2007, 2008) and the associated hypothesis that cultural modernization favors socioeconomic leveling in fertility by intensifying reproductive trade-offs in wealthy and well-educated strata.

Acknowledgments We are extremely grateful to all the families who took part in this study, the midwives for their help in recruiting them, and the whole ALSPAC team, which includes interviewers, computer and laboratory technicians, clerical workers, research scientists, volunteers, managers, receptionists, and nurses. In particular, we thank Jon Heron for his essential assistance with data management. The UK Medical Research Council, the Wellcome Trust, and the University of Bristol provide core support for ALSPAC. This research was funded by the UK Economic and Social Research Council. We thank Nathan Grawe, Laura Fortunato, Mhairi Gibson, Jane Lancaster, Rebecca Sear, and two anonymous reviewers for constructive comments on earlier versions of this manuscript.

Open Access This article is distributed under the terms of the Creative Commons Attribution Noncommercial License which permits any noncommercial use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.

References

- Barkow, J. H., & Burley, N. (1980). Human fertility, evolutionary biology, and the demographic transition. *Ethology and Sociobiology*, 1, 163–180.
- Becker, G. S., & Lewis, H. G. (1973). Interaction between quantity and quality of children. In T. W. Schultz (Ed.), *Economics of the family: Marriage, children and human capital* (pp. 81–90). Chicago: University of Chicago Press.
- Bentley, G. (1999). Aping our ancestors: comparative aspects of reproductive ecology. Evolutionary Anthropology, 7, 175–185.
- Bjerkedal, T., Kristensen, P., Skjeret, G. A., & Brevik, J. I. (2007). Intelligence test scores and birth order among young Norwegian men (conscripts) analyzed within and between families. *Intelligence*, 35, 503–514.
- Blake, J. (1989). Family size and achievement. Los Angeles: University of California.
- Bongaarts, J., & Watkins, S. C. (1996). Social interactions and contemporary fertility transitions. *Population and Development Review*, 22, 639–682.
- Boone, J. L., & Kessler, K. L. (1999). More status or more children? Social status, fertility reduction, and long-term fitness. *Evolution and Human Behavior*, 20, 257–277.
- Borgerhoff Mulder, M. (1987). On cultural and reproductive success: Kipsigis evidence. American Anthropologist, 88, 617–634.
- Borgerhoff Mulder, M. (1998). The demographic transition: are we any closer to an evolutionary explanation? *Trends in Ecology and Evolution*, 13, 266–270.
- Borgerhoff Mulder, M. (2000). Optimizing offspring: the quantity-quality tradeoff in agropastoral Kipsigis. *Evolution and Human Behavior*, 21, 391–410.
- Boyce, M. S., & Perrins, C. M. (1987). Optimizing great tit clutch size in a fluctuating environment. *Ecology*, 68, 142–153.
- Boyd, R., & Richerson, P. J. (1985). Culture and the evolutionary process. Chicago: University of Chicago Press.
- Bradshaw, J., Finch, N., Mayhew, E., Ritakallio, V., & Skinner, C. (2006). *Child poverty in large families*. Bristol: The Policy Press.
- Carey, A. D., & Lopreato, J. (1995). The evolutionary demography of the fertility-mortality quasiequilibrium. *Population and Development Review*, 21, 613–630.
- Cooney, T. M., & Uhlenberg, P. (1992). Support from parents over the life course: the adult perspective. Social Forces, 71, 63–84.
- Conley, D. (2001). Capital for college: parental assets and postsecondary schooling. Sociology of Education, 74, 59–72.
- Cronk, L. (1991). Wealth, status and reproductive success among the Mukogodo. *American Anthropologist, 93*, 345–360.

- De Vogli, R., Gimeno, D., Martini, G., & Conforti, D. (2007). The pervasiveness of the socio-economic gradient of health. European Journal of Epidemiology, 22, 143–144.
- Desai, S. (1995). When are children from large families disadvantaged? Evidence from cross-national analyses. *Population Studies*, 49, 195–210.
- Downey, D. B. (1995). When bigger is not better: family size, parental resources and children's educational performance. *American Sociological Review*, 60, 746–761.
- Downey, D. B. (2001). Number of siblings and intellectual development: the resource dilution explanation. *American Psychologist*, 56, 497–504.
- Eggers, S., Griesser, M., Nystrand, M., & Ekman, J. (2006). Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. *Proceedings of the Royal Society, B: Biological Sciences*, 273, 701–706.
- Ellison, P. T. (2003). Energetics and reproductive effort. American Journal of Human Biology, 15, 342– 351.
- Fieder, M., & Huber, S. (2007). The effects of sex and childlessness on the association between status and reproductive output in a modern society. *Evolution and Human Behavior*, 28, 392–398.
- Foster, C. (2000). The limits to low fertility: a biosocial approach. *Population and Development Review*, 26, 209–234.
- Gillespie, D., Russell, A., & Lummaa, V. (2008). When fecundity does not equal fitness: effects of an offspring quantity versus quality trade-off in pre-industrial humans. *Proceedings of the Royal Society*, *B: Biological Sciences*, 275, 713–722.
- Golding, J., Pembrey, M., Jones, R., & Team, A. S. (2001). ALSPAC—The Avon Longitudinal Study of Parents and Children, I: study methodology. *Paediatric and Perinatal Epidemiology*, 15, 74–78.
- Grawe, N. (2010). Bequest reciept and family size effects. *Economic Inquiry*, 48, 156–162. doi:10.1111/j.1465-7295.2008.00208.x. Published online April 2009.
- Hagen, E. H., Hames, R. B., Craig, N. M., Lauer, M. T., & Price, M. E. (2001). Parental investment and child health in a Yanomamo village suffering short-term food stress. *Journal of Biosocial Science*, 33, 503–528.
- Hagen, E. H., Barrett, C., & Price, M. E. (2006). Do human parents face a quantity-quality tradeoff? Evidence from a Shuar community. *American Journal of Physical Anthropology*, 130, 405– 418.
- Hart, C. L., & Davey Smith, G. (2003). Relation between number of siblings and adult mortality and stroke risk: 25 year follow up of men in the collaborative study. *Journal of Epidemiology and Community Health*, 57, 385–391.
- Hay, A. D., Heron, J., Ness, A., & The ALSPAC Study Team. (2005). The prevalence of symptoms and consultations in pre-school children in the Avon Longitudinal Study of Parents and Children (ALSPAC): a prospective cohort study. *Family Practice*, 22, 367–374.
- Hill, S. E., & Reeve, H. K. (2005). Low fertility in humans as the evolutionary outcome of snowballing resource games. *Behavioural Ecology*, 16, 398–402.
- Hopcroft, R. L. (2006). Sex, status and reproductive success in the contemporary United States. Evolution and Human Behavior, 27, 104–120.
- Irons, W. (1998). Adaptively relevant environments versus the environment of evolutionary adaptedness. Evolutionary Anthropology, 6, 194–204.
- Iacovou, M., and Berthoud, R. (2006). *The economic position of large families*. DWP Research Report No. 358. Leeds: Corporate Document Services for the Department for Work and Pensions.
- Kanazawa, S. (2003). Can evolutionary psychology explain reproductive behaviour in the contemporary United States? *Sociological Quarterly*, 44, 291–302.
- Kaplan, H. (1996). A theory of fertility and parental investment in traditional and modern human societies. Yearbook of Physical Anthropology, 39, 91–135.
- Kaplan, H., & Gangestad, S. (2005). Life history theory and evolutionary psychology. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 68–95). New York: Wiley.
- Kaplan, H., Lancaster, J. B., Bock, J., & Johnson, S. (1995). Fertility and fitness among Albuquerque men: a competitive labour market theory. In R. I. M. Dunbar (Ed.), *Human reproductive decisions: Biological and social perspectives* (pp. 96–136). London: Macmillan.
- Kaplan, H., Lancaster, J. B., Tucker, W. T., & Anderson, K. G. (2002). An evolutionary approach to below replacement fertility. *American Journal of Human Biology*, 14, 233–256.
- Keister, L. A. (2003). Sharing the wealth: the effect of siblings on adults' wealth ownership. *Demography*, 40, 521–542.
- Keister, L. A. (2004). Race, family structure, and wealth: the effect of childhood family on adult asset ownership. *Sociological Perspectives*, 47, 161–187.

Kohler, H. P. (2001). Fertility and social interaction. Oxford: Oxford University Press.

Lack, D. (1947). The significant of clutch size. Ibis, 89, 302-352.

- Lawson, D. W., & Mace, R. (2008). Sibling configuration and childhood growth in contemporary British families. *International Journal of Epidemiology*, 37, 1408–1421.
- Lawson, D. W., & Mace, R. (2009). Trade-offs in modern parenting: a longitudinal study of sibling competition for parental care. *Evolution and Human Behavior*, 30, 170–183.
- Lee, R. (2003). The demographic transition: three centuries of fundamental change. Journal of Economic Perspectives, 17, 167–190.
- Little, R., & Rubin, D. (1987). Statistical analysis with missing data. New York: Wiley.
- Livi-Bacci, M. (1986). Social-group forerunners of fertility control in Europe. In A. Coale & S. C. Watkins (Eds.), *The decline of fertility in Europe* (pp. 182–200). Princeton: Princeton University Press.
- Low, B. S. (1991). Reproductive life in 19th-century Sweden—an evolutionary perspective on demographic phenomena. *Ethology and Sociobiology*, 12, 411–448.
- Mace, R. (1996). Biased parental investment and reproductive success in Gabbra pastoralists. *Behavioral Ecology and Sociobiology*, 38, 75–81.
- Mace, R. (1998). The coevolution of human wealth and inheritance strategies. *Philosophical Transactions of the Royal Society of London, B: Biological Sciences*, 353, 389–397.
- Mace, R. (2007). The evolutionary ecology of human family size. In R. I. M. Dunbar & L. Barrett (Eds.), The Oxford handbook of evolutionary psychology (pp. 383–396). Oxford: Oxford University Press.
- Mace, R. (2008). Reproducing in cities. Science, 319, 764-766.
- Marmot, M. (2005). Social determinants of health inequalities. Lancet, 365, 1099-1104.
- McNamara, J. M., & Houston, A. I. (2006). State and value: a perspective from behavioural ecology. In J. C. K. Wells, S. S. Strickland, & K. N. Laland (Eds.), *Social information transmission and human biology* (pp. 59–88). London: Taylor and Francis.
- Meij, J. J., van Bodegom, D., Ziem, J. B., Amankwa, J., Polderman, A. M., Kirkword, T. B. L., et al. (2009). Quality-quantity trade-off of human offspring under adverse environmental conditions. *Journal of Evolutionary Biology*, 22, 1014–1023.
- Montgomery, M. R., & Casterline, J. B. (1996). Social learning, social influences, and new models of fertility. *Population and Development Review*, 22, 151–175.
- Nettle, D. (2008). Why do some dads get more involved than others? Evidence from a large British cohort. Evolution and Human Behavior, 29, 416–423.
- Nettle, D., & Pollet, T. (2008). Natural selection on male wealth in humans. American Naturalist, 172, 658–666.
- Newson, L., Postmes, T., Lea, S. E. G., & Webley, P. (2005). Why are modern families small? Toward an evolutionary and cultural explanation for the demographic transition. *Personality and Social Psychology Review*, 9, 360–375.
- Newson, L., Postmes, T., Lea, S. E. G., Webley, P., Richerson, P. J., & McElreath, R. (2007). Influences on communication about reproduction: the cultural evolution of low fertility. *Evolution and Human Behavior*, 23, 199–210.
- Northstone, K., & Emmett, P. (2005). Multivariate analysis of diet in children at four and seven years of age and associations with socio-demographic characteristics. *European Journal of Clinical Nutrition*, 59, 751–760.
- Penn, D. J., & Smith, K. R. (2007). Differential fitness costs of reproduction between the sexes. Proceedings of the National Academy of Sciences (USA), 104, 553–558.
- Pennington, R., & Harpending, H. (1988). Fitness and fertility among Kalahari !Kung. American Journal of Physical Anthropology, 77, 303–319.
- Pérrusse, D. (1993). Cultural and reproductive success in industrial societies: testing the relationship at the proximate and ultimate levels. *Behavioral and Brain Sciences*, 16, 267–323.
- Petrou, S., Kupek, E., Hockley, C., & Goldacre, M. (2006). Social class inequalities in childhood mortality and morbidity in an English population. *Paediatric and Perinatal Epidemiology*, 20, 14–23.
- Quinlan, R. J. (2007). Human parental effort and environmental risk. Proceedings of the Royal Society, B: Biological Sciences, 247, 121–125.
- Risch, T. S., Dobson, F. S., & Murie, J. O. (1995). Is mean litter size the most productive? A test in Columbian ground squirrels. *Ecology*, 76, 1643–1654.
- Roff, D. A. (2002). Life history evolution. Sunderland: Sinauer Associates.
- Rogers, A. R. (1990). Evolutionary economics of human reproduction. *Ethology and Sociobiology*, 11, 479–495.
- Rotkirch, A. (2007). All that she wants is a(nother) baby? Longing for children as a fertility incentive of growing importance. *Journal of Evolutionary Psychology*, 5, 89–104.

- Sear, R., Lawson, D. W., & Dickins, T. (2007). Synthesis in the human evolutionary behavioural sciences. Journal of Evolutionary Psychology, 5, 3–28.
- Singer, J. D., & Willett, J. B. (2003). Applied longitudinal data analysis: Modelling change and event occurrence. Oxford: Oxford University Press.
- Stearns, S. C. (1992). The evolution of life history. Oxford: Oxford University Press.
- Steelman, L., & Powell, B. (1989). Acquiring capital for college: the constraints of family configuration. American Sociological Review, 54, 844–855.
- Steelman, L., Powell, B., Werum, R., & Carter, S. (2002). Reconsidering the effects of sibling configuration: recent advances and challenges. *Annual Review of Sociology*, 28, 243–269.
- Strassmann, B. I., & Gillespie, B. (2002). Life-history theory, fertility and reproductive success in humans. Proceedings of the Royal Society London, B: Biological Sciences, 269, 553–562.
- Thorpe, K. J., Dragonas, T., & Golding, J. (1992). The effects of psychosocial factors on the emotional well-being of women during pregnancy: a cross-cultural study of Britain and Greece. *Journal of Reproductive and Infant Psychology*, 10, 191–204.
- Tuomi, J., Hakala, T., & Haukioja, E. (1983). Alternative concepts of reproductive effort, costs of reproduction, and selection in life-history evolution. *American Zoologist*, 23, 25–34.
- van Noordwijk, A. J., & de Jong, G. (1986). Acquisition and allocation of resources: their influence on variation in life history tactics. *American Naturalist*, 128, 137–142.
- Voland, E. (1990). Differential reproductive success within the Krummhörn population (Germany, 18th and 19th centuries). *Behavioral Ecology and Sociobiology*, 26, 65–72.
- Voland, E., & Dunbar, R. I. M. (1995). Resource competition and reproduction. Human Nature, 6, 33-49.
- Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist*, 100, 687–690.
- Winterhalder, B., & Leslie, P. (2002). Risk-sensitive fertility: the variance compensation hypothesis. Evolution and Human Behavior, 23, 59–82.

David W. Lawson is a research fellow at the Centre for Population Studies, London School of Hygiene and Tropical Medicine. He has research degrees in evolutionary psychology and biological sciences and received his Ph.D. in anthropology from University College London in 2009. His research interests focus on the behavioral ecology of the human family and the application of life history theory to parental investment strategies and child development in traditional and modern populations.

Ruth Mace is a professor of evolutionary anthropology at University College London. She is a fellow of the British Academy. Her research interests include a range of topics in human behavioral ecology and cultural evolution, including reproductive decision-making, life history evolution, parental investment and intergenerational transfers, the evolution of altruism, and also macro-evolutionary studies of human cultural diversity, including kinship and social organization, using cultural phylogenetics.