

# Life History Theory & Human Reproductive Behaviour

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The marvel of the natural world lies in its diversity. Variation in life histories, which, by clear Darwinian logic, will be subject to strong forces of natural selection, hold particular captivation for evolutionary biologists. For example, the number of offspring produced during a single reproductive bout (referred to as 'clutch size') ranges between a few relatively large offspring (most birds and mammals) to 10s or 100s of intermediate size (most insects and plants) to the 1000s of miniscule offspring produced by some marine invertebrates. Many species are 'iteroparous', spreading reproduction over sequential breeding periods, while, more rarely, species such as salmon and 'annual plants' like watermelon and cauliflower, structure their life-cycle around a single act of reproduction, closely followed by death. Reproductive maturity is reached relatively soon after birth in many species, while in others, including our own, offspring spend an extended period in immature or juvenile states, often heavily reliant on extensive parental care. Within the phenotypic constraints of a species, such life history parameters also demonstrate considerable plasticity across local ecological and demographic conditions. Life history theory is the principal analytical framework concerned with the study of this variation, and since its inception has fuelled an extensive research programme in evolutionary and behavioural ecology (Lessells, 1991; Roff, 2002; Stearns, 1992).

The fundamental concept of life history theory is that observed life histories are constrained by a combination of finite resource budgets and the 'Principle of Allocation', that is, resources (time, energy, effort) allocated to one function cannot be allocated to another (Cody, 1966). Thus, natural selection cannot simultaneously optimise individual life history

traits in isolation, but instead must optimise realisable trade-offs between competing dimensions of an organism's life history. At the macro level, these competing functions are normally recognised as survival, growth, and reproduction, but are more commonly analysed within finer sub-divisions, most notably, the trade-off between investment in current versus future reproduction, and between quantity of offspring and levels of parental care (Gadgil & Bossert, 1970; Stearns, 1992).

As a branch of evolutionary ecology, life history theory takes an optimality approach (see Parker & Smith, 1990) to understanding variation in observed life histories; recognising that the maximisation of inclusive fitness will be served by distinct phenotypic optima across varying ecological and demographic niches, and in relation to individual condition and resource access. Life history studies are thus principally concerned with deriving and testing predictions about the particular optima populations and individuals can be expected to evolve under natural selection of various alternative strategies. In recent years, increasing research attention has also been devoted to the mechanisms of life history adaptation and the developmental, physiological, and cognitive constraints which may prevent observed life histories reaching predicted optima (Partridge & Sibly, 1991).

In this chapter, I concentrate on the application of life history theory to the diversity of reproductive strategies observed in human populations. This area of research has traditionally been dominated by anthropologists and demographers adopting the theory and methods of evolutionary ecology (Hill, 1993; Hill & Kaplan, 1999; Kaplan et al., 2000; Low, 2001; Lummaa, 2007; Mace, 2000, 2007; Voland, 1998). Evolutionary psychologists and researchers of cultural evolution have also become active players in life history research, particularly in the context of 'culturally modern' populations, incorporating new hypotheses and research methodologies into the field (Borgerhoff Mulder, 1998a; Kaplan & Gangestad, 2005). I first overview the main trade-offs faced in human life history and the key socio-ecological factors that may shift the costs and benefits associated with their resolution. I focus this section on contemporary and historical hunter-gatherer and agriculturalist societies. Using the example of human family size (offspring number), I then focus in more detail on the issue of individual optimisation of life history in both traditional high fertility populations and those which have

undergone a demographic transition to modern low fertility. The chapter is rounded off with some thoughts on the key future directions for human life history research.

## Trade-offs in human life history

### Methodological Issues

The first step in any life history study is to identify and measure the underlying trade-offs that constrain the option set of reproductive strategies available to an organism. Quantifying trade-offs is, however, complicated by the problem of phenotypic correlations: individuals with access to a large pool of resources may be able to divert investments into multiple traits simultaneously, while individuals with relatively poor resource access will invest little effort in the same traits. Such variation can obscure a trade-off, leading to positive correlation between two competing functions, rather than the negative correlation predicted by the Principle of Allocation (van Noordwijk & de Jong, 1986).

Experimental methods, which manipulate single factors in isolation, are often used to get around this problem in animal studies. For example, in birds, the consequences of clutch size strategy have been explored by artificially manipulating the number of eggs per nest and measuring chick survival and recruitment rates against a control group (e.g., Gustafsson & Sutherland, 1988; Pettifor et al., 2001). Researchers interested in human life history must rely on observational methods, measuring covariation between life history traits and fitness-related outcomes from unmanipulated conditions, while statistically controlling for differences in individual resource base. This alternative method is widely acknowledged as problematic, as results will be “unreliable unless a strong case can be made that all relevant variables have been included in the analysis” (Roff, 2002, p. 149). Relevant heterogeneity between individuals is often difficult to measure, particularly in cases when intrinsic factors are important (including genetic differences). Thus, methodological concerns are a recurrent issue in discussions of human life history (e.g., Gagnon et al., 2009; Lawson & Mace, 2009; Sear, 2007).

### Trade-offs between growth and reproduction

Humans exaggerate the extension of juvenility which characterises primate taxa relative to other mammals (Pereira & Fairbanks, 2002). Unlike our primate cousins, feeding dependency also extends far beyond weaning, so that one or more elder offspring may require

provisioning while the mother simultaneously nurses a young infant (Bogin, 1997; Gurven & Walker, 2006; Lancaster & Lancaster, 1987). From a life history perspective, this relatively long period of juvenile dependence can be understood in terms of a trade-off between investments in growth-related benefits on the one hand and immediate sexual maturity and reproduction on the other. Delayed maturity has the potential to improve adult reproductive potential, because of physical benefits such as large body size (which also reduces offspring mortality; e.g., Allal et al., 2004; Sear et al., 2004) and, perhaps particularly fundamental to human resource and mate competition, because it facilitates brain development and increased investment in learning-based knowledge (Bogin, 1997; Kaplan et al., 2000). Yet, in the face of extrinsic mortality hazards, such as predation, food shortages or con-specific violence, delayed maturity can also increase chances of reproductive failure. A reduction in extrinsic mortality over the course of human evolutionary history is, therefore, considered a necessary precursor for the evolution of our relatively 'slow' life histories (Charnov, 1993). Comparison of chimpanzee to hunter-gatherer mortality rates suggests this reduction has been significant, with, for example, the probability of survival to age 15 for contemporary hunter-gatherer populations almost twice as high as that recorded for wild chimpanzees (Kaplan et al., 2000).

Differences in extrinsic mortality rates may also explain differences in growth between human populations. Human height is normally considered a product of differences in nutrition and environmental stress (leading many studies to use growth as a general biomarker for physical health and related aspects of the early rearing environment; e.g., Lawson & Mace, 2008). However, while such factors are robust predictors of growth patterns within populations, they correspond relatively weakly to cross-population variation in adult heights suggesting important genetic differences remain (Deaton, 2007). For example, pygmy populations found in regions of Africa, Southeast Asia, and South America, have notably small adult heights, defined as population mean male stature of less than 155cm (around 5 foot), in comparison to related populations with similarly poor levels of childhood nutrition (Migliano et al., 2007; Perry & Dominy, 2009). Migliano et al. (2007) argue that the unique growth pattern of pygmy populations is a direct consequence of their exceptionally high levels of childhood and adult mortality. Consistent with this hypothesis, modal age at first reproduction in pygmy populations is also exceptionally early, and women who reproduce at these earlier ages have

higher predicted fitness than comparative late starters (Migliano et al., 2007; see also Walker et al., 2006).

### **Trade-offs between current reproduction and future success**

Once mature, investment in current reproduction must also be traded off against the allocation of resources to future survival and reproduction. A simple formulation of life history theory therefore predicts, all else being equal, negative effects of early fertility on later survival and reproduction (Gadgil & Bossert, 1970; Kirkwood, 1977; Williams, 1966). An early test of this hypothesis using historical data on the British aristocracy provided apparent strong evidence that current versus future trade-offs constrain human life history, demonstrating a positive association between age at first birth and longevity and a reduction in number of offspring produced for women living beyond 80 years (Westendorp & Kirkwood, 1998). This study has, however, drawn serious methodological criticism, regarding analysis design and incomplete genealogies (Le Bourg, 2001), and related investigations have found it difficult to replicate their results, with now perhaps almost as many studies finding the predicted negative relationships between early fertility and later success as those finding null or positive relationships (Le Bourg, 2007).

Some of this variation may reflect context-dependency: Lycett et al. (2000), for example, in an analysis of a historical dataset of the German Krummhörn population, report that fertility had a negative impact on maternal longevity, but only amongst landless peasants (with wealthier families apparently able to simultaneously invest in high fertility and survival related maintenance). Methodological problems in controlling for such heterogeneity in resource base between families, often particularly difficult in historical samples, may account for null findings in some cases (Gagnon et al., 2009; Lummaa, 2007; Sear, 2007). The most recent research suggests the trade-off is detectable, providing fertility is relatively high and the sufficient adjustments are made for differences in socioeconomic and maternal health status; with a sophisticated comparative analysis of two historical datasets from Quebec and one from Utah demonstrating a negative effect of parity and a positive effect of age at last birth on postreproductive survival in all three populations (Gagnon et al., 2009).

The consequences of high investment in current reproduction can also be measured in comparison of mothers who produce singletons and twins. These studies are less susceptible to the problem of phenotypic correlations, because twinning rates can effectively be treated as random with respect to many socio-demographic factors which may otherwise confound associations between fertility and later outcomes (Lummaa, 2007). Accordingly, a number of studies have documented increased likelihood of maternal death at child birth in twin deliveries (Gabler & Volland, 1994; Haukioja et al., 1989; McDermott et al., 1995). There is also evidence that women bearing twins have increased post-reproductive mortality, and are more likely to fail to raise their next offspring, or to terminate reproduction altogether, as compared to mothers producing singletons (Helle et al., 2004; Lummaa, 2001; Sear, 2007).

Just as twins are more costly than a single birth, male foetuses also receive higher energy allocations during pregnancy. They have a faster rate of growth (Marsal et al., 1996), are heavier at birth (Anderson & Brown, 1943; Loos et al., 2001), and pregnant women carrying a male foetus have been shown to have a higher energy intake than those carrying a female (Tamimi et al., 2003). Some studies have also reported relatively long birth intervals following male births, suggesting increases in early post-natal investment practices such as breastfeeding (e.g. Mace & Sear, 1997). In light of these inequalities, higher reproductive costs of son relative to daughter production on future reproduction or survival might be anticipated. Support for a negative impact of sons on maternal longevity has been gathered from a number of studies, including historical populations in Finland (Helle et al., 2002), Belgium (van De Putte et al., 2004), Bangladesh (Hurt et al., 2006), and possibly Germany (Beise & Volland, 2002). The magnitude of effects and relative impact of the sexes is, however, far from uniform across studies, and in some cases differences are only apparent in particular subgroups. This suggests the increased physiological expense of male births, may interact to varying degrees with the wider costs and benefits of rearing offspring of each sex. For example, due to differing contributions to household tasks and later patterns of resource transfer at marriage. Future studies are required to disentangle these effects.

Humans are remarkable among other primates, and animals in general, because females experience menopause – the fixed and irreversible cessation of reproductive potential at around 50 years of age, several decades before the end of the life span. Thus, human

females have evolved to selectively invest resources into longevity at a cost to any chance of further reproduction, which at face value seems difficult to reconcile with an optimisation of life history. Why would natural selection not favour continued reproduction and earlier death? The 'grandmother hypothesis' provides one possible explanation, which has generated much debate in the literature (Hawkes, 2003; Mace, 2000; Marlowe, 2000; Peccei, 2001; Williams, 1957). According to this hypothesis, post-menopausal women are better able to enhance their lifetime reproductive success by assisting their current children to reproduce successfully than they would be having additional children of their own, which may be more costly at older ages due to increased difficulties in childbirth (which may also endanger current offspring) and less chance of surviving long enough to provide adequate post-natal care.

Because all women experience menopause we cannot directly examine the costs and benefits of alternative strategies. However, studies from a range of populations confirm the existence of significant grandmaternal effects on offspring fertility and the health and survival of grandchildren (Gibson & Mace, 2005; Hawkes et al., 1997; Lahdenpera et al., 2004; Sear & Mace, 2008). In fact, it has been suggested that it is this help from grandmothers, along with other extended kin, which has enabled humans to simultaneously maintain relatively high reproductive rate and extended juvenile dependency relative to other primates of similar body size (Hawkes, 2003). Modelling work based on observed life histories and grandmother effects in rural Gambia suggests that these effects may be sufficient to explain the evolution of human menopause (Shanley et al., 2007).

### **Trade-offs between quantity and quality of offspring**

Resources invested in increasing reproductive rate cannot be invested in advancing the development and competitive prospects of offspring. Life history theory therefore predicts a further trade-off between fertility and offspring survival and reproductive success (Lack, 1954; Smith & Fretwell, 1974; Williams, 1966; see also Box 6.1). This simple concept of a 'quantity-quality trade-off', albeit without specific reference to Darwinian fitness, is also central to economic models of the human family (Becker, 1981; Blake, 1989; Downey, 2001). Studies of child mortality provide strong support of quantity-quality trade-off models when spacing between births is narrow, with most populations demonstrating a negative effects of short birth intervals on child mortality (Gibson & Mace, 2006; Hobcraft et al., 1985; Rutstein, 1984).

These costs are probably best explained by poor recovery of maternal somatic resources between births and by dilution of the particularly intense care required in the first years of infant life. Accordingly, excessively short birth intervals are rare in human populations. Chances of early survival are also substantially reduced in children from multiple births (Gabler & Volland, 1994; Rutstein, 1984; Sear et al., 2001).

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**Insert Box 6.1 about here**  
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Considering associations between total family size and offspring outcomes across the full range of observed birth intervals presents a more complex picture. Studies of hunter-gatherer communities have not found strong evidence of quantity-quality trade-off effects. Among the !Kung, an African hunter-gatherer group on which the earliest studies of human life history were carried out (Blurton-Jones, 1986), researchers have failed to demonstrate higher mortality in children with many siblings (Draper & Hames, 2000; Pennington & Harpending, 1988). Among the South American Aché, number of siblings depressed likelihood of survival between the ages of 5 and 9 years. However, infant mortality below these ages was uninfluenced by parental fertility (Hill & Hurtado, 1996). Furthermore, in both populations, large sibships failed to depress female reproductive success and were actually associated with higher fertility for males (Draper & Hames, 2000; Hill & Hurtado, 1996).

Negative relationships between family size and child survival have been more effectively demonstrated in a number of contemporary African agriculturalist societies (Meij et al., 2009; Strassmann & Gillespie, 2002; see Figure 6.1, but see Borgerhoff Mulder 1998b) and historical European and American populations (Gillespie et al., 2008; Penn & Smith, 2007; Volland & Dunbar, 1995). There is also evidence of an association between family size and child anthropometric status among surviving children. Negative effects have been suggested in the South American Yanomamö (Hagen et al., 2001) and Shuar (Hagen et al., 2006), while in a cross-national analysis of 15 developing populations, Desai (1995) found height-for-age in children less than 3-years-old is significantly reduced by the presence of siblings close in age in almost all cases. However, despite using the same set of covariates for each country, effect magnitude was highly variable.

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**Insert Figure 6.1 about here**

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Studies of marital and reproductive success, focusing on the division of inherited capital such as land or cattle, also show clear costs of resource division between siblings which survive childhood. As inheritance usually goes to males these effects are particularly visible on sons. For example, Mace (1996) found a negative effect of older brothers on male reproductive success in the Kenyan Gabbra. This resulted from smaller initial bridewealth herds and later age at marriage in comparison with their elder brothers. Number of sisters however, had a moderately positive effect on male reproductive success. Similar effects have been demonstrated on the Kenyan Kipsigis (Borgerhoff Mulder 1998b). Gillespie et al. (2008) found that large sibships reduced survival, but not fertility among survivors in 18<sup>th</sup>-19<sup>th</sup> century Finland. However, this analysis did not test for sex-specific effects. In analysis of 19<sup>th</sup> century Swedish data, Low (1991) found that both men's and women's reported reproductive success decreased as number of siblings increased, but particularly for men, and particularly with respect to number of brothers. Voland and Dunbar (1995) show that in 18<sup>th</sup>-19<sup>th</sup> century Germany, number of same-sex siblings reduced likelihood of marriage, which likely further reduces reproductive success for both sexes.

In summary, a number of lines of evidence confirm that the human family is characterised by trade-off effects in the quantity and quality of children. However, for each outcome considered, be it survival, health or reproductive success, the effects of large family size appear somewhat variable and in a significant number of studies trade-offs are absent or positive effects are reported. Methodological issues may account for much of this variance. In particular, trade-offs may go undetected in the absence of sufficient controls of family level resources (van Noordwijk & de Jong, 1986). This may be a particular issue for studies of relatively egalitarian hunter-gathers who, unlike agriculturalist or wage-labour communities, lack obvious measures of relevant resource variation between families (Draper & Hames, 2000; Hill & Kaplan, 1999; see also Box 6.2).

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**Insert Box 6.2 about here**

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But should we anticipate a uniform pattern of trade-off functions across cultures? Children often contribute significantly to economic pursuits in traditional societies, such as foraging, and may play important roles as ‘alloparents’ (Kramer, 2005; Sear & Mace, 2008). While the benefits of these behaviours may rarely offset the net drain on family resources, engagement in these activities may modify the local costs of sibling resource competition. Wider patterns of cooperative breeding, whereby relatives share the burden of childcare may also alleviate trade-offs to varying degrees (Desai, 1992, 1995; Sear & Mace 2008). In many contexts, siblings may serve as valuable political allies, such as in providing an advantage in community disputes or access to neighbouring hunting or foraging territories (Draper & Hames, 2000). Environmental risk factors associated with local socioecology and levels of economic development will also influence relationships between parental care and offspring development, establishing different trade-off functions (Lawson & Mace, 2011; Quinlan, 2007; Winterhalder & Leslie, 2002). I discuss this point further in the context of modernisation later in the chapter. Finally, cross-culturally variable patterns of biased parental investment by offspring sex and birth order will alter the costs and benefits of siblings (considered in more depth by Sear, this volume).

## The optimisation of family size in traditional societies

### Mechanisms of fertility optimisation

The evolutionary ecology approach predicts that observed life histories represent ecologically dependent individual optima of fitness maximisation (sometimes referred to as the ‘individual optimisation hypothesis’: Pettifor et al., 2001). A number of mechanisms by which the human organism responds to local socioecology to optimise the quantity-quality trade-off have been proposed. At the physiological level, for example, automatic suppression of ovulation through lactational amenorrhea while nursing a young infant, or due to intense physical stress or nutritional deficit, prevents conception and subsequent dilution of parental investment at a time when current offspring are highly vulnerable (Bentley, 1999; Ellison, 1990; Ellison, 2003; see also Bribiescas, 2001).

At the psychological level, we can expect reproductive decision making to be regulated by equivalent cognitive mechanisms utilising environmental information on observed or expected relationships between parental investment and offspring development (Kaplan, 1996; Kaplan & Gangestad, 2005; but see Box 6.3). Experimental studies show that such

cognitive mechanisms are important regulators of fertility behaviour 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 adjust current clutch size, even when predation itself is not increased. In humans, behavioural pathways of fertility regulation may often be institutionalised in cultural practices, such as rules regulating marriage, inheritance, celibacy, contraception, and in extreme cases infanticide and abandonment (Hrdy, 1999; Kaplan, 1996). In modern societies, it has also be argued that we can add individual use of novel reproductive technologies including abortion and artificial fertility treatments to the list of strategic tools available to optimise reproductive timing and achieved family size (e.g., Lycett & Dunbar, 1999) .

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### **Predicted optima and observed fertility**

Animal behavioural ecologists have tested the individual optimisation hypothesis with the prediction that neither the experimental addition or removal of young will result in increased parental fitness relative to control broods (e.g., Gustafsson & Sutherland, 1988; Humphries & Boutin, 2000; Pettifor et al., 2001; Tinbergen & Daan, 1990). Anthropologists have had to make do with alternative methods. One approach has been to first determine the fertility level that leads to the highest fitness returns in some measurable currency (while controlling for differences in parental resources) and then to compare this to the population mode. If fertility is optimised, then optimal and modal fertility should converge.

Studies of the !Kung (Draper & Hames, 2000; Pennington & Harpending, 1988) and Aché (Hill & Hurtado, 1996) reveal positive linear relationships between number of children, and the lifetime reproductive success of the mother. This implies that both groups of hunter-gatherers failed to optimise family size, as higher fitness could have been achieved by increasing fertility beyond observed levels. Borgerhoff Mulder's (2000) study of the Kipsigis identified a quantity-quality trade-off in family size, with intermediate numbers of children maximising grandchildren for women, but not for men. For women, the calculated optima corresponded with the population mode. In the Dogon, Strassmann and Gillespie (2002) found family size had a clear negative effect on child survival rates, so that an intermediate level of fertility (eight offspring) optimised this measure of reproductive success (Figure 6.1). A large

majority of women had a completed fertility within the confidence limits of this estimate, leading the authors to conclude that observed family size optimised parental fitness. However, more recent studies of child survival attempting to replicate the results of Strassmann and Gillespie (2002) have found little evidence that intermediate levels of fertility maximize number of surviving children (e.g., Meij et al., 2009).

The mixed success of these studies may largely rest on the difficulty involved in calculating precise fertility optima with available data (Hill & Hurtado, 1996). Lifetime reproductive success, as measured by number of surviving children or grandchildren, is probably an effective proxy for fitness in many ecologies, provided mortality rates are relatively high (Jones, 2009). However, studies focusing on child survival alone will not detect negative effects of large family size, which become apparent in later life, such as through early death of the mother (Meij et al., 2009) or in future generations caused by the division of inherited resources (McNamara & Houston, 2006). Hence, such studies are likely to systematically overestimate the optimum family size. This line of reasoning is consistent with the fact that all studies that have failed to demonstrate a convergence between modal and optimal fertility have suggested that observed levels lie below the optimum.

### **Wealth and reproductive success**

A more generalised approach, that does not require the calculation of precise optima, is to consider covariation in the strength of trade-off effects and observed fertility. Life history studies typically operate under the assumption that negative effects of competition between offspring are at their strongest when resources are scarce (Tuomi et al., 1983; van Noordwijk & de Jong, 1986). Economic models of the family have also assumed that, since quantity-quality trade-offs are driven by 'credit constraint', increases in personal or societal wealth will reduce negative effects of high fertility on offspring (Becker & Lewis, 1973; Grawe, 2010). Empirical support for this position has been demonstrated in a number of animal studies (e.g. Boyce & Perrins, 1987; Risch et al., 1995).

In humans, costs of high parental fertility in individual offspring have been shown to be less pronounced in relatively wealthy strata in both contemporary African (Borgerhoff Mulder, 2000; Meij et al., 2009) and 18<sup>th</sup>-19<sup>th</sup> century European agriculturalists (Gillespie et al., 2008; Lummaa et al., 1998). Therefore, positive relationships between individual wealth and family size are anticipated, as when sibling competition is relaxed there are fewer costs to outweigh

the benefits of large family size. Consistent with widespread fertility optimisation, anthropologists and historical demographers have demonstrated strong positive relationships between socioeconomic status and fertility in practically all traditional societies where such relationships have been considered (Borgerhoff Mulder, 1987; Cronk, 1991; for a review, see Hopcroft, 2006).

## The optimisation of family size in modern societies

### The demographic transition

Demographic transition refers to the population shift from high mortality and fertility to low mortality and fertility which typically occurs in the economic development of a population from a pre-industrial to an industrialised economy. In classic models, this is a multi-stage process starting with a fall in death rates, followed in time by reduced birth rates, leading to an interval of first increased, and then decreased population growth (Coale & Watkins, 1986; Lee, 2003). The first demographic transitions occurred in northwest Europe, where mortality began a secular decline around 1800. It has now 'spread' to all areas of the world, with most developing populations in at least the early stages of transition, and the completion of a 'global demographic transition' projected by 2100 (Lee, 2003).

Initial mortality declines in modernising countries were largely driven by innovations in healthcare along with advancements in food storage and transportation which reduced rates and susceptibility to infectious disease and famine. Changes in mortality were mostly focused on infants and children, with death becoming increasingly concentrated in a relatively narrow band of older age. Following these advancements, fertility began to decline in most European countries between 1890 and 1920 (Coale & Treadway, 1986). However, there are notable cases where fertility decline has commenced without prior shifts in mortality, presenting a challenge to transition theories that envisage fertility decline as a direct response to mortality shifts. Less developed countries began to reduce fertility from around the 1960s, with fertility decline typically occurring more rapidly than for those in current developed countries (Lee, 2003). The total fertility rate has now fallen to below replacement level in practically all industrialised populations and many countries in East Asia.

Modern post-demographic transition societies immediately appear at odds with adaptive models of fertility optimisation (Borgerhoff Mulder, 1998a; Vining, 1986). 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. Current levels of resource abundance appear to buffer out any evolutionarily relevant costs of high fertility on offspring survival or reproduction. This is demonstrated by a number of studies applying traditional life history models to modern fertility. In all cases, researchers have failed to detect any trade-off between number of children and grandchildren, even in very large families, suggesting observed family sizes fall considerably below any fitness maximising optimum (Kaplan et al., 1995; Mueller, 2001; see Figure 6.2).

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Secondly, although there is wide variation in timing, speed and magnitude across societies, fertility decline within societies is generally characterised by markedly larger reductions of fertility in wealthy families compared to the rest of the population (Clark & Cummins, 2009; Livi-Bacci, 1986). As a consequence, modern fertility is not only dramatically reduced in comparison to traditional populations but is also typified by relative socioeconomic levelling (Nettle & 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; Lawson & Mace, 2009). Some studies have suggested that when education is held constant, positive correlations between income and fertility persist, at least for males (Fieder & Huber, 2007; Hopcroft, 2006; Nettle & Pollet, 2008). However, these relationships appear to operate on mating success, rather than reproductive success per se (that is, influencing levels of childlessness, rather than family size amongst reproducing individuals) and remain considerably weaker than relationships observed in traditional societies (Nettle & Pollet, 2008). Alternative evolutionary models, emphasising inherent limitations in evolved mechanisms of adaptation, have consequently gathered popularity as explanations of modern fertility decline.

### **Maladaptation to novel contraceptive technologies**

Adaptive behaviour 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). Modern fertility patterns may, therefore, be explained

by the interaction of ancestrally formed adaptations and novel socioecological factors. Taking this perspective, many evolutionary psychologists have argued that the widespread availability of efficient birth control technology in modern environments negates the ancestral association between sexual intercourse and reproduction (Barkow & Burley, 1980).

In support of this view, Pérusse (1993) has shown that wealthier men achieve higher copulation rates than their poorer counterparts, proposing that without the availability of contraception the wealthy would outreproduce the poor (see also Kanazawa, 2003). The importance of contraception in regulating fertility behaviour is however contested by evolutionary and economic demographers, not least because 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, 1998a; Lee, 2003). Studies documenting strong, socially recognised motivations for reproduction and the care of children distinct from sexual activity further dissuade from the simplicity of this hypothesis (Foster, 2000; Rotkirch, 2007).

### **Cultural evolution of fertility decline**

Researchers of cultural evolution have promoted their own accounts of modern fertility behaviour. These models have much in common with a rising number of social demographers who reject the individual-level rational choice perspective of economic demography in favour of models of cultural diffusion and social influence (see Bongaarts & Watkins, 1996; Kohler, 2001; Montgomery & Casterline, 1996). Boyd and Richerson (1985), for example, suggest that throughout our history, imitating behaviour associated with social prestige offered an efficient mechanism to enhance individual fitness. In traditional societies, imitation of esteemed patriarchs and matriarchs would thus cause individuals to strive to attain similar high fertility. Modernisation offers novel social roles of high prestige such as teachers and heads of organised workforces. Competition for such positions is advanced by increased investments in education and production away from the family, at the cost of limited fertility. Thus, imitation of prestigious individuals could consequently lead fertility levels to diverge from individual optima, sparking fertility decline. This hypothesis, however, fails to provide an effective explanation for why the first individuals decided to limit fertility in the early stages of demographic transition

(Borgerhoff Mulder, 1998a), nor does it take into account that social prestige is itself constructed by societal norms and values (Newson et al., 2005).

An alternative perspective, combining models of social learning and the importance of extended kin in human life history, has been offered by Newson et al. (2005). Here it is suggested that kin can be expected to place social pressure and rewards upon reproduction, at least when conditions are favourable, as this would lead to inclusive fitness benefits. Thus, traditional societies which are characterised by frequent and sustained interaction with kin, lead to high fertility norms consistent with fitness maximization. However, cultural modernisation dramatically changes the nature of social networks through the fragmentation of the extended family. Non-kin have less inclination to support our reproductive interests and, therefore, high fertility strategies are less likely to become socially favoured, encouraging low and potentially maladaptive fertility norms.

In support of this model, Newson et al. (2007) report that in role-playing experiments individuals adopting the role of friends, in contrast to relatives, are less likely to offer favourable advice about reproduction. The validity of the 'kin-influence hypothesis' ultimately rests on demonstrating the role of kin networks in actual rather than imagined reproductive decisions and in demonstrating influence above and beyond a response to the economic benefits of kin presence or absence. Few existing studies currently speak directly to this point. In one recent study, Mace and Colleran (2009) report that contraception use (normally considered a precursor to fertility decline) was uninfluenced by whether or not individuals in the wider kin network had previously used contraception or their presence or absence, once individual level economic factors had been taken into account.

### **Parental investment models of modern fertility**

While it seems obvious that fertility limitation has no meaningful influence on offspring survival or reproductive success in modern families, research from across the social sciences confirms that high fertility carries a number of important costs to both offspring and parents (Figure 6.3). For this reason, evolutionary ecologists, along with many economic demographers, have remained resistant to the view that modernisation leads to an



‘uncoupling’ of reproductive decision making from the real or perceived costs and benefits of rearing children (Kaplan et al., 2002; Lawson & Mace, 2010; Mace, 2007).

Lawson and Mace (2010), for example, demonstrate that high fertility in contemporary Britain is associated with increased maternal perceptions of economic hardship, even when controlling for a range of household level socio-economic measures. Family size also has a strong negative influence on allocations of care-time to individual children from both mothers and fathers; with family size having a larger influence on parental time investment over the first decade of life than any other covariate considered, including socio-economic indicators and parental age (Lawson & Mace, 2009). Studies throughout the developed world show that children in larger families perform significantly worse on IQ tests and on formal educational assessments throughout life, a pattern recognised as one of the most stable relationships in the study of education (Blake, 1989; Downey, 1995; Downey, 2001; Lawson, 2009; Steelman et al., 2002). There is also evidence that the presence of siblings is associated with deficits childhood growth, which may stem from reduced parental attention to healthcare or nutrition in early life (Lawson & Mace, 2008). Finally, number of siblings has an important negative effect on achieved socioeconomic status in adulthood, particularly on wealth ownership (Kaplan et al., 1995; Keister, 2003, 2004). Keister (2003), for instance, demonstrates that number of siblings is a strong determinant of the likelihood of receiving a trust fund or an inheritance (see also Cooney & Uhlenberg, 1992).

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**Insert Figure 6.3 about here**  
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In the presence of these quantity-quality trade-off effects, it is possible that modern low fertility remains adaptive in the long-run 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 lineage survival. Such a scenario has been formally modelled as theoretically plausible by a number of researchers (Boone & Kessler, 1999; Hill & Reeve, 2005; Mace, 1998; McNamara & Houston, 2006). Alternatively, Kaplan (1996) argues that modern low fertility is indeed 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).

Both perspectives share a key prediction which challenges the standard model of life history trade-offs – in order to favour low fertility in a time of economic prosperity and furthermore negative or null intra-population relationships between socio-economic status and fertility, cultural modernisation must establish unusually intense resource competition between offspring when resources are relatively abundant rather than scarce. Evidence for this reversal is accumulating, albeit sketchy, as until recently few studies have directly considered variation in trade-off functions in association with modernisation or between socio-economic strata within modern populations.

High levels of extrinsic risk in offspring survival and development characterises traditional populations leading to a substantial diminishing returns to parental investment, with a low saturation point beyond which ‘chance’ becomes the principal determinant of offspring success (Pennington & Harpending, 1988; Quinlan, 2007). As the traditional life history model assumes, this pattern is associated with reduced levels of resource competition between offspring when resources are relatively abundant, favouring high fertility norms. Cultural modernisation through the abolishment of extrinsic risks (that is, reductions in the incidence of famine, infectious disease, warfare, crime, and environmental catastrophes), buffers populations from environmental instability and may therefore create a higher degree of reliability in investment returns (Winterhalder & Leslie, 2002). As such, it is possible that higher levels of wealth may lead to a closer association between parental investment and offspring quality, and subsequently increased costs to resource competition between offspring, favouring family limitation (Kaplan, 1996; Kaplan et al., 2002). Gibson and Lawson (2011) consider this model in the context of a development initiative in rural Ethiopia that in some villages has radically reduced early childhood mortality – the installation of water taps (Gibson & Mace, 2006). In villages where tap stands have been installed, parents are more likely to invest in child education, indicating increased investment per offspring, and the likelihood of receiving education is more determined by position in the family, suggesting elevated costs to investment division (see Figure 6.4). In further support, Desai’s (1995) cross-cultural study of

childhood growth demonstrates that improved access to safe drinking water and health care facilities is associated with larger negative effects of sibship size on height.

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**Insert Figure 6.4 about here**  
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Modern skill-based wage economies and the welfare state may place additional rewards on fertility limitation when parental resources are in good supply (Kaplan et al., 2002; Lawson & Mace, 2010). This is because investments in skill-acquisition or direct transfers of wealth now also radically increase an offspring's ability to generate new wealth over the life course and further invest in their own status. Strong welfare states may also selectively reduce investment competition in the poorest families through guaranteed provisioning of basic schooling, healthcare and social opportunity; consequently families with potential to invest above this 'base' level (e.g., in private schooling, healthcare, and so on) may experience more substantial costs to investment division (Downey, 2001; Lawson & Mace, 2010). In support of these proposed mechanisms, Keister (2004) and Grawe (2010) both demonstrate that large family size is associated with negative consequences on the income generation and wealth ownership of offspring in middle and high socio-economic families in the US, but of relatively little consequence to children from impoverished backgrounds. Lawson and Mace (2010) have also reported that relatively high social class British mothers record larger increases in economic hardship associated with reproducing above the two child norm, suggesting that the perceived costs of high fertility are magnified in high socioeconomic strata.

It is currently impossible to determine whether or not small family sizes are adaptive in the long-term; we lack sufficient multigenerational data to test this model (see also Box 6.4). Nevertheless, in contrast to the popular hypotheses proposed by many evolutionary psychologists and cultural evolutionists (Barkow & Burley, 1980; Boyd & Richerson, 1985; Kanazawa, 2003; Newson et al., 2005; Perrusse, 1993), these effects suggest that modern low fertility may be best understood as a directed reproductive strategy of extended parental investment in sync with the local costs and benefits of raising socially and economically competitive offspring.

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**Insert Box 6.4 about here**

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## Conclusions and future directions

Four billion years of evolution by natural selection, from the earliest prokaryotes (single celled life forms) to the collection of successful organisms currently inhabiting our planet, has laid witness to a radical variety in reproductive strategies. Life history theory argues that this diversity, from the bird that always lays two eggs only for the first chick to murder the second (Mock et al., 1990; Simmons, 2002), to the chameleon that lives most its life as an egg (Karsten et al., 2008), or the ‘matrphagous’ spider whose first meal is always its mother (Kim et al., 2000), can be understood as competitive resource allocation tactics ‘designed’ to maximise Darwinian inclusive fitness.

Each species has a unique life history because each species is adapted to its own unique ecological and demographic niche. Populations vary within species, and individuals vary within populations, because natural selection rarely favours organisms ‘inert’ to local environment contingencies; instead it supplements genetic variation with high levels of phenotypic plasticity – reaction norms that shift developmental trajectories and behavioural responses favouring life history optimization at the individual level (West-Eberhard, 2007). Studies of human life history aim to elucidate both the ultimate origins of variation in human growth, mortality and reproduction, and the evolved proximate mechanisms regulating observed phenotypes. Emphasis is placed simultaneously on broad comparative study, including both cross-cultural and cross-species generalisations, and on detailed anthropological and sociological surveys at the local and individual level. It is acknowledged that not only will life history optima vary between environments, but also that adaptive responses will necessarily be limited by the imperfect design of both our physiology and psychology, which are perhaps particularly sensitive to patterns of adaptive lag in the face rapidly changing environments (Irons, 1998; but see Laland & Brown, 2006).

In this chapter, I have reviewed the main trade-offs in human life history and the evidence for fertility optimisation across both traditional and modern societies. It should be clear from the research summarised that life history studies are inherently interdisciplinary; while most of its practitioners are trained as biologists or anthropologists, a shared concern with differences in health, social status and schedules of fertility and mortality ensure

significant empirical overlap with neighbouring sciences. Theoretical overlap is also often substantial, with, for example, many evolutionary anthropologists and demographers adapting existing frameworks from economic models of fertility and family resource dilution (e.g., Kaplan, 1994; Lawson & Mace, 2009).

In contrast, explicitly evolutionary models of human behaviour do not always find much favour with the mainstream social sciences (Seegerstråle, 2000). There are multiple reasons for this, including the fact that the evolutionary approaches remain a young and partially fragmented field (Sear et al., 2007), that few researchers in the neighbouring sciences have the formal training in biology required to understand, critique, and incorporate Darwinian hypotheses, and regrettably the persistence of less rigorous forms of evolutionary psychology that capitalise on the popular appeal and controversy of some hypotheses, rather than adherence to the scientific method (for recent critiques, see Dickins et al., 2007; Gelman, 2007; Lawson et al., 2008).

Overcoming such difficulties is an important aim for future research. A dedicated focus on topics of social and public relevance represents one sure pathway to encourage greater interchange. Here, I have discussed a life history perspective on demographic transition and the effects of modernisation on family life (Bock, 1999, provides a more detailed discussion of how evolutionary models may be used to strengthen and unify outlooks across demography). Other researchers have emphasised the potential for life history theory to advance our current understanding of health inequalities; providing an overarching theoretical framework to study both inherent disease susceptibility and the motivations behind disease causing behaviours (Hill, 1993; Strassmann & Mace, 2008). Tucker and Rende Taylor (2007) provide a thoughtful discussion of how life history models, as a foundation of human evolutionary ecology, may also be used to critique (and ultimately improve) the implementation of government and non-governmental organization projects and policies aimed at improving public health and social welfare (see also Gibson & Mace, 2006). All of these research developments represent exciting and vital steps forward in establishing the value of a considered and integrative evolutionary perspective on human behaviour.

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### **Box 6.1. The evolution of sibling rivalry.**

The importance of resource competition between siblings in the natural world is also revealed by the evolution of sibling rivalry (Hudson & Trillmich, 2008; Mock & Parker, 1997). In extreme cases, facultative and obligate systems of siblicide have evolved (occasionally referred to 'cainism' following the Biblical account of Cain's murder of Abel). In many avian species, older siblings routinely kill younger hatchlings, a strategy which enables them to monopolise parental feeds (Mock et al., 1990; Simmons, 2002). Siblicide has also been documented at notable frequencies in several mammals, particularly when critical resources are scarce, including spotted hyenas (Wahaj et al., 2007) and vampire bats (Leippet et al., 2000). In my favourite example of sibling rivalry, Fraser and Thompson (1991) argue that domestic pigs have evolved early erupting canines as specialised 'sibling weaponry' to shift weaker sibling rivals off prime teats. The abstract of their manuscript (entitled 'Armed sibling rivalry among suckling piglets') has such unusual charm it deserves a full quotation:

*A piglet's most precious possession  
Is the teat that he fattens his flesh on.  
He fights for his teat with tenacity  
Against any sibling's audacity.  
The piglet, to arm for this mission,  
Is born with a warlike dentition  
Of eight tiny tusks, sharp as sabres,  
Which help in impressing the neighbors  
[sic];  
But to render these weapons less  
harrowing,*

*Most farmers remove them at farrowing.  
We studied pig sisters and brothers  
When some had their teeth, but not others,  
We found that when siblings aren't many.  
The weapons help little if any,  
But when there are many per litter,  
The teeth help their owners grow fitter,  
But how did selection begin  
To make weapons to use against kin?'*

*(Fraser & Thompson, 1991, p. 9)*

Anecdotal evidence suggests the rare occurrence of siblicide in humans also corresponds with cases of intense resource competition. History is full of examples of intra-family conflict in the succession to inheritance. For example, during the 15<sup>th</sup> -17<sup>th</sup> century it was judicial law that all surviving brothers were murdered at the appointment of a new ruling Sultan of the Ottoman Empire, with in the most famous case Mehmet III ordering the execution of 19 brothers. This grisly practice, later replaced by a more formalised system of primogeniture, was explicitly



intended to minimize disputes to the throne and associated political instability (Quataert, 2000). Whether or not more modest forms of sibling rivalry in humans, such as the common quarrels and physical fights between children and adolescents (see Kettrey & Emery, 2007), can be explained from a strategic resource competition perspective remains an open question for research.

**Box 6.2. Measuring social status in humans.**

Accurate assessment of differences in resource access between individuals presents a challenge to human life history research because social status is simultaneously multidimensional and dynamic. For example, Braveman et al. (2005) have critiqued the common treatment of indicators such as occupational coding, educational level, and income, as interchangeable socioeconomic measures in otherwise sophisticated studies of health and development. In reality these measures often vary with a surprising degree of independence, signifying distinct domains which have varied influence on the phenotype. They also note the inadequacy of income as the most commonly used measure of material wealth in affluent societies (e.g., see Nettle & Pollet, 2008). This is partly because income data is volunteered with weak reliability in survey research, but more crucially because it assesses current resource generation rather than total accumulated resources, which is largely determined by past economic activities and family inheritance (e.g., Keister, 2003). Income measures may be particularly inappropriate for older age individuals who may be retired or younger age individuals who are often enrolled in education and are rarely financially independent (the dominant sample population for many evolutionary psychologists). Thus, alternative measures of social status, which more directly assess wealth, such as property and goods ownership, neighbourhood quality, or measures of 'liquid assets' need to be considered more frequently (Braveman et al., 2005; Lawson & Mace, 2009).

Von Rueden et al. (2008) also challenge the common assumption that forager communities lacking significant material wealth or intergenerational inheritance can necessarily be considered 'egalitarian'. Using data from the Bolivian Tsimane, they document considerable variation along dimensions of physical condition, skill in resource accumulation, social support, and level of acculturation – each with unique relationships to multiple photo-ranked assessments of social status, including recognised respect, community influence and the likelihood of winning dyadic fights. Reiche et al. (2009) further note that conceptualising and measuring resource access at the individual level presents problems because resources in all societies occupy 'pooled energy budgets', shared between kin and non-kin. In light of these non-trivial points, researchers should experiment with multiple approaches to measuring social status in their own analyses and retain a critical eye in the face of frequent claims that relevant resource variation has been reliably 'controlled' by statistical adjustment.

**Box 6.3. Reproductive suppression and female eating disorders.**

A number of evolutionary psychologists have argued that female eating disorders, such as anorexia and bulimia, may have origins in an evolved mechanism of fertility regulation which was in fact adaptive in ancestral environments (e.g., Anderson & Crawford, 1992; Juda et al., 2004; Salmon & Crawford, 2008; Salmon et al., 2008). The theoretical foundation for this hypothesis is based on two observations. Firstly, in the face of poor ecological conditions, lifetime reproductive success may be improved by a postponement of reproduction until circumstances become more favourable (Wasser & Barash, 1983; Williams, 1966). Second, according to the 'critical-fat hypothesis' a reduction of body fat over a certain threshold leads to a termination of ovulation (Frisch & McArthur, 1974). As such, it is argued that voluntary weight reduction evolved as a strategy to delay reproduction when social or ecological cues predict poor reproductive outcomes and that this mechanism is activated at pathological levels by equivalent, but somehow amplified, cues in the contemporary West.

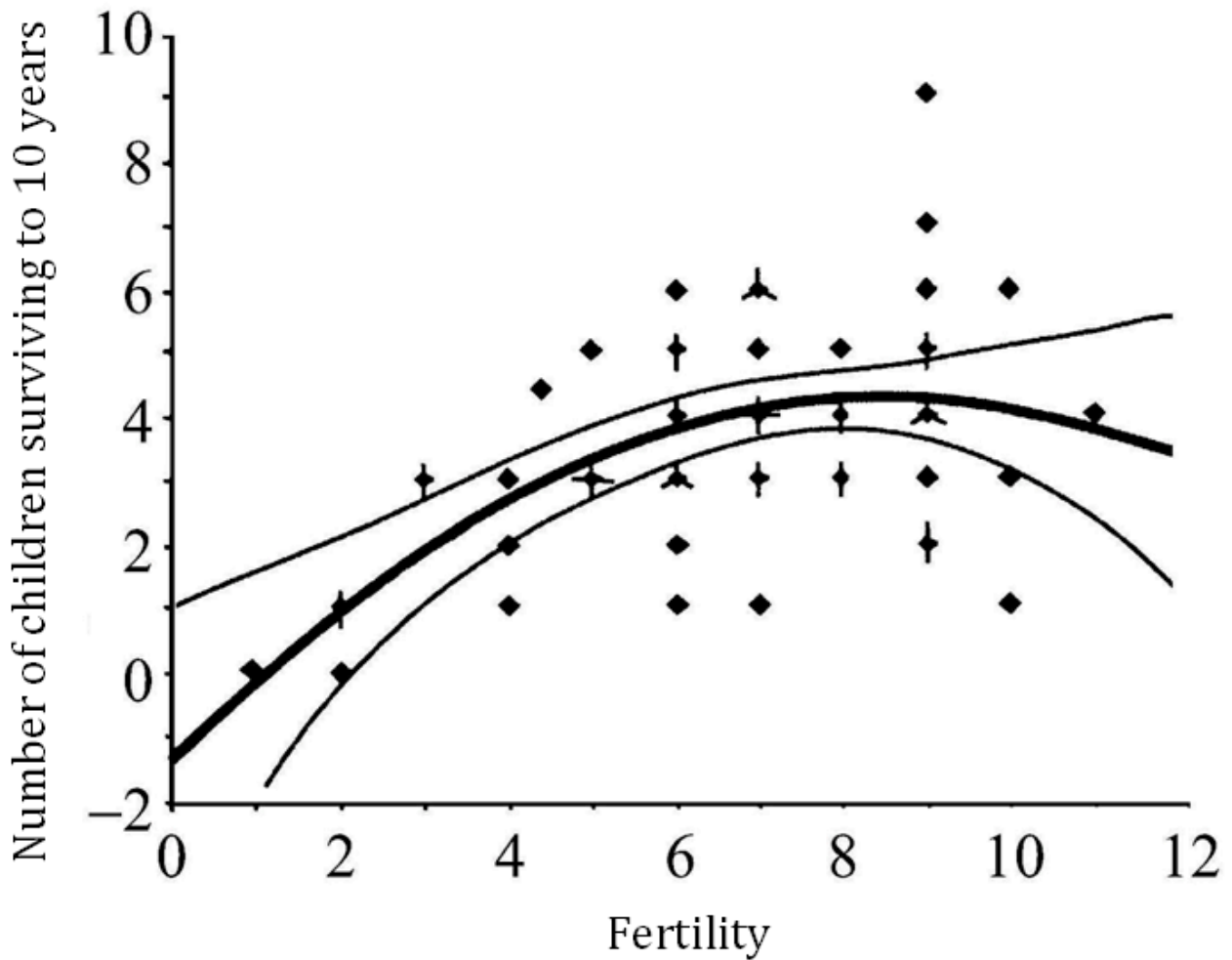
In my view, this 'reproductive suppression hypothesis' (RSH) is weakened by a number of fundamental problems poorly addressed by its supporting literature. Most importantly, while reproductive ecologists have indeed demonstrated that harsh environmental conditions are associated with temporary suppression of ovulation, this is ecologically enforced (e.g., due to local food shortages), occurring entirely through automatic physiological pathways (Bentley, 1999 Ellison, 1990, 2003). In no case has the voluntary denial of available food been recorded in response to environmental hardship. It is also contentious that a simple regulation of body-fat would provide sufficiently reliable grounds for fertility regulation, as the associated critical-fat hypothesis has been criticised as overly simplistic (see references in Mircea et al., 2007). Proponents of the RSH have also failed to conduct a formal cost-benefit model of the proposed ancestral strategy, yet clearly voluntary starvation in poor conditions, even over short periods, would elevate risks of mortality. Instead, the main evidence presented for the RSH has been repeated demonstrations of positive associations between disordered attitudes to dieting and various indicators of social stress and 'parental unreadiness' in Western women (usually North American college students). Such associations are consistent with, but hardly uniquely attributable to the RSH. Consequently, the RSH fits an unfortunate stereotype of evolutionary psychology as 'adaptive story-telling'; out of sync with current anthropological literature and advocated without adequate theoretical or empirical rigour.

**Box 6.4. Modern reproductive behaviour and adaptive reasoning.**

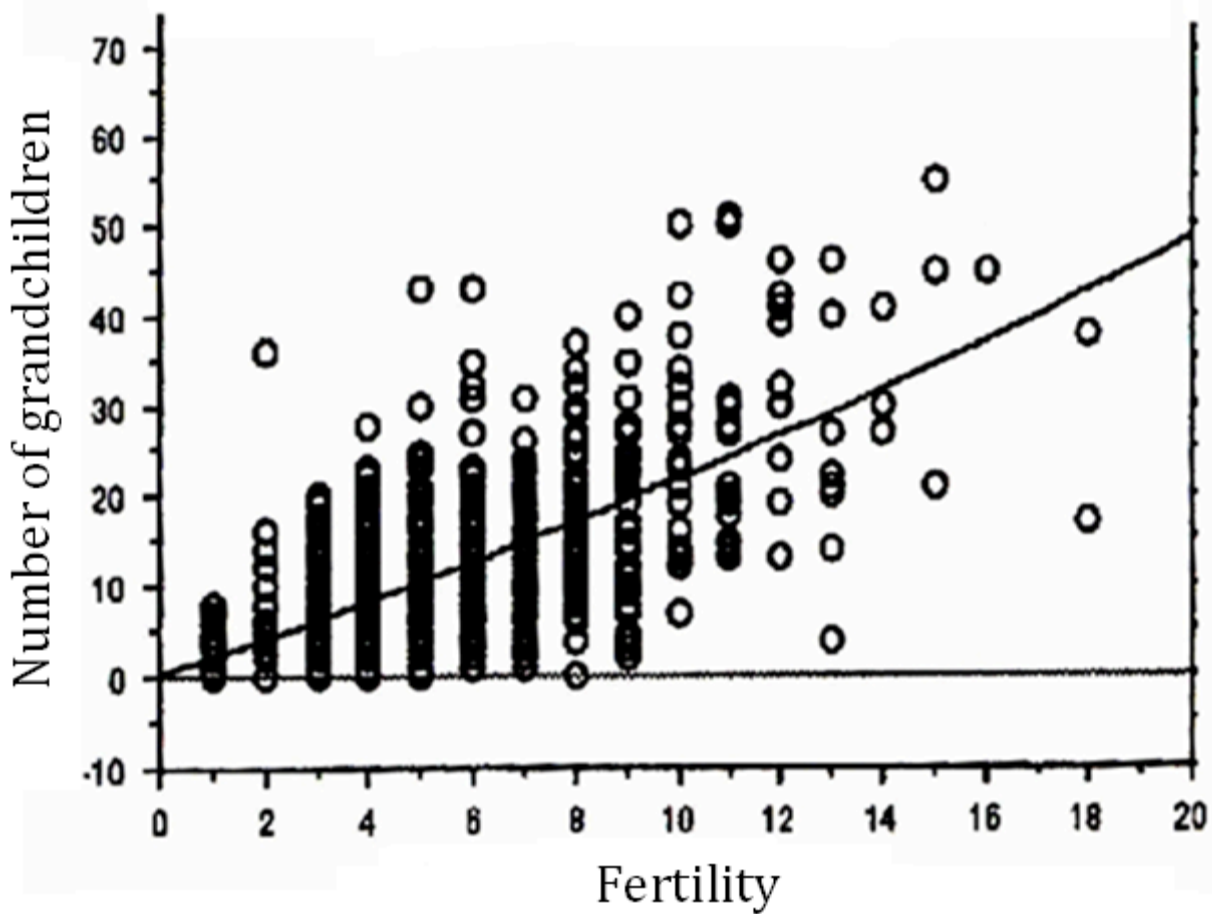
A number of researchers have modelled reproductive differentials in contemporary Western populations to deduce selection pressures currently acting on modern humans (e.g. Jokela, 2009; Nettle & Pollet, 2008) or alternatively to deduce the ancestral selection pressures which have shaped the extant human phenotype (e.g., Nettle, 2002). A life history perspective on reproductive behaviour suggests scepticism should be exercised in both cases. For example, Jokela (2009) finds that physical attractiveness is associated with high fertility in a modern population, while Nettle and Pollet (2008) find that male (but not female) income is positively correlated with fertility once negative effects of education have been taken into account. Thus, it has been argued that natural selection is currently acting positively on female and male attractiveness and male 'wealth' (see also Box 6.2). However, as we have discussed, under conditions of low mortality and high intergenerational transmission of resources it remains quite possible that small or intermediate family size will maximize long-term genetic fitness. This point is particularly pertinent to Nettle and Pollet (2008) because any reproductive gains to above average wealth will fail to be transmitted to offspring when a high fertility strategy is followed, due to the sharp division of inherited wealth between siblings (Keister, 2003; Lawson & Mace, 2010; Mace, 1998).

The deduction of past selection pressures from current fertility patterns is also problematic when it is acknowledged that behavioural optima necessarily vary between populations, particularly when socioecological differences are dramatic (clearly the case in the comparison of modern urban to ancestral hunter-gatherer demography). The potential for modern populations to suffer 'adaptive lag' in the face of environmental novelty also suggests that reproductive patterns are unlikely to be analogous (Irons, 1998). As an illustration, Nettle (2002) has suggested the sexual selection has acted in opposing directions on male and female height, explaining current levels of sexual dimorphism in stature. This conjecture is based on analyses of contemporary Western populations which have indicated relatively tall men are rated as more attractive and achieve higher fertility, while the reverse is true for women. However, Sear (2006) has critiqued this hypothesis because available data from traditional populations shows male height is not significantly associated to number of children and that female height is actually positively associated with reproductive success, largely due to the improved survival of their children (see also Monden & Smits, 2009; Sear, 2009).

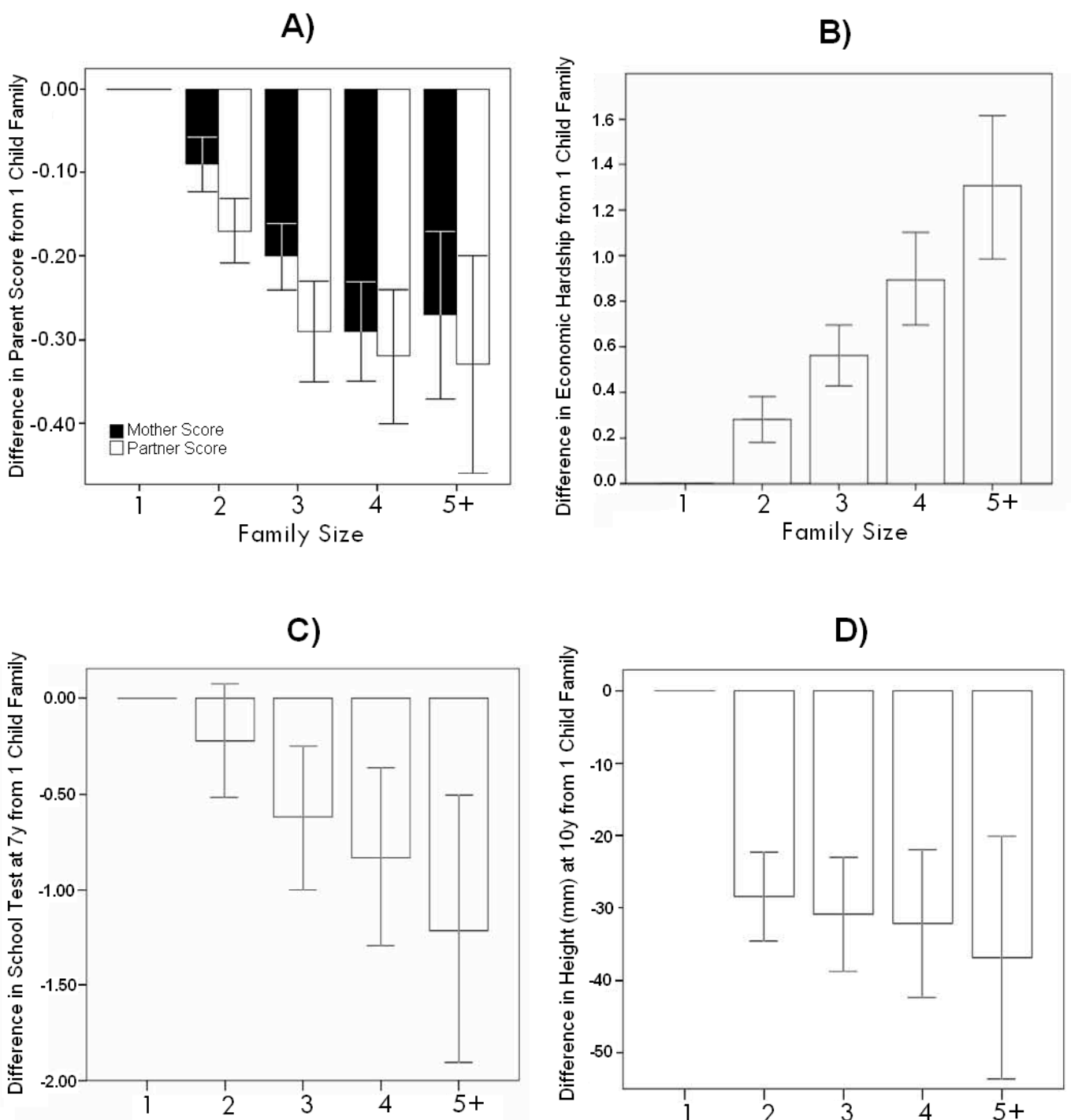
Figure 6.1. The relationship between female fertility and number of offspring surviving to age 10 years in the Dogon of Mali, plus 95% confidence limits. Each petal represents an additional data point. High fertility is associated with increased child mortality, with intermediate fertility maximizing number of surviving children. From Strassmann and Gillespie (2002).



*Figure 6.2.* The relationship between male fertility and number of grandchildren in Albuquerque, New Mexico. There is no indication of a trade-off between fertility and fitness as measured by number of grandchildren. Modal fertility is two, but number of grandchildren is maximized at the highest observed fertility. From Kaplan et al. (1995).



**Figure 6.3. Family size, parental investment and child development in contemporary British families.** The relationship between family size and **(a)** maternal and paternal allocations of care time between 1-9 years (from Lawson & Mace, 2009); **(b)** maternal perception of economic hardship from 0-7 years (from Lawson & Mace, 2010); **(c)** school test results at 7 years (from Lawson, 2009); **(d)** height at age 10 years (from Lawson, 2009; Lawson & Mace, 2008). Children with more siblings receive less time from parents, grow up in more economically stressed households and exhibit relatively poor physical and cognitive/educational development. Data are from the Avon Longitudinal Study of Parents and Children, a large cohort study ( $n = 14,000+$ ) of children born in 1991/1992. Confidence intervals are set at 95%.





*Figure 6.4.* An Oromo woman collecting water from a newly installed tap stand in Southern Ethiopia. Development projects are radically changing local mortality patterns in many parts of the world, and life histories are shifting in response (Gibson and Mace, 2006; Gibson and Lawson, submitted). Photo courtesy of Mhairi Gibson and Lucie Clech.

