Costs and Consequences of Reproduction

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Chapter 9
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Abstract The life history of women is characterized by several unusual patterns: women have a relatively late age at maturity compared to other primates, they produce offspring at short inter-birth intervals, and typically have many dependent offspring of varying ages to care for simultaneously. Women then lose their potential to bear children at menopause but can live a few decades afterwards. Such a reproductive strategy involves several trade-offs and costs of reproduction to future success that have to be optimized across the entire lifespan. This chapter summarizes evidence from humans on the costs of reproduction. First, I discuss the short-and long-term effects of investment in reproduction on the survival patterns of individuals. Second, I address how current reproductive investment affects the ability to invest in future reproductive events. Third, I review the evidence for such costs of reproduction and trade-offs changing with the age of the individual and across different environments. Trade-offs are predicted to be most severe among the very young and senescing females, and when resources are limited. Finally, I investigate the heritable genetic basis for individual differences in the consequences of reproduction, and how heritabilities and genetic trade-offs between traits vary with age and across environmental conditions.

9.1 Introduction

The fundamental evolutionary role of reproduction is to ensure genetic contribution to future generations. Ideally, females should start reproduction at maturation and continue increasing their family size with short inter-birth intervals across a long lifespan in order to maximize their lineage persistence across generations. However, such a reproductive strategy is rarely achieved and may not eventually give the highest fitness return because of several constraints and costs involved. First, although

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early age at first reproduction is among the most important life-history traits affecting between-individual variation in fitness and has a pivotal effect on family size and reproductive success in humans (Käär et al. 1996; Pettay et al. 2007), it is predicted to evolve to maximize fitness subject to both the benefits and costs of delayed reproduction (Stearns 1992). The costs of delaying reproduction include increased accumulated mortality hazard before reproduction, reduced reproductive span, reduced reproductive output, and longer generation time, whereas the benefits include larger body size, higher initial fecundity and lower offspring mortality brought about by longer growth (Kawecki 1993; Kozlowski 1992; Migliano et al. 2007; Stearns 1992). Second, because of constraints and costs of rapid reproduction to an individual's future reproductive success and survival, large overall family sizes in humans may not necessarily bring the highest fitness returns either (Gillespie et al. 2008).

The costs and consequences of reproduction in human women have interested scientists for over a century (Beeton et al. 1900). Reproduction is predicted to be associated with future health, breeding success, and survival because resources available to individuals in nature are usually limited. Consequently, production of offspring can be "costly" by reducing an individual's ability to invest time and resources in other important body functions, such as growth, immune defense, and body maintenance, and may lead to accelerated reproductive senescence and shorter lifespan (Stearns 1992; Williams 1957). Senescence is manifested as a decline in an individual's physiological and cellular function with age. Evolutionary theories suggest that physiological function decreases with age because, first, genes that have positive effects on fitness early in life will be selected for even if they have negative effects later in life and, second, because a weakening of selection with increasing age leads to an accumulation of mutations (Hamilton 1966; Kirkwood 1977; Medawar 1952; Partridge and Harvey 1985; Williams 1957).

Individuals vary in their consequences and costs of reproduction. In long-lived, iteroparous species that typically reproduce more than once, the relative cost of reproduction may change with age (Charmantier et al. 2006; Réale et al. 1999; Williams 1957), given that social rank, resource access, body condition, and residual reproductive value likely also vary with age. Young growing and old senescent individuals should thus suffer higher costs than prime-age ones, given that they may struggle to meet the energetic demands made by reproduction. The costs of reproduction may also change radically across different environments with differing resource levels (Monaghan et al. 2008), or with different amounts of help available from other individuals with raising the offspring, such as a partner or helpers-in-the-nest, which affect the level of parental investment made and, potentially, ageing rates (Bourke 2007). Rates of senescence might also differ between different life-history traits, or in males versus females, given that females typically invest more in reproduction by producing larger ova and, in mammals, through gestation and lactation (Trivers 1972). Finally, the costs of reproduction may also differ for genetic reasons: individuals may be differently able to bear the consequences of reproduction across different ages, and may also be differently genetically suited to reproduce in a given environment (genotype × environment interactions; reviewed in Wilson et al. 2008).

Humans are a particularly exciting subject with which to study effects of reproduction on senescence. This is because whereas most animals reproduce until they die, in humans, females can survive long after becoming unable to reproduce themselves (Hamilton 1966; Williams 1957), and, although males may remain reproductively capable, they do not often use their potential (Käär et al. 1998). In both historical and traditional hunter-gatherer populations, 30% or more of adult individuals are usually beyond the age of 45, given that most who survive childhood live past their childbearing years (Hawkes 2004). In comparison, in chimpanzee females fertility declines at about the same age as in humans to virtually zero at age 45 (Nishida et al. 2003), but their survival rates follow fertility so that in the wild less than 3% of adults are over 45 (Hill et al. 2001). In humans, aging is slowed down by allocation of more resources to cell maintenance and repair than is done by the nearest primate relatives (Hawkes 2003). Evolutionary life-history theory offers a framework to understand individual differences in the costs and consequences of reproduction and, in humans, such results have implications also for the social sciences, humanities, and public health. This is because although the human life-history is in many ways unusual and modern technology has allowed us to stretch the boundaries of reproduction, ultimately, the same biological principles that underlie life-history evolution in other species have also been documented to apply in humans.

This chapter will summarize evidence from humans on the costs of reproduction. First, I will discuss the short- and long-term effects of investment in reproduction on the survival patterns of individuals. Second, I will address how reproduction affects the ability to invest in future reproductive events. Third, I will review the evidence for such costs of reproduction changing with age and across different environments. Finally, I will investigate the heritable genetic basis for individual differences in the consequences of reproduction, and how these vary with age and across environmental conditions. Most research on the topic is conducted on women, but I will draw comparisons to men wherever such data is available.

9.2 Immediate and Delayed Effects of Reproduction on Survival

Both laboratory experiments on model species and a growing number of studies on natural populations of vertebrates have demonstrated that increases in reproductive effort, such as lower age at first reproduction or higher early-life fecundity, can result in reduced subsequent survival rates (reviewed in Nussey et al. 2008). In humans, the immediate risk of a woman dying from childbirth varies widely: In 2005, on average 9 women per 100,000 births died worldwide in developed regions, whereas the risk in developing regions was 450/100,000 and more than 2,000/100,000 in countries such as Sierra Leone (www.who.int). The probability that a 15-year-old female will die eventually from an (immediate) maternal cause is currently highest in Africa (at 1 in 26), while the developed regions have the smallest lifetime risk at 1 in 7,300. The major causes of maternal death worldwide include severe bleeding/hemorrhage (25%), infections (13%), unsafe abortions (13%), eclampsia (12%), obstructed labor (8%), other direct causes (8%), and indirect causes (20%). Maternal death, in turn, can have downstream effects, not only by cutting short the personal reproductive career, but also by affecting the quality of already produced offspring: several studies show the negative effect that mother loss has on their own infant and child survival (reviewed in Sear and Mace 2008). Thus, particularly in conditions with no modern medical care access, pregnancy and childbirth can reduce a women's longevity by exposing her to early death and have consequences for her fitness.

In addition to the immediate consequences of childbirth for survival, investment in pregnancy and breastfeeding is predicted to carry delayed long-term costs to female longevity by reducing resources available for body maintenance. Costs of pregnancy include resources invested in fetal growth, growth and maintenance of maternal supporting tissues, and maternal fat accumulation, while the costs of lactation include resources invested in milk synthesis and the maintenance of metabolically active mammary glands, and these costs generally outweigh the costs of pregnancy in women who exclusively breastfeed their baby (reviewed in Jasienska 2009). Studies documenting how increases in reproductive effort affect later-life survival have however been equivocal (reviewed in Le Bourg 2007). For example, in historical populations, some studies have been able to establish the expected negative effects of high total reproductive effort on female post-reproductive longevity (e.g. Gagnon et al. 2009; Jasienska et al. 2006a; Westendorp and Kirkwood 1998); but also many studies find no association or a positive correlation between total number of children and post-reproductive survival (Korpelainen 2000; Le Bourg et al. 1993; Müller et al. 2002); and sometimes this trade-off is manifested only among the poorest women (Dribe 2004; Lycett et al. 2000). Similar mixed results arise from studies on the association between total family size and longevity in contemporary populations (e.g. Doblhammer 2000; Hurt et al. 2004; Kumle and Lund 2000), or studies on the relationship between age at first reproduction and longevity (reviewed in Helle et al. 2002a, 2005).

Such results are puzzling because if limited resources should promote trade-offs between reproduction and survival, then we would expect to find the strongest evidence for such trade-offs from pre-healthcare populations. Moreover, although short inter-birth intervals are predicted to be particularly detrimental for future survival, studies investigating this association also show mixed results (e.g. Grundy and Tomassini 2005; Menken et al. 2003), and studies on the effects of reproduction on body condition or health in later life are also unequivocal (Tracer 2002). One possibility is that within each population, high-quality individuals have both higher breeding performances across their lifespan and higher probabilities of survival (van de Pol and Verhulst 2006), resulting in positive or "phenotypic" correlations (Daan and Tinbergen 1997) that are difficult to control for in a no-experimental study design. However, this does not explain why most studies that have investigated similar relationships between family size and longevity in men have generally found no significant relationships at all (e.g. Doblhammer and Oeppen 2003; Helle et al. 2004; but see Penn and Smith 2007) or positive effects of offspring of only one sex (e.g. Jasienska et al. 2006a). Across countries, however, birthrates are indeed related to a sex difference in lifespan: birthrate per female explains 17% of the variation in relative sex differences in lifespan across countries, and low birthrate results in females living relatively longer than males (Maklakov 2008).

An additional complication is that although the cumulative costs of reproduction are related to negative health outcomes such as increased risk of cardiovascular diseases, diabetes, and strokes even in women of good nutritional status, young age at first reproduction and high fertility may also lead to decreased mortality from certain diseases, such as breast and reproductive cancers (reviewed in Jasienska 2009). Depending on the population and overall risk of certain diseases as well as individual differences in the risk of suffering from specific health problems, the costs of reproduction may or may not outweigh the benefits of reproduction to health. Finally, it has also been suggested that extended periods of endogenous estrogen production following continued reproduction and breastfeeding until old age could stimulate biological systems to positively affect survival and health, and could also foster better survival chances through adoption of healthy behaviors or through social support in old age from younger children (Yi and Vaupel 2004).

Nevertheless, when socio-economic status is controlled for in the analyses and high reproductive effort is measured in terms of production of twins over singletons (Helle et al. 2004) or energetically more expensive sons over daughters (Beise et al. 2002; Helle et al. 2002b; Hurt et al. 2004; van de Putte et al. 2004), rather than by production of a large family size per se, high investment in reproduction appears to reduce a women's post-reproductive survival rates, for example due to increased susceptibility to infectious disease (Helle et al. 2004). It is thus possible that in a species such as humans mothers might be able to adaptively adjust their birth intervals or overall family size to match their available resource levels and current body condition to avoid having to pay high costs resulting from too expensive state-dependent reproductive investment, whereas production of twins over singletons or sons over daughters is less under the active control of the mother and more likely to lead to a realization of the costs of reproduction. Resolving the controversy surrounding this topic would benefit from twin designs comparing longevity of genetically similar individuals differing in their reproductive investment patterns, or studies involving large pedigree data sets that allow the associations between reproduction and survival to be investigated not only at the phenotypic, but also at the genetic level (for one example, see Pettay et al. 2005).

Many mechanisms have been identified as contributing to age-related deterioration in function (Nemoto and Finkel 2004). Processes that are widely believed to play an important role in this and could underlie life-history trade-offs involving longevity include the accumulation of oxidative damage to lipids, proteins, and DNA, which then interfere with cell and tissue function, as well as telomere attrition (reviewed in Monaghan et al. 2008). Increases in reproductive effort can impair immune function in the long term (Ardia et al. 2003), and an effective immune system itself may be costly to maintain (Sheldon and Verhulst 1996), and may constrain individual reproductive decisions. Direct evidence that high reproductive effort accelerates immunosenescence or facilitates telomere attrition in humans is however still lacking (but see e.g. Hanna et al. 2009; Helle et al. 2004).

9.3 Costs of Reproduction to Future Breeding Success

In addition to effects on survival, an increase in reproductive effort may manifest as reproductive senescence, i.e. reduced subsequent breeding success. In support of this, female collared flycatchers (*Ficedula albicollis*) that were subjected to experimentally enlarged broods early in life laid smaller clutches in old age (Gustafsson and Part 1990), and female red deer (*Cervus elaphus*) with high early-life fecundity showed stronger subsequent declines in offspring birth weight and delayed calving dates (Nussey et al. 2006). Such relationships between early life reproductive investment and later life survival, maternal performance, and rates of senescence have also been shown to have a genetic basis in natural populations of vertebrates (Charmantier et al. 2006; Nussey et al. 2008; Pettay et al. 2005; Wilson et al. 2008).

Few studies on humans have directly investigated the effects of maternal reproductive investment on her future breeding success, and to my knowledge such studies are entirely absent in men. That such effects are possible at least in women is illustrated by studies showing that increases in current reproductive effort (production of twins or more expensive sons) can reduce the mother's chances of a successful future reproduction (Lummaa 2001) and the quality of the subsequent offspring (Rickard 2008; Rickard et al. 2007, 2009). For example, inter-birth intervals tend to be longer after giving birth to a son than after giving birth to a daughter (Mace and Sear 1997), and mothers who previously produced a son thereafter give birth to offspring that have lower birth weight (Côté et al. 2003; Rickard 2008), smaller size at adulthood (Rickard 2008), and reduced mating and reproductive success (Rickard et al. 2007, 2009) compared to offspring born after a daughter. Moreover, increasing offspring quantity may reduce offspring quality in the short term (Meij et al. 2009) as well as their eventual contribution to maternal fitness (numbers of grand-offspring produced) (Gillespie et al. 2008). This evidence thus predicts that high investment in a current attempt has negative effects on investment in future reproduction, but studies investigating e.g. the effects of offspring birth weight (pregnancy investment) and breastfeeding length (post-natal investment) on future fertility and offspring quality are currently rare.

In women, "reproductive" senescence may also manifest post-reproduction, given that post-reproductive women continue gaining fitness by increasing the survival and/or reproductive capacity of both their own offspring and grand-offspring (reviewed in Sear and Mace 2008). As women age, their ability to affect positively the reproductive success of their adult offspring decreases and young grandmothers are the most helpful ones in aiding survival of their grandchild (Lahdenperä et al. 2004). However, it is not known whether this ability to gain fitness post-reproduction through grandmothering is modified by or traded-off with patterns of reproductive investment prior to menopause. Such effects would have important repercussions for calculating optimal allocation between reproduction and post-reproductive longevity, but are generally ignored in all the current models of menopause evolution (Rogers 1993; Shanley et al. 2007).

9.4 Costs of Reproduction with Age

Both the measures of reproductive performance and costs of reproduction can change with age. First, conception rate and baby birth weight are reduced in older mothers while offspring developmental and genetic problems and neonatal mortality increase (reviewed in Ellison 2001). In pre-industrial women, general offspring quality, as measured by their eventual contribution to the grand-offspring generation, has been documented to decline by as much as 30% from offspring born to mothers aged 17 to offspring born to mothers 40+ years (Gillespie et al. submitted). Such declines in fitness benefits of offspring produced at different ages were caused by both biological and social effects: while maternal age best explained declines in offspring survival to adulthood, increasing birth order and thus competition with siblings (Faurie et al. 2009) became more important in explaining declines in recruitment of adult offspring to reproduction (Gillespie et al. 2008).

Second, also the costs of reproduction to survival may vary with age: effects of birth order of the child on (immediate) maternal mortality risk have been found to follow a J-shaped function, with the risk of dying from childbirth declining after the first birth and then rising again in high-parity women (Knodel 1988). For example, in historical Utah, the risk of mortality after childbirth increased with age, and this risk was greater for women than men (Penn and Smith 2007). Changes in the costs of reproduction with age are predicted, given that not only social rank and thus external resource access commonly vary with age in all human societies, but also changes in body condition and individual residual reproductive value are likely to vary and lead to differences in the personal costs of reproduction. However, little is currently known of such processes, or the causes creating variation between individuals in their reproductive success with age and how previous reproductive effort modifies this. Without assessing the impact of early-life reproductive effort on survival and reproductive outcomes across all reproductive ages, the fitness implications of the long-term effects of early reproductive effort cannot be determined (Nussey et al. 2008).

9.5 Costs of Reproduction Across Environments

Ecological, social, and demographic conditions are likely to interact with the costs of reproduction and influence the rate at which women senesce. Environments with plentiful resources are predicted to be associated with earlier age at maturity and higher reproductive success and survival, whereas resource scarcity and limited energy available for reproduction is predicted to lead to constraints for the expression of optimal combination of these traits (Roff 2002; Stearns 1992).

Limited availability of resources should also promote trade-offs between fitness-related traits, and thus the optimal within-individual allocation of resources is likely to change across resource regimes (Noorwijk and de Jong 1986). In line with this, evidence from both wild animals and humans show that resource availability during reproduction not only influences the costs of reproduction for the breeder, but also the reproductive potential of offspring (Lummaa and Clutton-Brock 2002).

Costs of reproduction can be interpreted in a meaningful way only when they are analyzed in relation to the overall energy budget of the woman: high costs of reproduction will not have the same effects on women who have good diets and low levels of physical activity as on women in poor energetic condition (Jasienska 2009). Such physiological consequences of reproduction for women on different energy budgets are well-documented in humans (reviewed in Jasienska 2009). However, less is currently known of how resource variation affects the strength and direction of selection on human life history, despite this being one of the basic premises of life-history theory. One example is provided by a study on preindustrial Finns, demonstrating that the costs of reproduction were greater in inland areas, where winters are harsh and food was unpredictable, than in milder coastal areas where fish supplemented the diet: selection favored heritable dizygotic twinning in populations enjoying predictable food supply, whereas such an increase in reproductive effort was selected against in populations suffering from frequent famines. The differing selection pressure on multiple births likely led to the observed significant differences in twinning rates between populations with differing access to resources (Lummaa et al. 1998).

Moreover, in agreement with life-history theory, the opportunity for total selection, the strength of natural selection on life-history traits, and trait means differed in the same Finnish populations between women belonging to different wealth classes and thus with differing access to resources. Women from the poorest social class were more likely to have a reduced lifespan due to increased risk of dying from infectious diseases following increased reproductive effort, and experienced in general more profound trade-offs between life-history traits (Pettay et al. 2007). Similarly, even in modern developed countries, individuals with low socio-economic status have, on average, lower life-expectancy (e.g. Martikainen 1995). In historical times, opportunity for selection was higher and selection on earlier age at first reproduction stronger among the poorest mothers compared to wealthier mothers. This is in line with the prediction that selection should favor early reproductive effort in conditions where mortality is high. Further evidence that resource availability may affect selection on life-history traits in humans comes from studies on historical Germans and Swedes. In these populations, a negative relationship between parity and post-menopausal lifespan existed among poor landless women only, whereas in wealthier women, the relationship between parity and post-menopausal lifespan was positive (Dribe 2004; Lycett et al. 2000). A negative relationship between fertility and longevity may, therefore, be expected in women who, due to multiple pregnancies and breastfeeding, pay high costs of reproduction that cannot easily be compensated by increases in dietary intake and reduction in physical activity (Jasienska 2009).

Comparable differences in the costs of reproduction resources arising from social class differences between individuals could also be created, for example, by different amounts of help available from other individuals with raising the offspring, such as partners, grandparents, or other helpers-in-the-nest, that affect the level of investment made by the mother. Unfortunately, there are currently no studies investigating how such differences in the environmental conditions of breeders affect their life-history trade-offs, reproductive costs, and senescence in humans (but see Bourke 2007).

Environmental conditions during early life can have similar long-term effects, but little is known of whether the costs of reproduction and rates of senescence might be modified by the prevailing ecological conditions particularly at critical early stages of life. Poor early-life conditions such as maternal nutrition during gestation and lactation could lead to unfavorable developmental conditions for the offspring in utero (reviewed in Lummaa and Clutton-Brock 2002). This could represent an insult to the developmental process, ultimately reducing overall adult physiological condition. It is thus predicted that the life-history trade-offs will be most severe and the rates of senescence greatest among those women living in harsh ecological conditions, because the importance of contributing heavily to care will be greater in such circumstances and hence reproductive investment will be higher. That such effects are likely is suggesting by the growing evidence across species documenting density-dependent and density-independent aspects of the early environment accounting for large portions of variance in important life-history traits and, consequently, fitness (reviewed in Lindstrom 1999). For example, in humans, varying early environmental conditions, such as month or season of birth, predict longevity and reproductive performance (reviewed in Lummaa 2003). Furthermore, dietary intake prior to birth is associated with subsequent risk of adverse health (Hamdoun and Epel 2007), age at sexual maturation (Walker et al. 2006), ovarian function (Jasienska et al. 2006b), and lifespan (Moore et al. 1999), suggesting that early-life conditions influence development and that this has adverse effects later in life.

However, whether and how such early condition differences vary across ages and relate to senescence patterns is generally unknown. Evidence from red deer shows that rates of reproductive senescence are modified by both early environmental conditions (Nussey et al. 2007) and reproductive investment early in life (Nussey et al. 2006), with individuals born in poor conditions or investing heavily early in life showing greater rates of reproductive decline later in life. In many human societies, individuals reproduce across a long time-span and a range of environmental conditions. Given the ongoing demographic and nutritional transitions world-wide to higher energy diets and advancing maternal ages, such relationships are of potential importance in humans too to researchers from social, political, biological, and medical sciences and warrant further exploration.

9.6 The Genetic Basis for Costs of Reproduction Across Ages and Environments

What constrains the evolution of both high reproductive effort and long lifespan? To determine the potential evolutionary response to selection on traits such as reproductive output at different ages and across different environments, information concerning the genetic structure of the traits in question is necessary. This is because phenotypic correlations between reproductive traits and survival are particularly interesting only if they have a genetic basis, given that natural selection can only lead to an evolutionary response when it acts on a heritable character. For example, studies on wild populations of long-lived mammals have shown that, in poor environments, selection on survival can be stronger, but the amount of heritable genetic variation smaller (Charmantier and Garant 2005). Conversely, while there may be high heritable variation in good environments, selection may be relaxed in these conditions (Wilson et al. 2006), explaining why phenotypic trait means do not always correspond well to (directional) selection acting on them.

Unfortunately there are only a few studies investigating trade-offs in human life-history at both the phenotypic and genetic level, and none in men. This lack of information on the heritability and genetic constraints of reproductive traits in human populations has resulted in a limited understanding of whether the phenotypic selection documented could lead to evolutionary changes over time. The two exceptions include studies into the heritability of key life-history traits in contemporary Australian and rural historical Finnish women. In both populations, female life-history traits, such as age at menarche and menopause, reproductive rate and longevity, had significant additive genetic heritability, suggesting the possibility for a rapid evolutionary response to selection, and also 47% of the variance in fitness itself in Finns and 39% in Australians was attributable to additive genetic effects (Kirk et al. 2001; Pettay et al. 2005). Moreover, there were also detectable genetic constraints between reproductive traits and longevity (negative genetic trade-offs): genes related to capacity for a high birthrate appeared to also lead to reduced survival and shorter overall longevity of the mothers (Pettay et al. 2005). This supports the hypothesis that rate of reproduction should trade-off with longevity, and can maintain additive genetic variation in nature (Kirkwood 1977; Williams 1957). The fact that correlations between reproductive investment and longevity are often not present at the phenotypic level (see above) calls for further studies investigating such correlations at the underlying genetic level.

However, similarly to costs of reproduction, also heritabilities can be modified by age and environment. First, female fertility in humans shows clear changes with age, possibly affecting calculations of heritabilities. In young women, maternal effects may be important for successful reproduction, such as wealth of the parents, which correlates both with female body condition, and thus their age at menarche (reviewed in Voland 1998), and with marital success (Voland 1990). Furthermore, family help, such as the presence of grandmothers, may be an important determinant of female reproductive rate: daughters enjoying help from their post-reproductive mothers show reduced inter-birth intervals (Lahdenperä et al. 2004; Voland and Beise 2002) and increased breeding probability (Sear et al. 2003). Finally, female fertility also shows senescence with age: the natural conception rate falls rapidly already from the mid-30s onwards (Sievert 2001), and the risk of unsuccessful pregnancy (miscarriage) increases with age, while the quality of offspring, in terms of developmental and genetic problems, may decrease (Holman and Wood 2001). Consequently, a single over-lifetime estimate of heritability for traits may give too simplistic a view of their response to the documented selection pressures, because evolutionary theories of senescence predict that the additive genetic variance in fitness traits is age-dependent: aging leads to increase of additive genetic variance in late life (e.g. Charmantier et al. 2006).

Currently, the only evidence for the age-dependent changes in heritability of human life-history traits comes from a study by Pettay et al. investigating the historical pedigree records available for eighteenth and nineteenth century Finns (Pettay et al. 2008). A key female life-history trait, fecundity, had significant overall additive genetic heritability (0.31) across all ages, potentially permitting rapid evolutionary responses to selection (Pettay et al. 2005). However, this additive genetic variation in fecundity in women was age-dependent and increased with age, as suggested by the theories of senescence (Rose 1991). In contrast, family effects (nongenetic material inherited from parents) appeared important early in the reproductive career but diminished later on (Pettay et al. 2008). Contrary to many animals, women have high survival in later age classes (Hawkes 2004). The presence of age-dependent additive genetic variation suggests that the common practice of using a single estimate of heritability over all age classes may give an incomplete idea of whether and how selection can lead to an evolutionary change in trait mean values. It is also important in the light of the declining force of natural selection with age (Williams 1957). However, again, further studies on other populations living in differing ecological conditions and experiencing different age-specific reproductive rates and selection pressures would be helpful in clarifying the generality of these findings.

Heritabilities can also change across environments, and certain genotypes may be most successful in particular environments but not in others. Recently it has been increasingly demonstrated that environmental conditions can influence the genetic control of life-history traits such as survival and reproduction in laboratory populations (Sgrò and Hoffmann 2004). As such genotype–environment interaction can result in genetic correlations between life-history traits being environment-dependent (Wilson et al. 2006, 2008), trade-offs have to be examined across all environments experienced by a population. Such studies for human life-history traits are entirely lacking at the moment, although understanding life-history evolution requires examination of both the environmental and genetic relationships between fitness components across the ages and environments in which the traits are expressed.

9.7 Conclusions

In most animals, fitness is maximized by optimizing the trade-off between current and future reproduction, with the amount of selection on early reproduction relative to late reproduction influencing, in part, the rate at which individuals senesce and die. In contrast, in human women, menopause has been proposed to enable women to avoid reproducing at a time when the fitness costs begin to outweigh the benefits, while prolonged post-reproductive lifespan in turn offers an opportunity to increase one's overall genetic contribution to future generations by helping existing offspring to raise their families more successfully. Thus, by increasing current reproductive effort, mothers might not only reduce their future reproductive success but also their post-reproductive survival rates and ability to help their own adult sons and daughters in raising grand-offspring. Life-history theory consequently predicts that fitness in women should be governed by optimization of trade-offs both within the reproductive phase and between the reproductive and post-reproductive phases. We are only beginning to understand such processes, and the ultimate tests of this idea—that genetic trade-offs between rate of parity and post-reproductive lifespan increase with age—are yet to be conducted.

Understanding interactions between reproductive tactics, success, senescence, and lifespan in humans appeals to a large range of people both within and without the scientific community. First, recent changes in population age structure are a growing issue of concern in many "developed" societies, and current models have failed to predict demographic transitions in many developing countries. Second, although there have been dramatic gains in the survival rates of older people in Western countries over the last several decades, the scope for improvements remains an open question because our knowledge about the interaction of biology, behavior, and environmental conditions in determining rates of senescence and age-specific mortality rates is still limited. Moreover, it is likely that increasing knowledge of the human genome may lead to manipulations of genes and gene products, possibly resulting in boosts in lifespan. Better understanding of the forces that have evolved by natural selection to provide our species-typical cell and DNA repair mechanisms are important for these tasks, and this is provided by the life-history framework.

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