Chapter 10
Costs of Reproduction, Health, and Life Span in Women

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Abstract Reproduction in females is costly: pregnancy, breast-feeding, and childcare require energy, and thus energetic costs are indispensable feature of reproduction. Pregnancy and lactation also require many physiological changes, including in maternal immune system and increased levels of oxidative stress. Finally, genes involved in encoding traits related to reproduction often have multiple functions. Some of these genes have alleles that support reproduction but also increase risk of diseases later in life, and their carriers have higher mortality.

Results of studies testing relationships between reproduction and health and reproduction and life span are contradictory, possibly due to methodological problems and theoretical framework problems. There is a need for studies that would analyze these relationships at both genetic and phenotypic levels, and that would comprehensively calculate costs of reproductive investment, including not only number of children but also birth spacing, lactation, childcare, and extended reproductive effort.

10.1 The Principle of Allocation

Parental investment is costly and costs of reproduction are higher for human females than for males due to energetic and nutritional requirements of pregnancy and lactation, and traditionally female-dependent childcare. Energetic costs of pregnancy result from fetal growth, growth and maintenance of maternal supporting tissues, and maternal fat accumulation (Blackburn and Loper 1992). Energetic demands of lactation are a consequence of milk synthesis and the maintenance of metabolically active mammary glands (Lunn 1994). Human children require support also after weaning and in traditional societies became independent at about 15 years of age (Kramer 2005).

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If resources are limited, allocation to one function can only occur at the expense of other functions (Zera and Harshman 2001), and competition for common resources results in trade-offs among life history traits. Increased allocation to current reproduction should result in reduced future reproduction and/or reduced life span. Pregnancy and lactation take energy and nutrients away from other processes and cause multiple metabolic changes. Thus it is expected that female physiology will be negatively affected by the reproductive effort. Repeated reproductive events may negatively affect maternal health, especially at older age, and, ultimately, increase risk of mortality.

10.2 Energetic Costs of Menstrual Cycle and Pregnancy

Ovarian and uterine function in adult females must be constantly maintained. This maintenance requires energy but is not very expensive. During several days of the luteal phase of the cycle, an increase of 6–12 % in the resting metabolic rate has been reported in some women (Bisdee et al. 1989; Curtis et al. 1996; Meijer et al. 1992). An average basal metabolic rate (BMR) for a woman from an industrialized country is 1300 kcal/day (Leonard 2008); thus the increase due to menstrual cycle is between 70 and 150 kcal/day. Some additional energy beyond the regular metabolic needs is required to support regular menstrual function (Strassmann 1996a, b); these costs, however, are negligible in comparison to the much higher energetic demands of pregnancy and lactation.

For well-nourished women from industrialized countries, the estimated costs of pregnancy constitute an expense of an extra 90, 290, and 470 kcal/day, respectively, for the first, second, and third trimesters (Butte and King 2005). During the last trimester, the woman may require up to 22 % of additional energy over the prepregnant values (Butte et al. 1999).

10.3 Costs of Lactation and Childcare

The cost of lactation is a very important variable in calculations of total reproductive costs because, on average, 1 day of lactation places higher demands on maternal energetics than 1 day of pregnancy. Costs of lactation change with the age of the infant (Rashid and Ulijaszek 1999) and the frequency of daily feedings, but, on average, lactation requires additional 626 kcal/day (Butte and King 2005) and may last for a few years. Lifetime costs of lactation are usually neglected by research analyzing relationships between fertility and longevity of women. Data on duration of breast-feeding for individual women are not available from historical demographic records, and omissions of these costs may significantly bias the results of research on reproduction and longevity. Errors may be substantial when women from different socioeconomic classes are compared, since it is likely that there was a considerable variation in breast-feeding practices among such groups.

In addition to costs of pregnancy and lactation, there are also often significant costs which are associated with childcare or with an increase in intensity and duration of work necessary to obtain resources to support each additional child (Sujatha et al. 2000). Estimates of these costs are hard to find as well. Women who do not have any additional help clearly spend more time and energy as the number of children increases. However, as children grow older, they are able to provide childcare to younger siblings and become involved in housework, agricultural work, or work for wages (Biran et al. 2004; Kramer 2002; Nag et al. 1978). Therefore, the relationship between the number of children and the maternal costs of childcare is clearly not straightforward.

10.4 The Intergenerational Costs: Children and Grandchildren

Children not only impose biological costs but also provide some benefits to their parents, for example, by contributing labor to the household. In preindustrial societies, characterized by the absence of pension system or health insurance, having children was especially important for elderly parents (Tsuya et al. 2004). How children affect parental well-being depends on economic conditions and social structure of the population, especially family structure, and behavioral patterns of taking care of aging parents. For example, in the Liaoning Province in China between 1749 and 1909, women had 12 % higher mortality if they did not have any living sons, and the risk of mortality for women without sons increased further if women were widows (Campbell and Lee 2004). Having children had a positive effect on parental life expectancy also in some historical European communities (Tsuya et al. 2004).

Parental investment may continue for many years, and once parents complete their direct investment to children, they often became involved in helping to raise grandchildren. This prolonged investment requires additional energy and as such may increase burden associated with reproductive costs; thus well-being of parents is not only influenced by costs and benefits resulting from interactions with their children but, in later years, also with their grandchildren. Older people lived and, in some societies still do, with one of their children and his or her offspring. Costs and benefits of such interactions are important to consider when discussing health and mortality risks in relation to reproductive investment. While the impacts of grandparents on health and survival of grandchildren are widely studied (Sear et al. 2000; Hawkes et al. 1997; Voland and Beise 2002), less interest has been devoted to whether these interactions have any effect on the well-being of grandparents themselves. In patrilineal systems, cost and benefits of interactions with grandchildren may be different for grandmothers and grandfathers. Expectations toward grandmothers may be much higher than for grandfathers and may include childcare or physical labor (Pashos 2000). Grandfathers may feel entitled to a higher share of resources than those left for grandmothers which may be especially important when resources are scarce, and some studies report higher incidence of malnutrition in older females than in older males (Aliabadi et al. 2008). Even in modern families, grandmothers are expected to provide more care and support to families, as shown, for example, by a study investigating roles of grandparents in support networks in neonatal intensive care units in Scotland (McHaffie 1992).

Costs related to interactions with grandchildren may vary for maternal and paternal grandmothers. Maternal grandmothers, due to paternity uncertainty (Hamilton 1964), are expected to contribute more toward children of their daughters than to children of their sons. This prediction has been confirmed by many studies documenting that maternal grandmothers are more often the primary caregivers (Euler and Weitzel 1996; Michalski and Shackelford 2005; Sear and Mace 2008). Several studies documented benefits for grandchildren living with maternal grandmothers and lack of such benefits when children live with their paternal grandmothers (Hawkes et al. 1997, 1998; Jamison et al. 2002; Sear et al. 2000; Voland and Beise 2002). It is very likely that providing such benefits for children is not cost-free for their grandmothers. Childcare and resource acquisition are energetically demanding and may negatively affect nutritional status of grandmothers.

10.5 Reproductive Costs and the Overall Energy Budgets

Female zebra finches that are experimentally forced to have high costs of reproduction by laying more eggs do not seem to suffer negative metabolic consequences, provided that their diets are supplemented (Bertrand et al. 2006). It is not clear if similar relations should be expected for human females, but it is likely that 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.

Basal metabolism, measured by basal metabolic rate (BMR), is expected to rise in women who are pregnant or nursing a child. The BMR of a pregnant woman should increase during each of the four quarters of pregnancy, respectively, by about 3, 7, 11, and 17 % above the prepregnant values (Hytten and Leitch 1971). Empirical data usually support these theoretical predictions but only in women who have good nutritional status (Butte et al. 1999; Durnin 1991, 1993; Lunn 1994; Prentice and Prentice 1990; Prentice and Whitehead 1987). However, in limited energy environments, the physiology of women who are already pregnant or lactating may be forced to rely on energy-saving strategies in order to support energetic demands of the fetus or infant (Peacock 1991). Reallocating more energy to reproduction could be achieved by reduction in the maternal basal metabolism (Peacock 1991; Prentice et al. 1989, 1995).

In pregnant women from Scotland and Gambia, who are in poor nutritional condition, the BMR showed a significant decrease up to the 12th week of pregnancy. Later BMR increased and approached the prepregnant values by 22–26 weeks and continued to rise further, but even at delivery it was still much lower than the BMR of well-nourished Swedish women (Prentice and Whitehead 1987). Pregnant Nigerian women showed significant variability in BMR, which corresponded to variability in their nutritional status (Cole et al. 1989). Even well-nourished Western women show significant variation in the BMR responses to pregnancy paralleling differences in their prepregnant body fat (Prentice et al. 1989), and maternal adipose reserves serve as highly significant predictors of changes in the BMR (Bronstein et al. 1996). Reduction in the BMR at the beginning of pregnancy seems to be an important strategy for women in poor nutritional condition. Lowering the BMR considerably reduces energetic costs of pregnancy and allows women to allocate some energy into fat storage which may be critical for the energetic support of lactation.

Lactation is predicted to cause, on average, a 12 % increase in the BMR above the nonpregnant values (Hytten and Leitch 1971); however, during lactation, the BMR has been observed to increase, decrease, or remain at prepregnant levels (Forsum et al. 1992; Goldberg et al. 1991; Guillermo-Tuazon et al. 1992; Lawrence and Whitehead 1988; Madhavapeddi and Rao 1992; Piers et al. 1995). Variation in the BMR during lactation can be explained by differences in the nutritional status of the women (Prentice and Prentice 1990). Women from the Gambia during the first year of lactation showed a 5 % decrease in the BMR compared to the prepregnant values which saves about 200 kcal/day (Lawrence and Whitehead 1988). In comparison to women who increased their BMR during lactation, savings add up to about 380 kcal/day. The saved energy can be allocated into milk production. The savings from the reduction of the BMR, although not sufficient to cover the whole expense of lactation, are still substantial, since average daily cost of milk production for women in developing countries is about 480 kcal (Lunn 1994).

Reduction in basal metabolism suggests that some of the metabolic processes (e.g., components of the maintenance metabolism, like protein turnover, or immune function) are temporarily slowed down or even halted (King et al. 1994; Prentice and Whitehead 1987); thus a long-term reduction in the BMR may be detrimental to the maternal health.

10.6 Reproduction and Life Span

The question about the impact of reproduction on life span has been addressed by many epidemiological and historical demography studies (for review see Le Bourg 2007). Several studies described a U-shaped relationship between the number of children and risk of mortality (Green et al. 1988; Lund et al. 1990; Manor et al. 2000). In the historical Swedish population (1766–1885), the number of children ever born by a woman had a negative impact on maternal longevity (Dribe 2004). Giving birth to four or more children increased maternal mortality by 30–50 % in comparison to women with fewer children. Having four or five children, instead of none or one, shortened the woman's life span by 3.5 years. However, the negative impact of parity was restricted only to landless women, while those with better socioeconomic status were not affected by reproductive costs at all.

In a historical population of northwest Germany (1720–1870), the number of children had a negative impact on longevity but only for the group of poor, landless women (Lycett et al. 2000). Among other women, with higher economic status, a *positive* relationship between the number of children and longevity was described suggesting that trade-offs between costs of reproduction and longevity apply only for those women for whom such costs are a substantial part of their overall energy budget.

Gender of children may also be an important variable to consider when analyzing the costs of reproduction and longevity. Boys have faster rate of intrauterine growth and heavier average size at birth (Loos et al. 2001; Marsal et al. 1996) and, given larger body size, perhaps higher lactational demands (Hinde 2007). Women have longer interbirth intervals after giving birth to a son than after giving birth to a daughter (Mace and Sear 1997), and offspring born after brothers have lower birth weight (Cote et al. 2003), lower height at adulthood (Rickard 2008), and also lower number of surviving children (Rickard et al. 2007) than those born after sisters (but see Puskarczyk et al. 2015). This suggests that having sons may be more energetically expensive for mothers than having daughters and that the maternal organism may become more depleted by producing male offspring.

In Finnish Sami (Helle et al. 2002) and a Flemish village (Van de Putte et al. 2003), sons decreased maternal life span, while daughters did not. In four Polish small agricultural villages, however, analyses of parish records from 1886 to 2002 showed that both the number of sons and the number of daughters decreased maternal life span and did so to the same degree (Jasienska et al. 2006a).

Not all studies documented detrimental effect of reproductive investment on maternal life span, and, in fact, a number of studies of historical populations documented a positive association between the number of children and life span, as, for example, in the Amish population (McArdle et al. 2006) and German women of higher socioeconomic status (Lycett et al. 2000). In a French-Canadian cohort of women (seventeenth and eighteenth centuries), longevity increased with increasing number of children, especially for women with the late age at last birth (Muller et al. 2002), and this may suggest slower rate of ovarian and overall aging in some women (Dribe 2004). Others did not find either positive or negative significant relationships between the number of children and life span of mothers (e.g., Le Bourg et al. 1993).

10.7 Reproduction and Health: Obesity, Diabetes, Cardiovascular Diseases, and Osteoporosis

Reproduction requires not only additional energy but also nutrients. In addition, physiological and metabolic adjustments (e.g., immunological and increased oxidative stress) associated with pregnancy may cause permanent changes in the maternal organism, especially when pregnancies are numerous. Self-reported health status, a reliable predictor of mortality (Idler and Benyamini 1997), is lower for women with at least three pregnancies and especially for women with six or more pregnancies (Kington et al. 1997). Parity is positively related to the risk of obesity, impaired glucose tolerance, non-insulin-dependent diabetes, and cardiovascular diseases.

10.7.1 Cardiovascular Diseases, Diabetes, and Obesity

Many studies suggested that high parity is related to increased risk of cardiovascular diseases. The longitudinal Framingham Heart Study and the National Health and Nutrition Examination Survey documented a positive relationship between the number of pregnancies and the subsequent development of cardiovascular disease (Ness et al. 1993). In British women with at least two children, each additional child increased the risk of coronary heart disease by 30 % (Lawlor et al. 2003). In a population-based cohort Swedish study, women with five children had about 50 % higher risk of cardiovascular disease than women with two children (Parikh et al. 2010). Having gone through six or more pregnancies increased the woman's risk of all types of strokes by 70 % (Qureshi et al. 1997).

The risk of diabetes may increase with parity as well. Among rural Australian women, those with five or more children had 28 % higher risk of diabetes than women with three or four children and 35 % higher risk than women with one or two children (Simmons et al. 2006). In Finnish women, parity of five or higher was related to 42 % higher risk of diabetes compared to the average risk experienced by women in this population (Hinkula et al. 2006). In Brussels, both parity and early age at first birth were associated with diabetes-related mortality in women (Vandenheede et al. 2012).

Pregnancy is a risk factor for obesity, and postpartum weight retention occurs in 60–80 % of women (Martin et al. 2014). In a study of the US women, each birth was associated with a 0.55 kg of permanent increase in body weight (Brown et al. 1992), while other studies reported that maternal body weight increased by 0.4–3.0 kg after each pregnancy (Harris and Ellison 1997). Among women with parity of three or more, a higher proportion was overweight than in women with lower parity. In women from Utah, a dose–response relationship was observed between the number of children and risk of obesity (Bastian et al. 2005): each additional live birth increased the risk of obesity by 11 %. In a study based on data from 65 countries, sustained breast-feeding contributed to reduction of postpartum BMI but not among relatively wealthy women (Hruschka and Hagaman 2015).

In women from developing countries, however, repeated reproductive events cause a reduction of body weight. The "maternal depletion syndrome" refers to the long-term negative changes in the maternal nutritional status, as opposed to the short-term changes associated with a single pregnancy or breast-feeding (Winkvist et al. 1992). In Papua New Guinea, the nutritional status of women decreased with parity (Garner et al. 1994). This maternal depletion occurred even though birth intervals were relatively long (3 years on average) in this population. In Turkana from northwestern Kenya, women from both nomadic and settled populations had parity-related decline in fat reserves (Little et al. 1992). In another African population, the !Kung San, the higher number of surviving children was related to lower body weight in women, while in men those with more surviving children had higher body weight (Kirchengast 2000).

Improvement in socioeconomic status seems to increase the maternal ability to resist the stress of repeated reproductive events. In Papua New Guinea, the decline in nutritional status was substantial in women who were foraging horticulturalists, while such changes were not observed among wage earners (Tracer 1991). Toba women from Argentina, a well-nourished population undergoing a transition from semi-nomadic hunter-gatherer to a sedentary, peri-urban lifestyle, did not lose excess weight gained during pregnancy despite prolonged and intense breast-feeding (Valeggia and Ellison 2003).

10.7.2 Bone Density and Osteoporosis

During pregnancy and lactation, high levels of calcium are required to support the child's developing skeleton. Such high calcium requirements are often met by mobilization of calcium from the skeleton of the mother (Prentice 2000); thus it can be hypothesized that women who had high number of pregnancies and breast-fed their children would have lower bone mineral density and therefore higher risk of osteoporosis. Each pregnancy causes 3–4.5 % decrease of bone mineral density in the lumbar region (Black et al. 2000; Drinkwater and Chestnut 1991). Bone mineral density is regarded as reliable predictor of bone strength (Karlsson et al. 2005), and a decrease of about 10 % of initial density doubles the risk of fractures in women (Cummings et al. 1995). Lumbar bone density decreases further by 3–6 % during lactation (Karlsson et al. 2001; Laskey and Prentice 1997). Changes in bone density occurring during pregnancy and lactation are reversible (Karlsson et al. 2005; Laskey and Prentice 1997), at least in women from industrialized populations, and there seems to be no consistent relationship between the number of children and bone mineral density (Bererhi et al. 1996). The absence of such relationships may be due to a rather low fertility of women from industrialized countries. A large study in Italy, with over 40,000 participants, did not show any effects of having children on bone density, but it compared women who never had a full-term pregnancy to women who only had one or two children (De Aloysio et al. 2002). Among Tsimani women, forager–farmers of lowland Bolivia, higher costs of reproduction (higher parity, shorter interbirth intervals, and earlier age at first birth) were associated with reduced bone mineral density (Stieglitz et al. 2015).

The relation between parity and bone health could be confounded by lifetime estrogen status of women. Estrogen has positive effect on bones, and estrogen deficiency plays a crucial role in the development of osteoporosis (Raisz 2005); thus the number of menstrual cycles during which estrogen is produced should be positively related to bone mineral density (Somner et al. 2004). Early menarche and late menopause increase the total time during which women can become pregnant. Bone mineral density is positively correlated with the length of reproductive span. In natural fertility populations, women who have high parity also have the longest reproductive life spans.

In women who are in good nutritional condition, a negative effect of high parity on bone density may be not detectable, since it is counterbalanced by the effect of having many high-estrogen cycles which are beneficial for bone health. The protective effect of parity on hip bone mineral density was shown, for example, in a study on Amish women with high parity (7.6 live births on average) (Streeten et al. 2005). In these women parity correlated positively with the later age at menopause and higher cumulative estrogen exposure (calculated as the age at menopause minus the age at menarche). In addition, parity increase body mass and overweight women have more adipose tissue, which produces aromatase, an enzyme converting androstenedione to estrogens. This suggests that high-parity women may have, due to greater weight gain, higher levels of estrogen in postmenopausal years (Bray 2002), which promote higher bone density (Alden 1989; Nguyen et al. 1995).

10.8 Reproduction and Risks of Reproductive Cancers

Lifetime costs of reproduction are related to an increased risk of cardiovascular disease, diabetes, and stroke even in women who are in good nutritional status. Why then studies show contradictory results on the association between reproductive investment and mortality in women? These contradictory results may be explained by the fact that the same features of reproductive life which involve the highest metabolic and physiological costs of reproduction, i.e., early first birth and high parity, may also serve a protective function, leading to decreased mortality from other diseases.

Early age at first reproduction and high number of children are the most important factors protecting women against breast cancer and other reproductive cancers (Hinkula et al. 2001; Kvale 1992; MacMahon 2006; Mettlin 1999). Breast cancer risk is also decreased by breast-feeding (Kvale 1992; MacMahon 2006), especially in women from developing countries, because feeding sessions are more frequent than in developed countries and mothers are often in relatively poor nutritional state. Frequent nursing, however, is unlikely to cause long-lasting ovarian suppression when the mother is in a good nutritional condition (Valeggia and Ellison 2004). For these reasons (low frequency of nursing and good nutritional condition), women from economically developed countries, even when they are breast-feeding for a long period of time, experience a much earlier resumption of postpartum ovarian activity.

It is possible that contradictory findings of studies on relationship between reproduction and longevity in women partially result from the fact that reproduction increases risk of some diseases (e.g., cardiovascular disease and diabetes) but reduces risk of other diseases (e.g., reproductive cancers). These trade-offs between risks of different diseases are not the same in all populations. The risk of breast cancer increases due to high, lifetime exposure to estrogens (Bernstein 2002; Jasienska et al. 2000; Key and Pike 1988). Early pregnancy, by inducing the differentiation of breast tissue, reduces its susceptibility to neoplastic transformation (i.e., development of tumors) (Balogh et al. 2006), and each subsequent reproductive event suppresses menstrual cycles. In addition, the post-pregnancy period is characterized by low levels of endogenous estrogens, and it is thought that this may further suppress potential tumor growth.

In poor agricultural societies, however, women generally have low levels of estrogen and progesterone in menstrual cycles. Low nutritional status and intense labor postpone the age of sexual maturation and in later life periodically suppress ovarian function (Jasienska 2001, 2003; Jasienska and Ellison 1998, 2004; Panter-Brick and Ellison 1994; Panter-Brick et al. 1993). Poor developmental conditions during fetal and childhood periods are also related to lower hormone levels in adult women (Jasienska et al. 2006b, c; Nunez-de la Mora et al. 2007). Therefore, women in poor populations have low lifetime exposure to estrogens. In contrast, in economically well-off populations, women have high levels of hormones in menstrual cycles and only rarely experience ovarian suppression (Ellison et al. 1993). This suggests that in well-off women, reproduction may cause reduction in risk of breast cancer, while in relatively poor women, risk of breast cancer is low in general, due to low lifetime estrogen levels. Thus trade-offs between risks of different diseases that occur in relation to reproductive investment are not the same in well-off and poor women. In both groups, women with high parity may experience increased risks of cardiovascular diseases and diabetes, but in well-off women, these elevated risks may be outweighed by significantly decreased risk of breast cancer. Thus, for well-off women with high-parity reduction in life span may not be observed.

10.9 Genetic Trade-Offs Between Reproduction and Life Span

Genes involved in encoding traits related to reproduction often have multiple functions. Some genes have alleles encoding traits that support reproduction but also increase risk of diseases later in life, and their carriers have higher mortality. Such phenomenon when a gene contributes to enhanced reproduction or survival in younger age but poorer health in older age is known as antagonistic pleiotropy. Well-studied example of a gene that shows antagonistic pleiotropy is a gene *ApoE,* encoding apolipoprotein E that is involved in cholesterol metabolism. Carriers of *ApoE4* allele have higher levels of cholesterol and, consequently, have a higher risk of hypertension and of cardiovascular and Alzheimer's diseases (Song et al. 2004). Some studies suggested that this health-detrimental allele is maintained in populations because its carriers have some benefits in younger age (e.g., better

Table 10.1 Comparative costs and benefits of reproduction and their impact on health and life span in women with high parity but differing in socioeconomic status. In well-off women, reproduction increases risks of several diseases (e.g., cardiovascular, diabetes), but these risks are offset by significant reduction in risk of breast and other reproductive cancers. In poor women, reproduction increases risks of the same diseases, but these women have low lifetime risks of breast and reproductive cancers (due to low levels of hormones in menstrual cycles), even when they are not reproducing. In addition, in poor women, energetic and nutritional expenses of reproduction cannot be easily compensated and may cause more substantial damage to the maternal organism

	Poor women	Well-off women
Energetic costs of pregnancies	High	High
Energetic costs of lactations	High	Low/none
Nutritional ability to meet costs of pregnancy and lactation	Low	High
Levels of estrogen in menstrual cycles	Low	High
Risk of maternal depletion	High	Low
Risk of obesity	Low	High
Risk of cardiovascular diseases	Increased	Increased
Risk of strokes	Increased	Increased
Risk of diabetes	Increased	Increased
Risk of osteoporosis	Not affected	Not affected
Risk of breast cancer	Slightly reduced	Greatly reduced
Risk of uterine and ovarian cancers	Slightly reduced	Greatly reduced
Life span	Reduced	Not affected/increased

development of the cognitive function (Filippini et al. 2009) or protection against infectious diseases (Oria et al. 2010). Turns out that women with *ApoE4* allele have higher levels of progesterone in their menstrual cycle which means that they have higher potential fertility (Jasienska et al. 2015). This finding suggests that the presence of selected genes may confound results of studies analyzing relationship between reproductive investment and health and life span. Women with *ApoE4* allele may have higher parity and poorer health due to the presence of this allele. Poor health in high-parity *ApoE4* carriers may have nothing to do with energetic and physiological costs of reproduction. Further, this suggests that trade-offs between reproduction and health should be studied both at phenotypic and genetic levels (Stearns 1989).

10.10 When Does Reproduction Reduce Life Span?

There is convincing evidence that reproduction is costly and related to long-term changes in female physiology; however, a negative impact of reproduction on life span is not always expected (Table 10.1). Energetic and metabolic costs of reproduction cannot be calculated just by adding up all of the woman's children (Jasienska 2013). Women with a similar number of children often differ in costs of lactation, and this difference can be very substantial. They may also differ in their ability to meet energetic costs of reproduction, due to differences in lifestyle, dietary intake, and physical activity. High costs of reproduction and its negative effects on some diseases may be outweighed by reduction in risk of other diseases. The lifestyle maintained by women is an important factor to consider, as for some women, intense reproduction will substantially reduce their risks of reproductive cancers, while for other women, risks of these cancers are relatively low, even when they have low parity. Indirect, extended costs of reproduction, such as those paid by grandmothers taking care of grandchildren, may also change the overall lifetime ratio of costs and benefits of reproduction.

Therefore, in women from rich environments, high parity may not translate into reduction in longevity for several reasons. Women with high parity may have relatively low costs of reproduction if they do not breast-feed their children. In many European populations, women who had higher socioeconomic status were not expected to nurse their children at all, and wet nurses were commonly employed. In well-off women, even if they nurse their children, the costs of pregnancy and lactation are easily met by additional energy intake, especially when there are no energetic demands from physical activity. Furthermore, there are trade-offs between reproductive costs and benefits provided by protection against breast cancer. It is even possible that in well-off women, benefits may outweigh costs and high fertility may, in fact, be related to life span extension. Finnish grand multiparity women had higher mortality from all metabolic diseases, especially diabetes and cardiovascular diseases, than the average for the population, but these risks were clearly outweighed by lower mortality from cancers, since their *overall* mortality was slightly lower than the population average (Hinkula et al. 2006). A negative relationship between fertility and longevity may, therefore, be expected in women who due to multiple pregnancies and breast-feeding not only have high costs of reproduction but also when these costs cannot be easily compensated by increases in dietary intake and reduction in physical activity. The most pronounced negative relationship between reproduction and life span should be expected when the lifestyle (poor nutrition and high work demands) of the woman leads to low lifetime estrogen levels, and additional reduction in these levels caused by reproductive events is relatively insignificant.

Study Questions

1. Why do studies on a relationship between lifetime reproductive investment and health and life span in women report contradictory results?
2. How would you design a study on a relationship between lifetime reproductive investment and health and life span in women? What group/groups of women would you study? What kind of data would you collect?

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