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# **EVOLUTION OF PROLONGED LONGEVITY IN HUMANS**

by

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“Call it a clan, call it a network, call it a tribe, call it a family:  
Whatever you call it, whoever you are, you need one. “

*JANE HOWARD*

## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following articles which will be referred in the text by their Roman numerals:

- I Mirkka Lahdenperä, Andrew F. Russell, Marc Tremblay and Virpi Lummaa. Selection on menopause in two pre-modern human populations: No evidence for the Mother hypothesis.  
- *Submitted manuscript*
- II Mirkka Lahdenperä, Virpi Lummaa, Samuli Helle, Marc Tremblay and Andrew F. Russell 2004. Fitness benefits of prolonged post-reproductive lifespan in women. *Nature* 428: 178-181.
- III Mirkka Lahdenperä, Duncan O. S. Gillespie, Andrew F. Russell and Virpi Lummaa. Severe intergenerational reproductive conflict in humans and its implications for female menopause.  
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- IV Mirkka Lahdenperä, Andrew F. Russell and Virpi Lummaa 2007. Selection for long lifespan in men: benefits of grandfathering?  
- *Proceedings of the Royal Society of London: Biological Sciences* 274(1624): 2437–2444
- V Mirkka Lahdenperä, Virpi Lummaa and Andrew F. Russell. Natural selection on the longevity of men.  
- *Submitted manuscript*

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## 1. INTRODUCTION

Evolution by natural selection provides a framework for understanding the variation in form and function that we observe in the natural world (Darwin 1859, Fisher 1958). In particular, the theory of natural selection suggests that the form and function observable today are the currently winning trait combinations from generations of reproductive competition with others. While most of evolutionary theory is tested using extinct and extant animals, there has been a recent appreciation that also humans can be subject to evolution by natural selection, and can be fruitfully used to test evolutionary theory (Blaffer Hrdy 1999, Dunbar & Barrett 2009, Hawkes & Paine 2006). Indeed, humans, especially those living in conditions of natural fertility/mortality, have a number of advantages over animals as a model species because of our advanced understanding of the anatomy and physiology, and because measuring lifetime reproductive success of whole populations (including dispersers) is possible. Finally, as we shall see, humans have an exceptional life-history that not only provides a significant test of Darwinian selection, but also promises to advance our understanding of selective forces driving evolution.

### 1.1 The puzzle of human life history

Human life-history differs in many distinct ways from other mammals (Alvarez 2000, Charnov & Berrigan 1993, Hawkes 2003, Hawkes & Paine 2006). Offspring are born helpless and have high infant mortality and childhood is notably prolonged, although relatively long childhood is also found in other apes (Perreira & Fairbanks 1991). Young children depend entirely on parental provisioning of care, shelter and sustenance, and nutritional dependency may continue until puberty (Kaplan & Lancaster 2003). Nevertheless, although children need protracted care and high investment, they are born at relatively short intervals compared to other apes. For example, chimpanzees (*Pan troglodytes*) give birth to a new offspring on average with an interval of 5.5 years, orangutans (*Pongo pygmaeus* and *P. abelii*) with an interval of 8 years and humans every 3-4 years in populations with natural fertility (Robson et al 2006, Wich et al. 2004). The short birth interval in humans results in a family structure with a number of offspring at different stages of dependency, and hence needing to be cared for simultaneously.

Human lifespan is the longest of any terrestrial mammals (Paine & Hawkes 2006). Surprisingly, however, all women worldwide lose their ability to reproduce around age of 50 (Pavelka & Fedigan 1991), making the long post-reproductive lifespan one of the most exceptional traits in human life-history. In women, senescence of reproductive function differs from other physiological functions (Hill & Hurtado 1991), given that

women can still live decades after menopause. An age-specific decline in fertility is not unknown among animals (Packer et al. 1998, Ricklefs et al. 2003) and iteroparous animals are generally expected to exhibit declining fertility as a function of overall senescence (Hamilton 1966). However, even female primates, our nearest relatives, retain fertility close to the end of their lives (Caro et al. 1995, Pavelka & Fedigan 1991), resulting in a maximum post-reproductive lifespan in these species of a few years (Cohen 2004). Short-finned pilot whales (*Globicephala macrorhynchus*) and killer whales (*Orcinus orca*) are the only other species known to experience a non-facultative and total cessation of reproductive capacity well before the end of their maximum potential lifespan (Marsh & Kasuzya 1984, Pavelka & Fedigan 1991, Ward et al. 2009); living, like humans, several decades after a clear menopause.

The recent increase in human life expectancy in developing countries is not the only factor explaining long lifespan of humans. Until the last decades, increases in life expectancy have reflected reductions in infant and juvenile mortality, rather than increases in the proportion of post-menopausal women (Hawkes 2004). In both historical populations and hunter-gatherer populations with natural fertility and mortality, a third or more of women are usually found above 45 years (Gurven & Kaplan 2007, Hawkes 2004). This is very unusual compared to other primates; in chimpanzees, less than 3% of adults are over the age of 45 (Hill et al. 2001) although the fertility patterns in chimpanzees and humans is very similar, approaching to zero at the same age (~50 years) (Thompson et al. 2007). Thus, the reproductive and somatic senescence are clearly coupled in female chimpanzees but not in women (Thompson et al. 2007). A life-history with such a long post-reproductive lifespan is puzzling because evolutionary theory suggests that individuals should reproduce until death to maximize the number of descendants in future generations (Hamilton 1966, Williams 1957) and there should not be selection for living beyond one's reproductive capacity. If this is the case, how can we understand menopause and a women's long post-reproductive lifespan from an evolutionary viewpoint? And what explains the very similar lifespan of men and women, despite the fact that, contrary to women, men's overall senescence is more clearly coupled with their reproductive senescence? The aim of my thesis is to resolve the evolutionary puzzle of prolonged longevity in both men and women.

## 1.2 Framework to resolve the puzzle

To understand the evolution of female menopause and more generally, the length of human lifespan, we need to apply a life-history approach incorporating kin-selection theory. The life-history theory of evolution postulates that many traits and behaviors can be understood in terms of the effects of natural selection on the key maturational and reproductive characteristics during lifespan (Cole 1954, Gadgil & Bossert 1970,

Lack 1954, Williams 1966, reviewed in Roff 1992, 2002 and Stearns 1992). Thus, life-history theory provides a tool for explaining the diversity of traits and life cycles among and within individuals. During its lifespan, an individual should maximize its genetic contribution to future generations, a task that can be accomplished through various combinations of reproductive traits in varying environmental conditions. Life-history theory thus provides a framework for studying why some traits have evolved or why they are expressed in certain way. The key questions include: At what size should an individual start to reproduce? How many offspring should it produce, and of what sex and size? How many times should an individual reproduce during its lifespan and when should it senesce and die? Central to all of these questions is how these features are affected by other traits, for example how longevity is affected by fecundity or by the sex of the offspring produced. Such negative correlations, or trade-offs, between traits are explained by the fact that individuals have limited amounts of energy and time; investment in one trait will take resources from another trait. Trade-offs can exist, for example, between maintenance and reproduction, and we expect natural selection to favor the most optimal combination of investment that will maximize fitness.

Another central theory for studying human evolution is kin-selection theory (Hamilton 1964). This theory aims at explaining why individuals indulge in apparently altruistic behaviours; reconciling this contradictory behavior with the benefits of providing care to individuals which share the same genes by descent. This theory thus supposes that individuals behave more altruistically toward their relatives, because they share a relatively higher proportion of genes by descent than non-relatives. Consequently, by helping a relative to reproduce, an individual can indirectly transmit its genes to the next generation. According to Hamilton's rule ( $rb-c>0$ ), individuals are expected to help their relatives ( $r$ , the coefficient of relatedness), when the fitness costs of helping ( $c$ ) are smaller than the fitness benefits ( $b$ ) weighted by relatedness ( $r$ ). Individuals are also more likely to provide care to the offspring of others if they have no offspring of their own (Russell 2004, Sear et al. 2000). By combining life history theory and kin-selection theory, we can study in what circumstances and why natural selection may have favoured the evolution of menopause in women, as well as prolonged longevity in both sexes.

### **1.3 Kin-selection based life-history hypotheses for the evolution of menopause and post-reproductive lifespan in women**

Kin-selection and life-history theories have individually been successfully applied to understanding the evolution of menopause and exceptional longevity in humans. Several hypotheses have been formulated to explain the occurrence of menopause and post-menopausal lifespan in women. Some explanations have proposed that these traits result from a physiological trade-off favoring efficient reproduction early in the fertile part



of life (Pavelka & Fedigan 1991, Peccei 2001a, Wood et al 2001), whereas others have suggested that menopause and post-menopausal lifespan in humans are by-products of increases in lifespan or life expectancy due to improved nourishment, medicine and hygiene and thus are not evolutionarily meaningful (Symons 1979, Washburn 1981, Weiss 1981). Such suggestions are however not upheld by the current knowledge that prolonged longevity in humans had already evolved in late Pleistocene (Caspari & Lee 2004) and is therefore not a recent phenomenon (Gurven & Kaplan 2007). In his patriarch hypothesis, Marlowe (2000a) proposed that female menopause is a by-product of selection for greater male longevity. This would be explained both by the fact that males are capable of maintaining a high status and being reproductively active in older years, but also by the fact that genes associated with longevity are not on the Y chromosome and hence also benefit females. It has also been suggested that the high nutritional provisioning of older males to reproductively active women and children could increase male mating success in old age and would have hence indirectly resulted in female increased longevity (Kaplan et al 2000). These explanations are not very likely, as it is difficult to envision how selection on one sex would give rise to a greater response in the other sex, given that female lifespan is on average slightly longer than male's in almost all populations worldwide (Møller et al 2009).

The more plausible explanations for the evolution of female menopause and longevity include adaptive hypotheses concerning the women themselves. Several authors have proposed that menopause is the result of selection for a post-reproductive lifespan that allows increased maternal investment in existing offspring ("Mother hypothesis", Lancaster & Lancaster 1983, Peccei 1995, 2001b, Williams 1957) and grand-offspring ("Grandmother hypothesis", Hawkes et al. 1989, 1998, 2003, Hill & Hurtado 1991, Rogers 1993, Turke 1988). Recently, a third hypothesis suggested that menopause and the minimal reproductive overlap between generations of women might be the outcome of reproductive competition between generations (Cant & Johnston 2008). Below, I conduct a detailed investigation of these main adaptive explanations for the evolution of female menopause and longevity in women.

### **1.3.1 The Mother hypothesis**

The first adaptive explanation for the evolution of menopause is the Mother hypothesis, which proposes that because humans have an unusually long period of dependence and unusually high numbers of dependent offspring simultaneously, individual selection should favour mothers who shut-down their reproductive system earlier in the face of increasing risks of reproducing with increasing age and concentrated on rearing their already existing offspring (Lancaster & Lancaster 1983, Peccei 1995, 2001b, Williams 1957). The Mother hypothesis relies on the existence of high risks for both the offspring

and the mother that are associated with continuing to reproduce in old age. In line with this assumption, previous evidence supports a potential rise of maternal mortality with higher maternal parity and age (Donoso & Villarroel 2003, Knodel 1988, Loudon 1992, Temmerman et al. 2004, Ujah et al. 2005, Yerushalmy et al. 1940). In addition, old-age pregnancies have highly elevated risk of stillbirth or fetal loss (Wood 1994) and the fetus has higher risk of birth defects (for example chromosomal abnormality) (Heffner 2004, McNamara 1982, Reddy et al. 2006).

To fully understand the importance of this hypothesis in explaining menopause and subsequent prolonged survival, we are in dire need of studies examining the costs to the mother and her dependent children of continued reproduction in older age. This would consist, first, in assessing whether the costs of reproduction, measured as the rate of maternal death from childbirth, increase to an unbearable level with increasing maternal age and, second, it would mean identifying how and until what age the dependent children's survival and future fitness are affected by maternal death. Finally, given the length of the need for parental care in human offspring, maternal death in child-birth should not only have a significant negative effect on the survival probability of the current child, but it should also affect the survival of all previous offspring that still depend on their mother for sustenance. Although recent studies (reviewed in Sear & Mace 2008) show overwhelming support for the importance of the mother on the child's survival pre-weaning, the nature of the interaction between maternal death and offspring age on offspring survival and future reproductive potential has not yet been explored. Understanding such an interaction would however allow us to estimate whether the costs of continued reproduction with age can be high enough to favour women who end their reproduction early. It would also give us a better idea as to how long women should live after ceasing reproduction to ensure the survival and success of their offspring. Such analyses would clarify to what extent a typical post-reproductive lifespan in women may have evolved simply as a result of the lengthy need for maternal care in human children.

### **1.3.2 The Grandmother hypothesis**

The Grandmother hypothesis aims at explaining the evolution of long post-reproductive lifespan rather than the evolution of menopause. It proposes that in our evolutionary past, older women who stopped reproducing early gained an evolutionary advantage when they devoted their remaining reproductive effort towards increasing the success of their own adult offspring and grand-offspring (Hawkes et al. 1989, 1998, 2003, Hawkes & Blurton Jones 2005, Hill & Hurtado 1991, Rogers 1993, Turke 1988). Grandmothers could thereby increase their offspring's lifetime reproductive success and hence their own biological fitness, such that natural selection would favor a longer post-reproductive lifespan in women.

According to the Grandmother hypothesis, helping grandmothers could reduce their daughter's age to first reproduction and shorten her inter-birth intervals, leading her to produce more children with increased chances of survival. As a result, a grandmother who would live longer would pass more genes copies to future generations, and a lengthy post-reproductive period in women would thus represent a clear fitness advantage. The Grandmother hypothesis originally suggested that older women could, in particular, provision their daughter's weaned offspring (Hawkes et al 1998). However, in humans, the relative contributions of post-menopausal women to food production appear to vary from group to group, and while in some societies it can be very important (Hawkes et al 1997), it is not essential in others (Hill & Hurtado 2009, Kaplan et al 2000). In addition to food provisioning, evidence from contemporary human populations shows that grandmothers may assist philopatric offspring through a transfer of knowledge and by participating in household tasks and child care, and that such help may indeed increase both offspring breeding probability (Sear et al. 2003), as well as grandchild nutrition and survival (Hawkes et al. 1997, reviewed in Sear & Mace 2008).

While previous studies aiming at testing the Grandmother hypothesis have focused on the one-sided benefits of living grandmothers on their grandchild's survival or offspring life history traits (age at first reproduction, mean inter-birth interval), little has been done to evaluate the importance of the fitness-increasing-effects of long post-reproductive lifespan on the total fitness gained by the helping grandmothers. Crucially, we need studies, first, that incorporate all mechanisms through which the post-menopausal women can increase offspring success and thus their own fitness and, second, that evaluate the grandmother's subsequent fitness benefits acquired from living after ceasing reproduction. This would require measuring how the length of the post-reproductive lifespan is related to the number of grandchildren. Such assessment are however difficult to carry out because data encompassing the complete reproductive histories of several generations of individuals are scarce.

### **1.3.3 The Reproductive Conflict hypothesis**

A recent third hypothesis for the evolution of menopause in humans (referred here as the "Reproductive Conflict hypothesis") suggests that the early reproductive cessation and thus the very minimal reproductive overlap between generations in humans results from reproductive competition between generations (Cant & Johnstone 2008; Cant et al. 2009). The onset of menopause coincides with the age at which a female can become a grandparent and face reproductive competition from the younger generation (Cant & Johnstone 2008). Reproductive competition between females is known to take place in many cooperatively breeding animals where cobreeding with other females involves costs (Clutton-Brock et al. 2001, 2006, Koenig et al. 1995). This leads to the reproductive

separation of generations, but breeding status is usually obtained by older females (French 1997, Wasser & Barash 1983, but see Richardson et al. 2007). The reversed pattern of older women stopping reproduction early could be explained by costly human offspring (Hawkes & Paine 2006) and an ancestral human history of female-biased dispersal patterns (Marlowe 2004, Oota et al. 2001, Seielstad et al. 1998). Indeed, we expect mothers-in-law to lose the competition for reproduction against their typically co-residing daughter-in-law, for she will be 0.25 related to offspring produced by her son and daughter-in-law, while the daughter-in-law will be unrelated to offspring produced by the original mother. Thus assuming competition over reproduction, conflict should be resolved in favour of reproduction by the subordinate rather than the dominant, leading ultimately to the evolution of menopause (Cant & Johnstone 2008).

Whether a reproductive conflict between generations that is based on mathematical modeling (Cant & Johnstone 2008), is a potential force favoring earlier reproductive cessation in women (*sensu* “Reproductive Conflict hypothesis”), needs to be investigated with empirical data from humans. We should first evaluate whether both parties, the grandmother and the offspring, incur costs as a result of reproductive overlap and thus experience lower reproductive success. We should also evaluate whether these effects are sufficiently high enough to favor the evolution of menopause given the other known costs of continued reproduction (eg. Heffner 2004, McNamara 1982, Reddy et al. 2006, Temmerman et al. 2004, Ujah et al. 2005, Wood 1994). Finally, we need to better understand whether costs increase when there is a reproductive overlap between mothers and daughters-in-law, as compared to mothers and daughters. Taken together, these results would significantly increase our knowledge on the ancestral dispersal patterns in humans and the adaptive significance of menopause.

## **1.4 Evolution of longevity in men**

Men, in contrast to women, have a life-long ability to reproduce, but despite this their longevity is very similar to women, differing on average by a few years only (Austad 2006, Kruger & Nesse 2004, Møller et al. 2009). The majority of studies examining the evolution of human longevity have been conducted on women, whilst selection pressures affecting male lifespan have seldom been considered. For example, the Grandmother hypothesis fails to explain why men live up to nearly the same age as women (Kaplan 2000). Long lifespan in men could either have evolved through similar selection pressures as female longevity or through completely different selection pressures. First, male longevity could be a consequence of selection favoring longer post-reproductive lifespan in women, because daughters and sons both inherit genes affecting levels of cellular maintenance and repair from their mothers (Hawkes 2004). Second, similarly to women, lifespan of men might be a consequence of the provisioning of prolonged care

to their own offspring and grand-offspring (“Grandfather hypothesis”). This is a possible mechanism even though there is little general evidence that men over the age of 50 years provide any benefits to their grandchildren (reviewed in Sear & Mace 2008). Third and as suggested by Williams (1957), male lifespan may be maintained by the ability of males to reproduce throughout their lives and hence by the direct fitness benefits acquired from producing offspring at an old age (from now on referred to as “Continued reproduction hypothesis”). Some (Bonduriansky et al. 2008, Charlesworth 1997, 2001, Marlowe 2000a, Kaplan et al. 2000, Tuljapurkar et al 2007) have stressed the importance of males and male mating strategies on the evolution of human longevity and hypothesized that selection on male reproduction late in adult life could be strong enough to account for the prolonged lifespan in both sexes (see also section 1.3). However, reproductive potential may not be equivalent to reproductive fitness, especially since male fertility above age 50 differs considerably between populations with different mating systems: men in polygynous populations have higher fertility at advanced ages compared to men in monogamous populations where male fertility is restricted by their wife’s menopause (Paget & Timaeus 1994). Nevertheless, men in monogamous societies may be able to maintain reproduction by remarrying after the menopause of their first wife.

To identify the selection pressures that have shaped male longevity in humans, we should examine both potential grandfather effects, as well as fitness benefits from continued reproduction with male age. However, such studies remain rare. In particular, to fully investigate whether grandfathers significantly improve offspring reproductive success as well as their own inclusive fitness at an old age, we should study whether longer male lifespan increases the total number of grandchildren and through which process this might take place (e.g. by decreasing offspring’s age at first reproduction and thus reproductive tenure length or by shortening the offspring’s inter-birth intervals). Second, although a male’s ability to breed until death follows general animal patterns (Bribiescas 2006, Pavelka & Fedigan 1991), the realized fitness effects of reproducing at an old age should be investigated. The lack of such studies has significantly hampered our ability to evaluate the evolutionary forces that have led to evolution of prolonged longevity in men.

## 1.5 Aims of the thesis

The aims of this thesis were to resolve the following questions:

- (i) Do reproductive costs increase with increasing maternal age for mothers themselves and for their dependent offspring? Are these costs sufficiently high to explain the evolution of menopause and the decades-long post-reproductive lifespan in women? (Test of the Mother hypothesis I). More precisely, I examined:

- (1) whether and how risk of death in childbirth increased with the mother's age when repeated births across women's lifespan are included in the analysis; (2) when does the death of the mother significantly reduce offspring survival and do all dependent offspring of different ages experience a higher risk of dying after maternal death; and (3) does the loss of the mother have long-term effects on offspring future adulthood survival and fitness?
- (ii) Do women gain fitness benefits by prolonging lifespan post-reproduction and can these effects explain the extended lifespan after menopause (test of the Grandmother hypothesis **II**)? More precisely, I studied: (1) whether prolonged post-reproductive longevity is associated with greater grandchild production and hence greater fitness, (2) whether the presence of post-reproductive grandmother increases offspring lifetime fitness (offspring's number of children produced and raised to 15 and individual  $\lambda$ - a fitness measure incorporating the timing of reproduction and the lifetime reproductive output); and (3) the mechanisms through which a post-reproductive grandmother could increase offspring reproductive success (offspring's age at first reproduction, inter-birth intervals and reproductive tenure length, and the grandchildren's survival).
- (iii) Is there reproductive overlap between generations and does this result in reproductive conflict between generations that is a selective force of sufficient strength to explain the evolution of menopause in women (test of the Reproductive Conflict hypothesis **III**)? More precisely, I examined: (1) the degree of potential reproductive overlap between generations; (2) the costs of reproductive overlap between generations to the reproductive success (survival of offspring) of both parties (the offspring's generation, as well as the grandmother's generation); and (3) the effect of reproductive overlap on the selection favouring menopause at age 50 in women.
- (iv) Do men gain fitness in late in life by grandfathering and could this select for longevity in men (test of the Grandfather hypothesis **IV**)? More precisely, I evaluated the effects of the presence of the father on: (1) the key life-history traits of his sons and daughters (age at first reproduction, inter-birth intervals and reproductive tenure length); (2) correlates of their fitness (lifetime fecundity, offspring survival and lifetime reproductive success); and (3) whether longer living grandfathers obtain more grandchildren and whether men's long lifespan could have evolved through grandfathering effects.
- (v) Can men in a monogamous society gain fitness by breeding throughout life by remarrying? Is the continued reproduction throughout adult life likely to be the main selection pressure for long lifespan in men? (test of the Continued

reproduction hypothesis **V**). More precisely, I investigate whether the men who are able to remarry after spousal death and to reproduce until older age, have higher fitness in older age than men who do not remarry. This would imply that the evolution of men's long lifespan could result from the benefits of late reproduction of males.

By providing answers to these gaps in our previous knowledge, I hope to increase our general understanding of the puzzling life-history in humans and in particular the evolution of menopause in women and prolonged longevity in both sexes.

## **2. MATERIALS AND METHODS**

This thesis is based on analysis of demographic records of two historical human populations, Finland and Canada.

### **2.1 The Finnish data**

The complete Finnish church records, originally collected for tax purposes since the 18<sup>th</sup> century, are the main source of data in this thesis. The Lutheran Church was obliged by law to maintain registers of all births and baptisms, movements, marriages, deaths and burials all over the country since the mid-18<sup>th</sup> century (Luther 1993). These data contain accurate and exceptionally complete demographic information on survival and reproductive details for three full generations from five geographically distinct communities. Three of the study parishes are from south-west archipelago (Hiittinen, Kustavi and Rymättylä) and two from inland (Ikaalinen and Pulkkila) with contrasting living conditions between these two areas. The main source of livelihood in pre-industrial Finland was farming but this was supplemented by fishing leading to greater predictability of food in the archipelago (Lummaa et al. 1998). The data includes the occupations for the fathers (for example tenant farmer, fisherman, landowner, servant), which provides an opportunity to compare the survival and reproductive details between families of different socio-economic levels (rich, average, poor).

Overall for Finland, I used data for 653 women born during 1702-1823 and these women's 635 spouses born during 1704-1822. These couples gave birth to 4,515 children born 1732-1863, of whom 1,652 married and reproduced in the population. These offspring gave birth to 7,846 children born 1757-1906. This relatively comprehensive demographic data set that includes 13,649 individuals has benefits compared to more traditional sources of data used in human behavioral ecology studies, such as anthropology surveys from hunter-gatherer populations. In those cases, the number of people is usually small and the given ages of individuals are estimates and not accurate written information, thus making ages for older individuals' especially unreliable (Hill & Hurtado 1996, Gurven & Kaplan 2007). The study period in Finland ended before the start of industrialism and before more liberal economics, birth-control methods and higher standards of living improved survival markedly (Soininen 1974), thus these data reflect natural survival and fertility conditions among these people.

The Finnish data set is especially useful for studying how individuals affected each other's life across generations as the typical family house contained both the parents and the family of one child, and thus several generations (Moring 1993, 1996). Extra-pair



affairs and missing information on such instances, that might confound the results of this study, are unlikely to be high, because in pre-industrial Finland divorce was rare and extra-marital affairs were a strict taboo for the Lutheran church and punishable (Sundin 1992). Thus, the rate of extra-pair paternity in our study population was probably as low as the 1.7-3.3% suggested for modern populations with high paternity confidence, or at least substantially lower than the median of worldwide extra-pair paternity rate of 9% (Anderson 2006). This Finnish data set is used in all chapters of this thesis (I-V).

## 2.2 The Canadian data

In this thesis I also used two datasets that include demographic information from pre-modern Quebec, Canada. Both of these datasets were obtained using the BALSAC population register based at the University of Quebec, Chicoutimi (BALSAC Project 2009). The register contains demographic and genealogical information collected from baptism, marriage and death certificates from all individuals in the Saguenay region of Quebec during the 19<sup>th</sup> and 20<sup>th</sup> centuries (Bouchard et al. 1995, Bouchard 2008). The opening of the Saguenay region to sustained settlement began in the early 1830's, with founders coming mainly from the adjacent region of Charlevoix (south of the Saguenay) (Gauvreau et al. 1991). The population is mostly French-speaking and Catholic, and until the beginning of the twentieth century, mainly agricultural (Bouchard 1996).

In the first data set from pre-modern Canada (chapter I), we obtained data for 14,923 children born 1891-1929 to 1,642 mothers and 1,627 fathers. The second data set (chapter II) includes 3,290 women born in the Saguenay region between years 1850-1879 and their 29,895 children of which 16,618 married and reproduced in the population and all their 100,074 grandchildren. Benefits of health care were not apparent in the region until after the 1930s and individuals experienced natural fertility and mortality (Gauvreau 1993; Gauvreau et al. 2007). The data also contains information of the occupation (for example farmer, blacksmith, merchant, journeyman) of the father in each family, allowing us to rank child socio-economic status as for the Finns (rich, average, poor). The families were usually nuclear and the inheritance system followed an equalitarian principle, although sons, rather than daughters, tended to inherit the land. There was no preference for a given son in the transmission of family land. The population was monogamous, illegitimate births were very rare (less than 1%), and all children were baptized (Bouchard 1996). These Canadian data provide a useful replicate of the Finnish data set. Also the family type had already changed from a traditional multi-generational household structure to a nuclear family, whereas the former was still the most usual household type in Finland during the study period. These contrasts together with very large data sets from both countries allow me to estimate more efficiently the evolution

of menopause and prolonged lifespan in humans in different environmental and social conditions. The Canadian data sets are used in chapters (I & II).

## 2.3 Studied life-history traits

The most often studied fitness measures as well as key-life-history traits in this thesis are:

- i) *lifetime fecundity* was measured as the lifetime number of children born to the individual.
- ii) *lifetime reproductive success* (LRS) was measured as the number of children that survived to adulthood (i.e., to 15 years).
- iii) *individual lambda* ( $\lambda$ , McGraw & Caswell 1996), which in addition to lifetime reproductive success also considers the timing of reproduction and hence provides an alternative for an individual-level fitness estimate.
- iv) *Number of born grandchildren*, the total number of grandchildren ever born to an individual gives a more accurate estimate of an individual's inclusive fitness than the previous fitness measures.
- v) *Age at first reproduction* (AFR) is the age at which an individual produced her/his first child.
- vi) *Mean inter-birth interval* (IBI) is the average time interval between all the births of an individual.
- vii) *Age at last reproduction* (ALR) is the age at which an individual produced her/his last child.
- viii) *Reproductive lifespan* (also *reproductive tenure length*) is the time (in years) between the births of individual's first and last child.
- ix) *Longevity* is the age at death of an individual who lived beyond age of 50 years.

## 2.4 Data analysis

Here I briefly describe the statistical methods used in the chapters of this thesis. More detailed information is given in the methods section of each chapter (I-V).

### 2.4.1 Analyses of life-history traits and longevity

I used several types of multivariate analyses when investigating life-history traits and longevity in pre-industrial Finland and Canada. One type of analysis was the analysis of variance (GLM procedure, SAS). Some statistical analyses were also performed using generalized linear mixed models (GENMOD procedure, SAS) when data was

non-normally distributed and when repeated terms had to be included into the model. However, the most commonly used type of analysis was maximum likelihood method in general linear mixed models (MIXED procedure, SAS). This statistical approach is very useful for studying life-history evolution in humans, because it allows us to control for many potentially confounding effects in the analysis, including fixed effects (e.g. time period, living area, socio-economic status, presence of relatives), as well as random effects (parent or grandparent identity).

#### **2.4.2 Survival analyses**

In chapters (II, IV, V), I conducted a survival analysis using the Kaplan-Meier-method to estimate survival functions between groups. More accurate survival analysis of Cox proportional hazards model was used in chapters (III, IV) (Allison 1995, Collet 2003). This analysis provides a benefit of censoring and time-dependent covariates. Therefore it is useful in analysing survival among humans using data collected from church records, whose exact death dates are unknown but for whom we know for example their age at last birth and thus their survival until that point. Also the effects of some covariates can change during the studied age interval (lifespan) and the assumptions of proportional hazards can be checked by including time-dependent covariates as explanatory variables in the model (Collett 2003). In chapter (I), I used discrete time survival analysis (also known as event history analysis), which allows a sensitive analysis of the effects of time-dependent variables, such as the presence of relatives, on the probability of dying over time (Singer & Willett, 2003). This analysis allowed me to estimate the child's risks to die for each year from birth to independency in the presence of a living relative compared to the absence of a relative. In addition to enabling the use of censoring in the discrete time survival analysis, this also enables the controlling of repeated measures, ie. children, from the same mother/father.

#### **2.4.3 Problems with correlative data analysis**

When analyzing correlative data of life history traits, for example fitness and longevity, interpretation of causality and direction of the effects can be difficult. The best way to overcome this problem would be experimental manipulation of certain life history traits, for example brood size, to investigate the change in other life history trait, such as longevity, to assure that the correlation between these traits is not the result of better quality individuals having larger broods (van Noordwijk & de Jong 1986). This is not possible in humans and of course when having historical data sets. However, there are ways for one to minimize this problem. First, in this thesis and in each analysis, I have controlled for several confounding effects on each response variable, such as individual's socio-economic status, temporal and geographical differences in living

conditions, all of which are strong correlates of health and likely to have an impact on longevity estimates. In addition, I controlled for many other confounding variables in the analyses, like individual's sex, birth-order or marital status (more in detail in chapters **I-V**). Second, mixed model analysis allows me to investigate the effects of the presence of a relative (for example the mother or grandmother) on offspring survival or life-history traits within the family that experience similar health and living conditions. Third, for some analysis, for example in Figure 1a of chapter (**II**), I did not limit myself to showing the correlation between grandmother's longevity and total number of born grandchildren (controlling for many significant terms), but in addition I also performed a set of analyses on the offspring generation to show how the positive effects on offspring fitness were manifested by the grandmother living in the family. Furthermore, I used a natural experimental setting to show that offspring that lived apart from their currently living mother had reduced success compared with those that lived close to their alive mother (in the same village), despite being from the same family. The result did not change when we controlled for the number of children born before menopause for each woman. We can therefore be assured that the result is due to helpful grandmothers and the positive effect of their longer lifespan on the number of grandchildren, and not only the result of phenotypic correlations of higher quality and longer living women having more children and grandchildren. It is therefore unlikely that between-family differences in health or living conditions could have severely confounded our results.

### 3. RESULTS AND DISCUSSION

#### 3.1 Evolution of menopause and post-reproductive lifespan in women

##### **Mother hypothesis**

In chapter (I), I found little support for The Mother hypothesis, which proposes that female menopause evolved when the costs of reproducing late in life exceeded the benefits. In particular it proposes that maternal survival is required for the duration of their offspring's period of dependence (i.e. up to 15 years). Maternal mortality in childbirth increased with age in pre-industrial Finland and Canada, reaching 1-2% at the age of 50 years, imposing a slight cost of continued reproduction with advancing age. This finding is in line with previous studies from contemporary Nigeria and historical Germany (Knodel 1988, Ujah et al. 2005). Also, I found that loss of mother had a clear negative impact on a child's survival when under three years, a finding that is supported by many previous studies (reviewed in Sear & Mace 2008). However, maternal death had little effect on offspring survival after these first years of life. Therefore, although the maternal death in childbirth would have negative consequences for the current child, I found no evidence to suggest that it has negative consequences for any previous offspring. Thus, the 1-2% risk of dying from childbirth is unlikely to have given rise to women benefitting from stopping reproduction early and for the evolution of menopause. Also, although human children are costly and need high investment until adolescence (Kaplan et al 2000), I found no evidence for the idea that mothers are required until maturity in order to secure the survival of their offspring. Hence it is unlikely that the maternal care alone could explain the markedly extended post-reproductive lifespan in human females.

##### **Grandmother hypothesis**

I found compelling evidence from pre-industrial Finland and Canada (chapter II) that selection may have acted to increase post-reproductive longevity in women. Post-reproductive grandmothers gained two extra grandchildren for every ten years they survived after menopause (age of 50 years, Pavelka & Fedigan 1991) in both countries, despite the vast differences in culture and demography between Finland and Canada. The longer living grandmothers gained more grandchildren by decreasing their offspring's age at first birth, shortening their first three birth intervals and increasing their grandchildren's survival. This resulted in greater fitness for offspring, as the number of children born during their lifetime, the number to adulthood and individual lambda (fitness measure incorporating both the number and timing of children) were all elevated in the presence of a living grandmother. Importantly, these differences were only present

when the living grandmother was residing in the same village as her offspring. This strongly suggests that my findings with the larger dataset are not products of uncontrolled confounding effects. Although, the Grandmother hypothesis has been studied widely and gained support from hunter-gatherer populations as well as from contemporary and historical populations (reviewed in Volland et al. 2005), this was the first evidence that a longer post-reproductive lifespan increases the inclusive fitness of a grandmother (by measuring the number of grandchildren). This work suggests that the post-reproductive lifespan is actually a fitness enhancing trait and not an evolutionary enigma.

### **Reproductive Conflict hypothesis**

In chapter (III) I present the first empirical support for the Reproductive Conflict hypothesis (Cant & Johnstone 2008), indicating that significant costs can exist for both parties if reproduction over-laps between generations (i.e. mother and offspring). In pre-industrial Finland this effect was particularly large if the mother and daughter-in-law reproduced simultaneously, resulting in decreased reproductive success of both of them because of lower survival of the offspring and grand-offspring. The fitness calculations considering the costs of continued reproduction with maternal age have previously failed to show that this would have lead to evolution of menopause (Hill & Hurtado 1991 and 1996, Rogers 1993, but see Shanley et al. 2007). My study implies that severe costs exist when breeding alongside a reproducing offspring, a fact which has not been considered in previous calculations. Quantitative models taking into account all the costs of continued reproduction in old age (chapters I, III) as well as the benefits from investments in kin during post-reproductive period in human females (chapter II) should thus prove helpful in resolving the long-standing evolutionary puzzle of menopause at 50 in human females.

## **3.2 Evolution of longevity in men**

### **Grandfather hypothesis**

In chapter (IV), I found no evidence that longer living men would increase their fitness through enhancing their adult offspring's reproductive output, on the contrary to grandmothers (chapter II). In pre-industrial Finland, the father reduced adult offspring age at first reproduction and birth-intervals, but did not increase reproductive tenure lengths. Also, a father's effect on offspring's fitness was minimal as the presence of a father increased only the first born son's lifetime 'fecundity' and had no influence on offspring lifetime reproductive success. Overall, in contrast to my results for women (wives of the here studied men) in the same strictly monogamous population, men did not gain extra fitness, i.e. increase the number of grandchildren, through grandfathering. This strongly suggests, again, that the findings for women are not a result of confounding

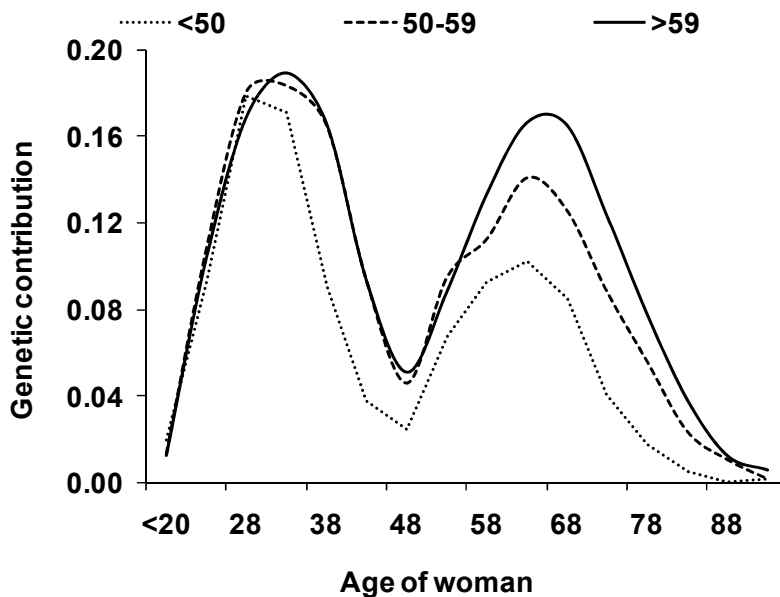
living conditions, for example. Because the paternal investment (and thus also the grandpaternal investment) is expected to be highest in monogamous populations (Marlowe 2000b), our results suggest that the general importance of Grandfather hypothesis in shaping male lifespan during our more promiscuous evolutionary past (Dupanloup et al. 2003) is small.

### **Continued reproduction hypothesis**

I investigated the Continued Reproduction hypothesis (Bonduriansky et al. 2008, Graves 2007, Marlowe 2000a, Tuljapurkar et al 2007, Williams 1957) for the evolution of male longevity in pre-industrial society of Finland (chapter V). I found that men showed behaviours that were consistent with attempting to gain fitness throughout adult life, but accrued little fitness after their first wife reached menopause. Men were three times more likely to remarry after spousal death than women, and they continued to marry still late in life, on the contrary to women. Men were likely to remarry significantly younger women. This resulted in that remarried men were able to produce offspring up to ten years later than those who did not remarry, and thus subsequently had higher lifetime 'fecundity'. However, the offspring from first marriages had lower survival when men remarried, presumably because of a reduction in care received by these offspring. Consequently, the lifetime reproductive success as well as the total number of grandchildren 'born' to men who remarried and reproduced with several wives was not higher than that of other men. Altogether, I found no evidence to suggest that men gained significant fitness after the age of 51 years due to strict monogamy. My results suggest that men would possibly accrue fitness throughout life if they were permitted to remarry following spousal menopause, but without spousal death. By using longevity data from societies world-wide, I found support for the implication that in polygynous societies where men are permitted to reproduce throughout life, men have significantly longer relative life-expectancy than do men in monogamous societies. My results suggest that the old, and often discussed but not previously empirically tested, Continued reproduction hypothesis is the likely explanation for the evolution of male longevity in humans.

## 4. CONCLUSIONS

The menopause and subsequent slow aging resulting in prolonged longevity in women have been puzzling from the viewpoint of traditional evolutionary theory. The framework of combined evolutionary theory and kin selection theory has been profitable in this thesis aimed at resolving the puzzle. I found clear support that at least some part of the post-reproductive lifespan in women has been favored by natural selection during the ancestral history of humans. In addition to chapter (II), this claim is supported by several studies world-wide showing beneficial effects of grandmothers on their offspring's reproductive success (reviewed in Voland et al 2005, also for example Jamison et al. 2002, Leonetti et al 2005, Sear et al. 2002, Voland & Beise 2002). Figure 1 illustrates the evolutionary significance of post-reproductive lifespan in pre-industrial Finnish women. Fitness, measured by the genetic contribution to future generations, that was gained from grandchildren reached the same levels during post-reproductive years as did the gains from producing one's own children during their reproductive period, and the women who lived longest (>59), clearly gained most grandchildren during their post-menopausal years. The recent senescence theories of exceptional human aging pattern have also shown that not only the births but these inter-generational transfers between generations can shape the aging-rate in social species and should be incorporated in the senescence models of humans (Chu et al. 2006, Lee 2003, 2008).



**Figure 1.** The age-specific genetic contribution of women in pre-industrial Finland. The genetic contribution is calculated as the number of children born each age\*0.5 plus born grandchildren\*0.25. The lines describe the average genetic contribution in each age of women who died before age of 50 years (<50), died between 50-59 years (50-59) or died after age of 59 years (>59) ( $n=637$ ).



There are reasons to suspect that the menopause has been adaptive during our evolutionary past. Central in estimating this are the costs of continued reproduction with advanced maternal age and the benefits of stopping reproduction early. In chapter (I), I found that the costs for maternal mortality from childbirth increased slightly with age, but to ensure the survival of dependent children the maternal presence was needed only during the first two years of life. Thus, there are costs from reproducing in old age but these costs are not transferred to all offspring as has been previously assumed. The findings in chapter (III) highlight another important key in the puzzle, as conflict between generations resulting from over-lapping reproduction is one potential evolutionary force for increasing the collective costs of continued reproduction with age. However, this hypothesis should be further tested in other societies with different types of dispersal pattern to see how general these findings are. Further, the benefits of maternal and grandmaternal investments after menopause can also outweigh the benefits from continued reproduction (see also Figure 1a). The adaptive significance of menopause is also supported by the findings that, first, the age of menopause is at least partly genetically determined (Kirk et al. 2001, Pettay et al. 2005) and second, the mechanism of menopause involves rapid attrition of ovarian follicle stock around age of 45 years, although the stock of oocytes could last until age of 70 years without this peculiar speeding-up process (Faddy et al. 1992) and clearly contrasts the mechanisms of reproductive senescence in close relatives (Atsalis et al. 2008).

The long lifespan in men is unlikely to have been affected by fitness increasing grandparental effects in old age (chapter IV), on the contrary to grandmothers (II). Furthermore, it is likely that the male longevity is an evolved property of life-long reproduction (V). Also it is possible that the male lifespan is at least partly affected by the selection on greater longevity of women, because offspring of both sexes inherit longevity genes from the longer living grandmother. I thus suggest that the senescence models should incorporate both sexes (Tuljapurkar 2007) instead of only one, to produce a model corresponding to real human aging patterns. Moreover, I suggest that further studies on both sexes should be conducted by using evolutionary and kin-selection framework on societies world-wide with differing social and cultural environments to clarify the selection pressures behind the menopause and prolonged longevity in both sexes of humans. Also for comparison and generality of these findings, it would be important to investigate similar patterns as discovered in this thesis also in other species that have evolved a clear menopause and prolonged post-reproductive survival (short-finned pilot whale and killer whale), as well as fitness maximization patterns across lifetime and reproductive and survival senescence in similarly long-lived mammals without a clear menopause (e.g. elephants, *Loxodonta africana* spp and *Elephas maximus* spp, chimpanzees).

These results have several wider implications across disciplines. These results highlight the importance of cooperative breeding (Blaffer Hrdy 1999, 2009) during human

evolution and the high impact of other group members on others in differing ecological and social conditions. Nowadays, the traditional multi-generational family pattern has dramatically changed over the past decades to nuclear family types in many developed countries and this can have also effects on offspring reproductive decision making as well as on family sizes. Also, 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 in both sexes is still limited. Moreover, if the increasing knowledge of the human genome leads to manipulations of genes and gene products in purpose to increase our lifespan, the better understanding of the natural evolutionary forces behind our exceptional life-history and longevity is essential.

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