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Testing Behavioral Ecology Models with Historical Individual-Based Human Demographic Data from Norway

Thesis for the degree of Philosophiae Doctor

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Photo 1: Where it all started. The Plains of Serengeti.

Photo Credit: Gine Roll Skjærvø

Cover photo Paper I: My father's ancestors at a funeral at Brattgjer, Sør-Trøndelag in 1903.

Photo Credit: Unknown

Cover photo Paper II: View of Reine in Lofoten. The village my mother's father grew up.

Photo Credit: Stein Roll (2013)

Cover photo Paper III: My father as a child with his family

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Cover photo Paper IV: Four generations. The first generation is my maternal grandparents.

Photo Credit: Unknown

Cover photo Paper V: Grandmother and grandfather with three grandchildren.

Photo Credit: Fotograf Schrøder, Trondheim (1986).

Cover photo Paper VI: What will the future bring?

Photo Credit: Stein Roll (2009)

To my family, then and now

Where it all started. The Plains of Serengeti.
Photo Credit: Gine Roll Skjærvø

Contents

Acknowledgments

During my years in ecotoxicology research, we asked proximate questions – how things work. Ten years ago, Prof. Eivin Røskaft introduced me to the ultimate questions. They address the evolutionary significance of a behavior – Why are things the way they are. I was thrilled by the new perspective. Two equally important pieces in the puzzle of life. I want to thank Eivin for his clear mind, enthusiasm, kindness and humor that have stimulated my focus into interesting and important issues regarding behavioral ecology and human behavior. Eivin is a big picture person. Therefore, I'm grateful, and to some extent impressed by his patient during my 'deep into details'- periods. He always managed to help me see The Forest. Eivin has influenced me at all stages during the work with the thesis and it would never have been completed without him. Thank you.

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Trondheim, October 2014

Gine Roll Skjærvø

Summary

Behavior varies widely among animals, both within and between species. An evolutionary perspective may help us understand the origin of this diversity. Behavioral ecology models seek to explain much of variation in behavior as adaptations formed by natural selection. In addition to provide answers why behavior varies under different ecological conditions, behavioral ecology also provides insight into the underlying proximate mechanisms. Although theory has made enormous progress in explaining the diversity of animal behavior, it has often been difficult to empirically test theory on long-living wild mammals. This is because generations times are typically long so that adequate transgenerational data is difficult to obtain. Humans, however, have recorded our own history for hundreds of years and represent a unique model species for testing behavioral ecology theories. In this thesis I use individual-based demographic data from two populations (inland and coastal) in historical Norway (1700-1900) to test predictions from such theories. I focus on life history traits like brood size (twins or singletons) and menopause, and explore how environmental factors (wealth, ecology, maternal parity, and solar activity) can explain variation in human behavior. First, I tested if parent-offspring conflict (POC) could explain why twins are so rare in humans (Paper I). One prediction from POC theory is that twins increase inclusive fitness by the death of a co-twin ('offspring win'), while twin mothers benefit from the survival of both twins ('parent win'). However, the results indicated that 'parent win' but not 'offspring win'. Thus, POC could not be a selective force shaping brood size in humans. Next, I studied the interactional effects of status and ecology on women's fitness (Paper II). The positive effect of wealth on fitness was stronger in the inland agricultural than in the coastal fishing society, indicating that the fitness consequence of wealth may depend on local

ecology. The variation in diet may be the proximate explanation for the differences. Prenatal levels of testosterone decreases with maternal parity. I predicted that maternal parity may be important for offspring's subsequent life histories (Paper III). I found that within mated pairs, the difference between the parity of their mothers was a strong predictor of each couple's fitness. Sons born to mothers of low parity married to daughters from mothers with high parity had a much higher number of grandchildren than e.g. sons of mothers with high parity married to daughters of mothers with low parity. The results suggest that the environmental conditions before birth can have fitness effects that span generations. Why do women stop reproduce long before they die (Paper IV)? I tested the 'Reproductive Conflict Hypothesis' (RCH) that predicts that both younger and older generations should experience fitness costs with co-breeding. Contrary to predictions, younger and older women who co-breed had more grandchildren than those who did not co-breed. I conclude that menopause might be understood in the light of both ageing and increased lifespan. Theory predicts that sexual selection is thought to act more strongly on males than on females. This is poorly studied in humans. I found that wealth/status was an important factor for the probability of obtaining a new partner, ultimately influencing the strength of sexual selection (quantified with the Bateman gradient) on both men and women in these populations (Paper V). Finally, I tested the hypothesis if high solar activity during early development affects human life history (survival, fertility and lifetime reproductive success (LRS)). The results show that a high solar activity (large number of sunspots) at birth decreased the individual's survival to adulthood (in both sexes) and fertility (in low status women). On average, the lifespan of individuals born in a solar maximum period were 5.2 years shorter, than those born in a solar minimum period. To sum up, in this thesis I have focused on fundamental paradigms within behavioral ecology and demonstrated how their theoretical predictions can be tested using two human populations. As this procedure was successful, it may inspire future research in other human populations to be carried out with a similar procedure.

List of papers

This thesis is based on the following papers:

I. **Skjærvø GR**, Stokke BG, Røskaft E. (2009.) The rarity of twins: a result of an evolutionary battle between mothers and daughters - or do they agree? Behavioral Ecology and Sociobiology 63:1133–1140.

II. **Skjærvø GR**, Bongard T, Wiken Å, Stokke BG, Røskaft E. (2011). Wealth, status, and fitness: a historical study of Norwegians in variable environments. Evolution and Human Behavior 32: 305–314.

III. **Skjærvø GR**, Røskaft E. (2013). Early conditions and fitness: effect of maternal parity on human life history traits. Behavioral Ecology 24: 334–341.

IV. **Skjærvø GR**, Røskaft E. (2013). Menopause: no support for an evolutionary explanation among historical Norwegians. Experimental Gerontology 48: 408-413.

V. **Skjærvø GR**, Røskaft E. (2015). Wealth and the opportunity for sexual selection in men and women. Behavioral Ecology, doi:10.1093/beheco/aru213.

VI. **Skjærvø GR**, Fossøy F, Røskaft E. (2015). Solar activity during fetal life and reproductive success in men and women. Proceedings of Royal Society B, doi: 10.1098/rspb.2014.2032.

Declaration of contribution

I contributed to the initiation, design and data collection and data analyses for papers I-VI. Eivin Røskaft contributed to the initiation, design and data collection for papers I-VI. Frode Fossøy contributed to the initiation, design and performed the statistical analyses in Paper VI. Finally, I was also responsible for the writing of Papers I-VI, supported by comments and contributions from all the respective co-authors.

Chapter 1. Introduction

Expression of behavioral traits varies widely among animals, both within and between populations. What is the origin of this diversity, and why is it maintained? Behavioral ecology (henceforth BE) provides a framework for understanding much of these variations as adaptations formed by natural selection. It includes topics as how animals find and defend resources, choose mates and reproduce, and care for their offspring. BE tries to understand the causes, functions, development and evolution of such behavior (Davies et al., 2012). The causes of behavior include both the ecological conditions that affect behavior, and the internal hormonal and neural mechanisms that control behavior (proximate explanations) (Flatt and Heyland, 2011). The functions of behavior include its immediate effects on animals and its adaptive value (ultimate explanations) in helping animals to survive or reproduce successfully in a certain environment. The development of behavior relates to how behavior changes over the lifetime of an individual, and how these changes are affected by both experience and genes. The evolution of behavior can be measured in terms of how behavior patterns change over generations (Davies et al., 2012).

Most of the theories within BE have typically been tested on wild animals. However, as we shall see, BE models can also be tested on humans and further help us understand the extraordinary diversity of human behavior. To fully understand behavior, we must obtain both ultimate and proximate explanations (Brown, 2013). The ultimate questions ask how fitness consequences of some behavior strategies will vary according to the ecological condition. Hence, we expect that organism behave optimally by the means of maximizing their fitness in the ecological conditions that they live in (the adaptationist stance) (Grafen, 2006). Phenotypic plasticity is another central aspect within BE and is defined as the tendency for organism with the same genotype to produce different phenotypes (behavioral strategies) under different environmental conditions. Thus, behavioral strategies are not necessarily dependent on genotype, but the ability and extent of phenotypic plasticity has a genetic basis. The function of plasticity is to maximize fitness. Learning can be a mechanism coupled with plasticity. Learning can be selected for, because it can influence an individual’s decisions to behave locally adaptive in variable or changing environments (Pigliucci, 2005; Scheiner, 1993). These assumptions enable behavioral ecologist to make testable a priori predictions on which behaviors should succeed best in specific environments (Clarke and Low, 1992; Nettle et al., 2013).

When testing predictions from BE it is common to measure the fitness consequences of the behavioral strategies that individuals adopt. However, no general measure of fitness exist (Stearns, 1992). This generally means that every study will have to define the appropriate measure of fitness according to the question asked (Kozlowski, 1993; Wolf and Wade, 2001). Early theories within BE had often less complex predictions than more recent ones. For instance, many studies established that female reproductive success depends on access to resources while that of males rests on access to partners, and that sexual selection (competition for mates) is thought to act more strongly on males than on females (Bateman, 1948; Trivers, 1972). However, with time, it has been apparent that the picture is more complex, because the reproductive strategies of males and females are fined-tuned to circumstances, due to phenotypic plasticity. A detailed understanding of the socio-ecological factors such as type of mating systems (monogamy, polygamy) and access to resources that may influence sexual selection is of particular importance (Ahnesjo et al., 2001). In addition to mating strategies, BE study life histories. An individual’s life history is its lifetime pattern of growth, reproduction and mortality. For instance, when should an organism start reproducing, when should it stop growing, how many offspring should be produced, and what size and sex should one produce? Life history is about the scheduling of major events (life history strategies). Because resources are limited, individuals face trade-offs; energy spent on, for example, reproduction cannot be invested in growth. Furthermore, biological processes take time. An individual must face the risk of dying before reaching maturity. Thus, the trade- offs involving time and energy mean that every individual's life history is an evolutionary compromise. The basic assumption in life history theory is that natural selection has selected for an optimal combination of the life history traits that maximize fitness. Thus, different life histories, like other adaptive behavior, evolve to maximize the contribution of genes to the following generations (Roff, 2002; Stearns, 1992).

Understanding the environmental causes and evolutionary consequences of variation in mating and life history strategies is needed to improve the models that explain and predicts the variation in such behavior. Empirical tests of theories in BE (particularly life history theory) in large mammals (>10 kg) are rare, because they require long-term individual-based data, such as age of first and last reproduction, number and sex of offspring and age at death. This is difficult to carry out because long-lived large mammals occur at low densities and are difficult to track over sufficiently long time period. Humans, on the other hand, have several features that make them suitable as a model species to test BE theories (Clarke and Low, 2001; Nettle et al., 2013). First, they can be tested on a wide range of human behavior decisions across and within a range of societies. Second, human life history is assumed to be exceptional in many distinct ways from other primates and mammals: long gestation; children are dependent for many years; late menarche; long reproductive and post-reproductive periods. This long duration of different life stages, make it possible to explore if the environment during different life stages have any potential fitness effects (Low, 2000). Third, among mammals the human species is the most studied one regarding internal (hormonal) and external (culture) mechanisms (Flatt and

Heyland, 2011). Traditionally, this has not been of great interest within BE. Although, recent debate emphasizes that an integration of these mechanisms will make our understanding of behavior more complete (e.g. Brown, 2013). Finally, it is possible to collect human data over several generations in entire populations, and therefore, in contrast to most wild animals, we can measure complete life-histories and long-term fitness for each individual. In general, such data is hard to acquire because it is time consuming to collect and analyze information from historical records that are reliable, because high quality sources are rare.

The goal of this thesis was to advance one step further from traditional BE studies in order to understand the variation in behavioral strategies and examine, with a unique historical individual-based dataset (see methods for details), how natural selection and ecological conditions (social, ecology and access to resources and conditions during prenatal life) interact to shape men's and women's lives. As mentioned above, theoretical frameworks help us interpreting the interactions between the individuals and their environment and how they maximize fitness. In Chapter 2, I give a short introduction to the BE models, with the assumptions and predictions that are most relevant to this thesis.

Chapter 2. Questions asked and theories tested

Can Parent-Offspring Conflict explain the rarity of twins? (Paper I)

Brood size (the number of offspring produced per reproductive cycle) is an important life history variable (Stearns, 1992) which is expected to be optimized by natural selection. Theory (Parent–Offspring Conflict) further predicts that the parent should in general be interested in having a larger brood size than each individual offspring (Trivers, 1972). This can result in a potential conflict of interest between parents and offspring over parental investment. Parent–Offspring Conflict (POC) is a theoretical genetic conflict of interest over how parent should invest in different offspring (Trivers, 1972). Because parents are 50 % related to their offspring, they are expected to equalize their investment among them. Offspring, on the other side, are 50 % related to their siblings and 100 % related to themselves so they try to get more care than the parents will give them since they always will have benefits of receiving extra parental care. Thus, the two parties have different optimal levels of parental investment which is the basis of the conflict. There is evidence that POC can lead to a brood size different from what is optimal from the parents' perspective (Mock and Parker, 1997). More specifically, in the most extreme situations, the reduction of brood size by siblicide is found in several seabirds, but less well studied in mammals (Mock and Parker, 1997). In humans, the most common brood size is one, and twins are rare. Could POC be a potential selective force maintaining the low twinning rate in humans? We hypothesize that the rarity of twins, and thus singletons as the most common brood size, results from an evolutionary conflict over parental investment between twins and their mothers (Figure 1) (POCH). In particular, it is the child's wish that the mother gives birth to singletons (or one twin dies), while the mother will increase her fitness by giving birth to twins who survive to adulthood. This has not been empirically tested in humans. In part, this thesis investigate whether both parties, the mother and the twins, increase own inclusive fitness at the expense of the other party in the different outcomes of the conflict (e.g., one twin survival vs. two twins survival) (Figure 1). These results will increase our knowledge about the selective forces shaping the optimal brood size in a long-lived mammal.

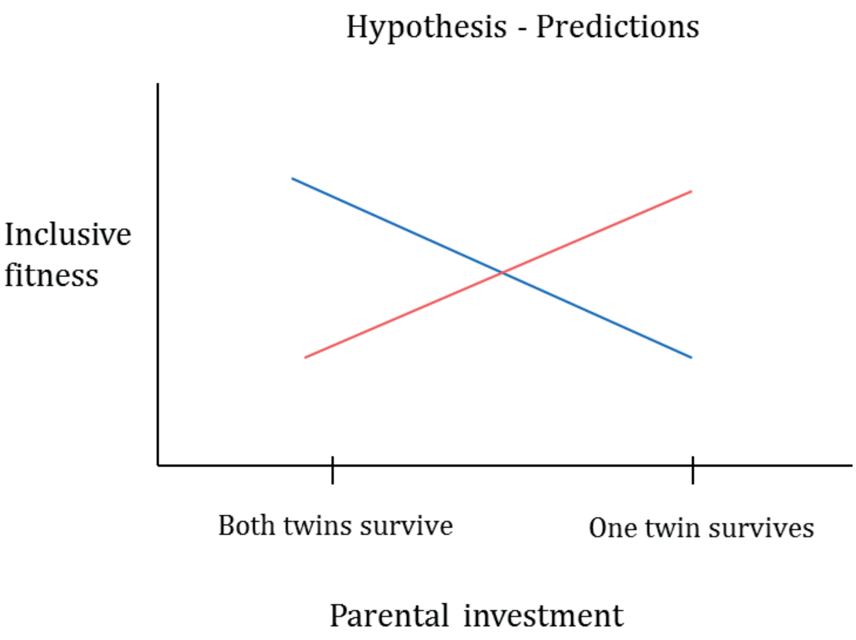

Figure 1. Parent–Offspring Conflict Hypothesis (POCH): a mother's optimum is that both twins survive, because she will increase her inclusive fitness by giving birth to twins. A twin's optimum is that one twin survives, because offspring will always have benefits of receiving extra care, therefore it is their wish that the mother gives birth to singletons.

Can the fitness consequence of status depend on local ecology? (Paper II)

The ecological conditions are rarely constant. The plasticity of behavior and life-histories are thus important for long-living animals that can experience a variety of different environments during their lifetime. Status or dominance is an important condition that can explain variations in life histories and fitness, because individuals with varying status have different access to resources (including quality and amount of food) that in turn is essential for survival and reproduction (Roff, 2002; Stearns, 1992). Such associations are reported in a range of animal species (Boutin, 1990; Ellis, 1995; Gende and Quinn, 2004; Murray et al., 2006; Vogel, 2005) including humans (Clarke and Low, 1992; Gillespie et al., 2008; Hopcroft, 2006; Low and Clarke, 1992; Lummaa, 2001; Pettay et al., 2007). No studies on humans have investigated how local ecology can modify the fitness consequences of status, using the number of grandchildren as a measure of fitness, or investigated potential proximate mechanisms (variation in diet) mediating such effects. Both these aspects are addressed in this part of the thesis.

Early conditions and fitness I - Can maternal parity have an impact on offspring fitness (Paper III)

The environment often set limits for fitness and evolution of life history traits and we know that the environment experienced before birth is of great importance (Lindstrom, 1999). This is evidenced by several long-term studies in a variety of species (Metcalfe and Monaghan, 2001), including humans (Barouki et al., 2012; Bateson et al., 2004; Lummaa and Clutton-Brock, 2002). One aspect of the early environment that can impose variation in life history trait, but less considered (but see, Lummaa et al., 2007; Monclus et al., 2014) , is the level of testosterone to which the developing young are exposed. Maternal parity (the number of previous births) can be a proxy for the level of testosterone a fetus is exposed to, because the prenatal level of testosterone is shown to decline with increasing parity (Carlsen et al., 2003; Rohrmann et al., 2009; Toriola et al., 2011; Zumoff et al., 1995). Thus, maternal effects during early development may be significant drivers of the offspring subsequent reproductive success and parental fitness.

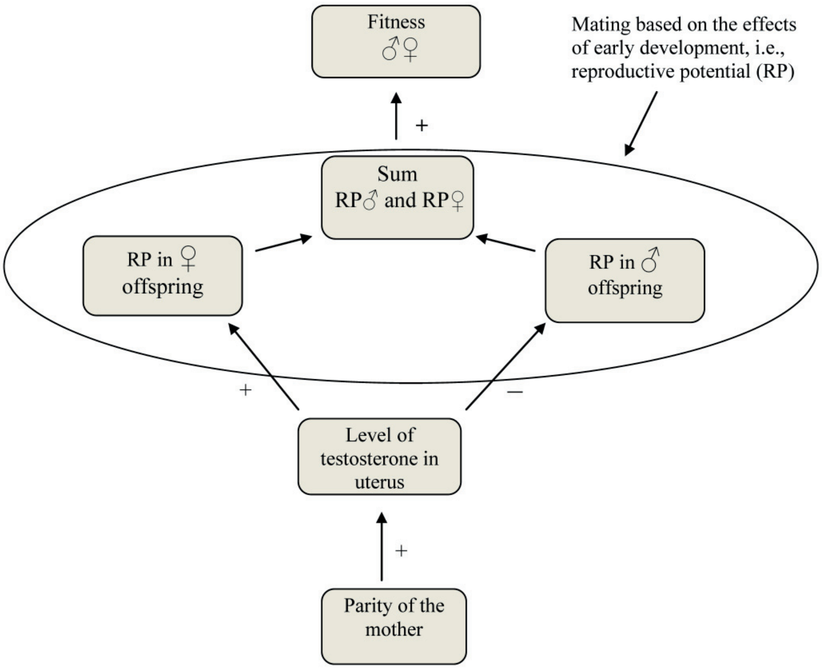

Figure 2. A schematic representation of the consequences of maternal parity effects on offspring's subsequent fitness by means of the effects of early development on RP (reproductive potential). Environmental conditions, such as testosterone level *in uterus,* may affect the RP of male and female offspring in opposite directions. The sum of each RP to both the individuals in a couple (tot-RP) may influence the fitness of that couple.

Here, we hypothesize that maternal parity can have a positive effect on fitness via daughters and a negative effect on fitness via sons, driven by fetal testosterone exposure. High exposure to testosterone during fetal development will result in the masculinization of offspring, a trait likely to be beneficial, in terms of reproductive potential, for first borne sons but detrimental to first borne daughters (Figure 2). This part of the thesis examines for the first time how maternal parity influences children’s subsequent life-histories and pair-specific fitness (number of grandchildren).

Can a conflict between reproducing generations explain the evolution of menopause? (Paper IV)

Traditional theory predicts that evolution should synchronize ageing in the reproductive and somatic systems, and individuals are therefore expected to have a short life after reproductive cessation (menopause) (Hamilton, 1966; Williams, 1957). However, some female mammals (Hodgen et al., 1977; Pavelka and Fedigan, 1991) stop reproduction before they die, and humans (Low, 2000) have, relative to lifespan, an extremely long post-reproductive life. Why do women stop reproducing so many years before they die? This question has attracted much attention from researchers in a number of fields who have suggested a variety of hypotheses. For example, recent life history theory proposes that menopause in humans is ether adaptive (Lahdenpera et al., 2011) or non-adaptive (Peccei, 2001). One of the adaptive hypotheses is the ”Reproductive Competition Hypothesis” (RCH) (Cant and Johnstone, 2008). RCH proposes that menopause has evolved because of conflict between reproducing generations (older and younger generations co-breeding) in environments where resources are scarce. Cant and Johnstone (2008) argues that there is a minimum reproductive overlap between generations in humans, because women cease reproduction (menopause) at the same time as the younger generation starts to reproduce. Thus, reproductive cessation reduces costly competition. Costly co-breeding among females in other cooperatively breeding animals is known (Clutton-Brock et al., 2006). The main prediction from the RCH is that reproductive overlap between generations may impose fitness costs to both older and younger females. While previous empirical studies aiming at testing the RCH have measured the fitness costs in terms of infant mortality and fertility (Lahdenpera et al., 2012; Mace and Alvergne, 2012), little has been done to evaluate the effect of reproductive competition on a long-term measure of fitness. This section of the thesis will therefore test the main prediction from the RCH by using a more long-term measure of fitness (number of grandchildren).

Can sexual selection operate on both sexes in a monogamous population, and under what circumstances? (Paper V)

Theory and empirical evidence suggest that female reproductive success depends on access to resources while that of males rests on access to partners, and that sexual selection (competition for mates) therefore act more strongly on males than on females (Bateman, 1948; Trivers, 1972). However, with time, it has been apparent that the picture is more complex, because the reproductive strategies in males and females are fined-tuned to circumstances, due to phenotypic plasticity. A detailed understanding of the socio-ecological factors such as the degree of access to resources and type of mating systems (monogamy, polygamy) that may influence sexual selection is of particular importance (Ahnesjo et al., 2001). As a species, humans have mating patterns that vary (restrict monogamy, serial monogamy, polygamy and polyandry) depending on the social and ecological conditions (Marlowe, 2000). Humans therefore offer an exceptional opportunity to test hypotheses from sexual selection theory. Predictions from such hypotheses have been tested in several human populations but have received mixed support (Brown et al., 2009; Courtiol et al., 2012; Jokela et al., 2010; Moorad et al., 2011; Pettay et al., 2014). Furthermore, most of them have focused solely on men in polygynous mating systems. Thus, little research on sexual selection has been done simultaneously in men and women, and the same goes for how wealth influences sexual selection. Therefore, this part of the thesis will explore how wealth affects the degree of sexual selection in both men and women in monogamous populations, on two distinct episodes of human sexual selection (marry once and remarry). Our data consist of four categories of individuals that vary in the degree of wealth (based on differences in landownership and subsistence (agricultural or fishing) and importantly, men and women inherit wealth from their dead spouses and therefore have control over these resources when widowed, and remarriage was common after widowhood (Dupaquier, 1981).

We predicted that sexual selection might be able to act on the ability to remarry in women as well as men when they were landowners. Hence, the opportunity for sexual selection can act in a monogamous mating system. There are many ways to measure sexual selection. Here we use the Bateman gradient (β_{ss}), calculated by regressing the number of children born on number of marriages (Arnold, 1994; Moorad and Wade, 2013) which is the standard comparative metrics method in sexual selection.

Early conditions and fitness II - Effect of solar activity at birth on infant survival and women's fertility (Paper VI)

High solar activity during prenatal life can be an environmental factor that may have detrimental effects on survival, fertility and lifetime reproductive success later in life (Bancroft et al., 2007; Llabres et al., 2013). This is because ultraviolet radiation (UVR) can suppress molecular processes essential for the development of healthy and fecund individuals during gestation (Dahms and Lee, 2010; Diffey, 1991; Halliday, 2005; Jablonski and Chaplin, 2000). However, we currently do not know much about how early exposure to high UVR affects life history traits and fitness in mammals, because such research is almost explicitly done on aquatic species. The activity of the sun cycles in its energy output, is measured as sunspots. This means that individuals born in peak years are exposed to high levels of UVR during development (Figure 3). In addition, there are several ecological conditions that can modify the detrimental effect of high UVR, such as gender and status. Concerning gender, within BE it is general consensus that boys are more vulnerable during development than girls (Clutton-Brock et al., 1985). Regarding status, in historical Norway, women of low status were most likely to be exposed to more UVR than high status women, because they worked out in the fields. Moreover, the quality of diet is generally better among high-status than low-status women. High-quality food, in contrast to low-quality-food, is rich in antioxidants that can reduce the negative effects of the UVR. In line with these assumptions, we expect that children of poor women born in years with high solar activity have decreased infant survival and fertility, and that boys should be more affected than girls. Previous research on humans concerning these effects are sparse and none have used individual-based data and therefore have been unable to control for the time spent out in the sun (poor vs. rich women). Therefore this section of the thesis will use sunspot- and individual-based life history data to examine the effect of UVR during gestation on infant mortality and reproduction later in life. In addition, by accounting for status and sex in the models enable us to understand how solar activity during early life affects life-histories to individuals differently according to such circumstances.

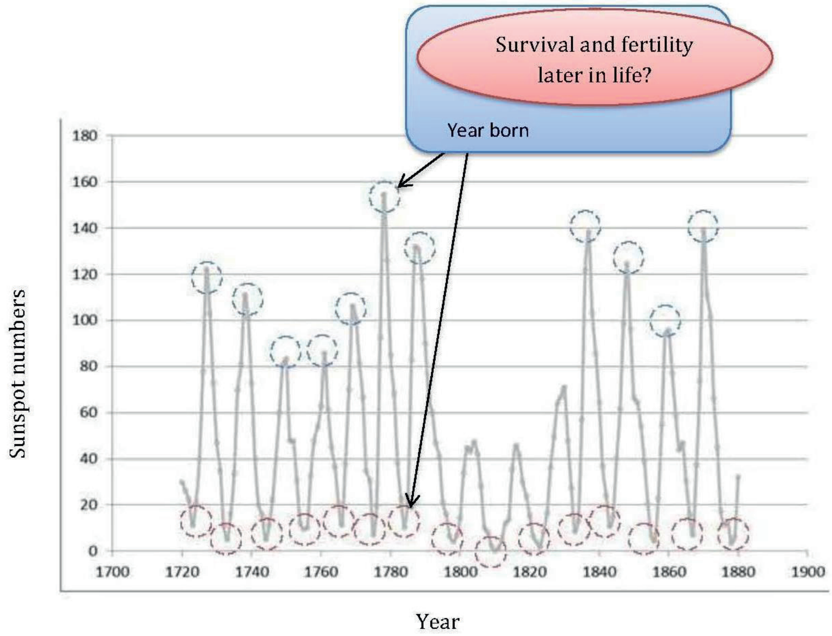

Figure 3. Average sunspot numbers per year from 1720 to 1880. Environmental conditions, such as exposure to UV radiation (measured as sunspot numbers) during development *in uterus,* may affect the survival, fertility and LRS of male and female offspring. Individuals born in years with high solar activity ◌ may a lower fitness than those born in years with low solar activity ◌ .

Chapter 3. Aims

The overall aim of my thesis was to improve our understanding of BE models and the diversity of behavior regarding mating and life history, using humans as an example. This was addressed by using historical individual-based human demographic data from Norway. The findings are expected to make an important contribution to our understanding of the selective forces and internal mechanisms causing the variation in animal life histories.

More specifically, the thesis addresses the following questions:

Can parent-offspring conflict explain the rarity of twins? (Paper I)

Can the fitness consequence of status depend on local ecology and may the dietary patterns be a proximate explanation? (Paper II)

Can maternal parity have an effect on offspring's subsequent (individual and pair-specific) life histories and fitness? (Paper III)

Can a conflict between reproductive generations explain the evolution of menopause? (Paper IV)

How influences wealth sexual selection in men and women in a monogamous society? (Paper V)

Does high UV radiation during gestation affect infant survival and reproductive performance later in life, and does status and gender modify this relationship (Paper VI)?

Chapter 4. Materials and methods

Here I first describe the study system and data collection used in the papers. Then I give a brief description of the life history traits studied. Detailed descriptions of the different study designs and statistical methods used to test the predictions are found in the individual papers and in the references cited therein.

Demographic data

This thesis is based on demographic data, collected from local history books, from two populations in central Norway. Soknedal (inland) and Smøla (coast) are located 100 km apart at the same latitude (63° N) and have similar climates. Data are of high quality and consist of complete demographic information on survival and reproductive details for three generations. Both populations were comprised of two distinct socioeconomic groups with each individual belonging to either a low (poor) or high (wealthy) status group based on landownership. The populations had different access to resources. The coastal fishing society had stable access to resources through fishing, which benefited both poor and rich, while the resource assess in the agricultural inland population was more unpredictable. Importantly, the consequences of differences in such ecological factors and means of subsistence may emerge on the stratification of the society. More specifically, we assumed that the costal population was less stratified than the inland population. Preindustrial Norway was highly monogamous, and both men and women married late. Overall, I used data for 9171 individuals born between 1670 and 1900, to 1870 fathers and 1924 mothers. Of all the children, 2006 (22 %) died before the age of 20 years, 5159 married (72 %) and 1422 emigrated (20 %) (These numbers varies across populations and status groups; see individual papers for details). The time period of the data originated from individuals born before the population experienced the demographic transition. This is important in an evolutionary study, because the connection between both fertility and mortality, and wealth seem to be violated after the demographic transition (Low and Clarke, 1992).

Life history variables studied

Fitness is the currency for natural selection. Yet measuring fitness is not straight forward. In this thesis I have measured fitness differently according to the available data and question raised in each paper. This is indicated by 'Fitness in Paper I-VI' in the list below.

The most often used fitness and life history traits recorded are:

1) **Age of first reproduction (AFR):** the age (in years) when a man/woman produced the first child
2) **Fertility or number of children born (NCB):** the total number of children produced in a lifetime. Fitness in Paper V and VI.
3) **Mean birth interval:** the average time in months between giving births for an individual
4) **Age of last reproduction (ALR):** the age (in years) when a man/woman produced the last child
5) **Reproductive period (RP):** the number of years between an individual's first and last child
6) **Survival of children:** the survival proportion of children born that survived to an age of 20 years (NAC/NCB).
7) **Number of adult children (NAC) or lifetime reproductive success (LRS):** NCB that survived to an age of 20 years. Fitness in Paper I and VI.

8) **Number of married children(NMC):** NBC that married

9) **Number of grandchildren (NGC):** the total number of grandchildren produced in a lifetime. Fitness in Paper II, II and IV.

10) **Age of death:** the age in years at death of individuals that married

Chapter 5. Main results and discussion

The focus of the research included in my thesis was to test models within behavior ecology with human demographic data from historical Norway, and to understand the variation in reproductive behavior and life histories in animals, in addition to give insight into the selective pressures affecting evolutionary processes. In the following section, I discuss the general findings of each research question asked. Figure 4 provides an overview of the research questions asked in the different papers (blue), the design to test hypotheses (red), the fitness measure (green) used and main results (arrows) in this thesis.

The rarity of twins: a result of an evolutionary battle between mothers and daughters - or do they agree? (Paper I)

We found no evidence supporting the POCH, which suggests that a parent – offspring conflict could be responsible for the rarity of twins in humans (Fig. 4). We tested the predictions that 1) twins had higher inclusive fitness than their mothers in families where one of the co-twins died (offspring win) and 2) mothers had higher inclusive fitness than twins in situations when both twins survived (parent win) (Fig. 1). In families where both twins survived, twin mothers had significantly higher inclusive fitness (5.5) than twins (3.8) (‘parent win’). However, in families where one twin died, twins had not significantly higher inclusive fitness (6.3) than their mothers (5.5). With no support for ‘offspring win’, we cannot conclude that there is an evolutionary conflict between twins and their mothers.

Twins who grew up with a co-twin had lower fertility (2.5) than twins growing up as singletons (6.3). Further, because twins growing up as singletons had more children (6.3) than the sum of the two twins growing up together (5.0), mothers might gain more grandchildren when one of the twins died. Our finding, thus, suggests that both mothers and twins might actually benefit by the death of a co-twin. Alternatively, the rarity of twins might be explained by the Insurance Egg Hypothesis (IEH) rather than the POCH. The IEH states that a tendency to produce more than one egg at each menstrual cycle (strategy of twinning) is insurance for the high abortion rates in humans. Conceiving twins is therefore a maladaptive by-product of selection for polyovulation (Anderson, 1990; Forbes, 2005).

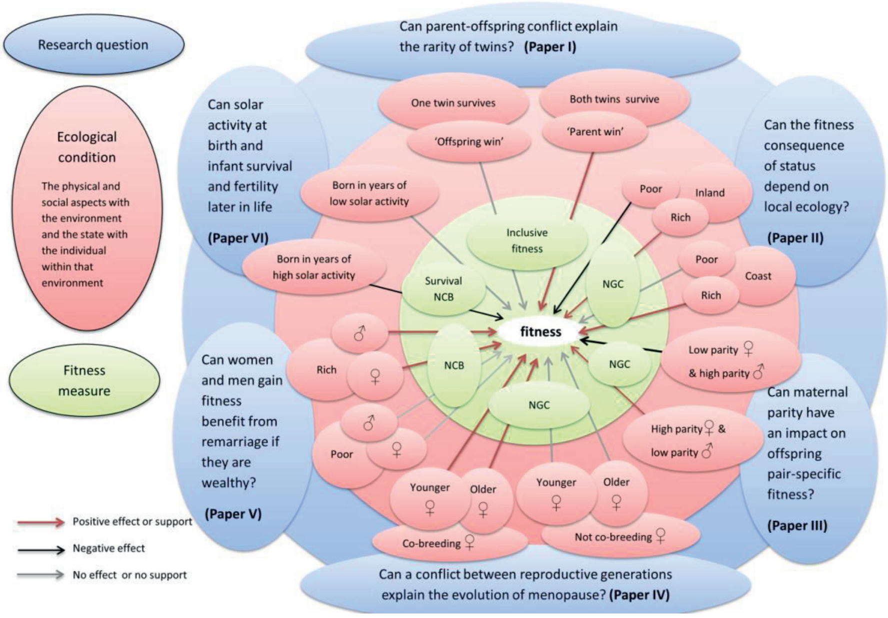

Figure 4. Research questions asked in the different papers (blue), the environmental condition and/or subgroup in the 'natural experiment' designed to test hypotheses (red), fitness measure (green) and main results (arrows: red is significant positive effect on fitness; blue is significant negative effect on fitness; and grey is no effect on fitness) in this thesis

Our results are in accordance with predictions and former empirical findings supporting (Gabler and Voland, 1994; Haukioja et al., 1989; Helle et al., 2004a; Lummaa et al., 1998; Sear et al., 2001) the IEH: twins decrease the mothers' fitness; mothers of twins have longer reproductive lives than mothers of singletons; and that twins are costly in terms of high mortality and low fertility. Finally, when the costs raising twins are more relaxed, due to for example environmental predictability, the frequency of twins rises (Helle et al., 2004b; Lummaa et al., 1998). To conclude, having twins incurred fitness costs to both mothers and twins, indicating that twins are maladaptive in these populations.

Wealth, status, and fitness (Paper II)

Our results are in agreement with life history theory and replicable research that both status (Reviewed in Low 2000; Hopcroft 2006), and ecology (Low and Clarke, 1991; Low and Clarke, 1992), independently influence women's life histories, including fitness (number of grandchildren) (Fig. 4). We also wanted to investigate if local ecology could modify the association between status and fitness. In this paper we used the number of grandchildren born as a fitness measure. Indeed, we found that local ecology (inland or coastal) modified the effect of status on women's fitness. Our novel findings show that the differences in fitness (grandchildren) between poor and rich women were larger in the inland (7.8 vs. 16.8) than at the coast (12.0 vs. 16.1), thus, the effect of status were stronger in the inland agricultural than at the coastal fishing population. Thus, the poor agricultural females had impaired fitness. We also investigated possible between-area fitness differences for females who married upwards in the social hierarchy. Our results indicate that poor agricultural females marrying upwards in the social hierarchy still had impaired fitness. Together, these findings indicate that the effects in question tended to span generations.

The underlying life history variables that partly explained these differences were: age of first reproduction, fertility and the rate of married children. Thus, poor inland women had fewer grandchildren in part because they had lower fertility because they began reproduction later and because their children married at a lower rate. This is supported by other studies that have documented that poor women, compared to rich ones, had lower fertility (Gillespie et al., 2008; Low, 1991; Mace, 1996; Pettay et al., 2007). Furthermore, poor agricultural women started reproduction later than rich ones, partly because they married late because they needed time to acquire resources needed to establish a household (Low, 1991; Pettay et al., 2007). The marriage probability of the children of poor inland women was the most important variable explaining the differences found in this study. We suggest that these children could appear less attractive as mates with low reproductive potential due to adverse environmental conditions such as malnutrition during early development (reviewed in Lummaa, 2003). This effect arose because the poor agricultural women most likely had an unbalanced diet high in carbohydrates and low in both proteins and fat, compared to the other women in this study (Dyrvik et al., 1979; Grøn, 1942). Increasing evidence emphasizes the importance of balanced diet for both fertility (Chavarro et al., 2009) and fitness (Hayward et al., 2012; Nenko et al., 2014). This work indicates that the fitness consequence of wealth may depend on local ecology (Shenk et al. 2010), and that the diet can influence human life history across several generations.

Early conditions and fitness: effect of maternal parity on human life history (Paper III)

This part of the thesis examines for the first time how maternal parity influences children's subsequent life histories and fitness (number of grandchildren). Maternal parity can have a positive effect on fitness via daughters and a negative effect on fitness via sons, driven by fetal testosterone exposure, since testosterone decline with increasing parity (Carlsen et al., 2003; Rohrmann et al., 2009; Toriola et al., 2011; Zumoff et al., 1995). High exposure to testosterone during fetal development may result in the masculinization of offspring, a trait likely to be beneficial, in terms of reproductive potential, for first borne sons but detrimental to first borne daughters (Fig. 2). Indeed, our results supported these predictions. We found that within the mated pairs, the difference between the parity of their two mothers was a strong predictor of each couple's fitness. Specifically, pairs consisting of low-parity boys (masculine) and high-parity girls (feminine) had at least four more grandchildren than couples formed by high-parity boys (less masculine) and low-parity girls (less feminine) (Fig. 4).

Moreover, we hypothesize that fetal testosterone may be important in mate choice, because it may influences children's attractiveness later in life. Theory further predicts an association between attractiveness and reproductive success if mate choice are based on preferences that signal partner quality (such individuals have relatively high fitness) (Apicella et al., 2007; Jokela, 2009; Manning et al., 2000; Pawlowski et al., 2008). Further analyses showed that these high fitness couples had many grandchildren because they had long reproductive lives where they produced high number of children that grew up, successfully married and had children themselves. Our finding suggests that both maternal effects and the environmental conditions before birth can have long-term effects on fitness that span generations.

Menopause: no support for an evolutionary explanation (Paper IV)

In this part of the thesis we found little support for the 'Reproductive Conflict Hypothesis' (RCH) that predicts that both younger and older generations should experience fitness costs with overlapping reproduction (Cant and Johnstone, 2008). Contrary to predictions, we found that younger women (21 % was daughters and 79 % was daughters-in-law) that co-bred with the older generation had significantly more grandchildren (Fig. 4), because they had more married children, compared to those who did not co-breed. Although, we found that the child mortality was higher among older women that co-bred with younger women (Lahdenpera et al., 2012; Mace and Alvergne, 2012), we did not find any evidence that co-breeding had any long-term effect on the number of grandchildren. Thus, we did not find any intergenerational conflict over reproduction in these populations.

Our result contradicts recent empirical research among historical Finns, confirming that intergenerational co-breeding can be costly (in terms of child mortality and inclusive fitness) (Lahdenpera et al., 2012; but see Snopkowski et al., 2014). More specifically, when mothers-in-law and daughters-in-law co-bred, both child survival and inclusive fitness decreased, but when mother and daughters co-bred, there were no decrease in child mortality or inclusive fitness. Obviously, in the Norwegian societies there was reproductive cooperation within families where in-laws co-bred, rather than conflicts. Besides from methodological differences (e.g. definition of reproductive overlap), variation in resources and marriage, residence and inheritance norms between the two different societies may be potential factors that could explain the observed differences (Mace, 2013). Our further analyses indicate that older females that co-bred with the younger generation started reproduction at an early age, and therefore probably were of high quality (Van de Pol and Verhulst, 2006). We suggest that younger women may partly have enhanced fitness because they copied behavior of the high-quality and experienced reproductive women from the older generation. Young women became better parents by this copying behavior. Thus, the adaptation is to copy an older and more experienced woman in the way she rears her offspring. Finally, we discuss the troubling assumptions of the adaptive explanations for menopause (see original manuscript), and propose that menopause might be understood in the light of both ageing in general as well as our increased lifespan, and that menopause is not unique to humans.

Wealth and the opportunity for sexual selection in men and women (Paper V)

The aim of this part of my thesis was to examine whether behavioral ecology models can predict short term reproductive strategies (mate once or mate more than once) and long-term consequences of wealth in males and females (Fig. 4). Specifically, we tested if sexual selection could act on the ability to marry and remarry in a monogamous population and explored how the degree of wealth (four different subpopulations) could influence it. We calculated Bateman gradients for the two distinct episodes of selection ('marry once' and 'remarry') across the subpopulations. Men and women were analysed separately.

First, we found evidence for sexual selection on 'marry once', with an intensity that corresponds well with studies of other monogamous populations (Courtiol et al., 2012; Jokela et al., 2010; Moorad et al., 2011). Interestingly, we found that for 'married once' neither gender nor wealth was important. This suggests that men and women who managed to marry once improved their RS at a similar degree independent of wealth in these populations. Second, for 'remarried', wealth effects were significant, while sex was not. In other words, when women were in the possession of wealth they increased their number of children as much as men did by remarriage, ultimately influencing the strength of sexual selection on both men and women (Fig. 4). These results contradict traditional theory and previous studies on preindustrial Finns (Courtiol et al., 2012) and contemporary Americans (Jokela et al., 2010) reporting a significant selection on remarriage in men but not in women (but see, Pettay et al., 2014), and that wealth was unimportant for remarriage (Courtiol et al., 2012). Nevertheless, it should be noted that there is another study (using preliminary data) that found that sexual selection might be able to act on the ability to remarry in women, but not men, in a horticultural population in Tanzania (Borgerhoff Mulder et al. 2009). Together, this indicates the need for a further examination of the sexual selection and resource distribution relationship in other human populations.

Further analyses revealed that a woman's remarriage age greatly influenced her odds of having children in the second marriage, which declined sharply after the age of 35 (Low, 1991); which is consistent whit the decline in fertility with increasing age (Velde and Pearson, 2002). For men, the pattern was different. To reproduce in a second marriage, the man's age was important, as was marrying a younger (on average 10 years) woman than themselves.

To conclude, socially imposed monogamy can reduce the potential for sexual selection (Moorad et al., 2011). Even so, these results illustrate that sexual selection can operate on both sexes in a preindustrial Norwegian monogamous population and that wealth was important for the ability to remarry; while it was not for marry once. These findings improve our understanding of the socio-ecological factors influencing the reproductive strategies and thus sexual selection in men and women.

Solar activity during fetal life and reproductive success in men and women (Paper VI)

Here we tested the hypothesis if high solar activity during early development affects human life history (survival, fertility and lifetime reproductive success (LRS) (Fig. 4). Specifically, we examined if these associations were stronger in boys compared to girls, and if the effects of high solar activity during development were stronger before, rather than after 20 years of age. The results show that number of sunspots at birth decreased an individual's subsequent: 1) survival to adulthood (in both sexes) and 2) fertility including LRS (in low status women) (Fig. 4). On average, the lifespans of individuals born in a solar maximum period were

5.2 years shorter, than those born in a solar minimum period. This is in line with previous studies (Lowell and Davis, 2010). Importantly, in contrast to data used in previous studies, the longitudinal individual-based data enable us to measure age specific mortality. We report the results of the first study showing that solar activity at birth significantly increased infant mortality, and not adult mortality, in each gender. In addition, fertility and LRS were reduced among low-status women born in years with high solar activity. This is the first evidence that solar activity at birth may have consequences on human lifetime reproductive performance both within and between generations. Furthermore, we suggest that the proximate explanation for the relationship between high solar activity and infant mortality may be an effect of folate degradation in the pregnant women caused by UVR. Folate is necessary for DNA synthesis (Kim et al. 2009). It is common consensus that a low level of folate during pregnancy is associated with higher morbidity and mortality (Osterhues et al. 2013). Increased folate degradation in solar maximum periods could therefore result in low levels of folate in pregnant women (Borradale et al. 2014; Lucock et al. 2014) and, consequently, increased subsequent infant mortality (Jablonski & Chaplin 2000).

UVR is a global stressor with potentially ecological impacts and the future levels of UVR are expected to increase due to climate change and variation in atmospheric ozone (Williamson et al. 2014). Our novel results are thus highly relevant and contribute to a deeper knowledge of the effects of UVR for animal life histories and human health.

Different fitness measures

In paper II, III and IV NGC was used as a fitness measure. There are both some theoretical and methodical issues that need to be discussed in relation to the use of this measure. Fitness is usually measured as offspring quantity (here NCB or NAC). However, offspring quantity may be a poor measure of fitness, if the quality of offspring vary non-randomly in terms of reproductive quality (e.g. attractiveness to mates and fertility), which is found in several high-fertility populations (Alvergne et al., 2010; Gillespie et al., 2008; Lawson et al., 2012; Low, 1991; Strassmann and Gillespie, 2003). There are two main reasons why the reproductive quality of offspring may vary non-randomly in traditional societies like the societies used in this thesis. First, resources are scarce and distributed unequally between people in such societies. Offspring who vary in, for example, nutrition during development will most likely vary in quality. Secondly, traditional societies are characterized by high fertility rates. Thus, the reproductive consequence of the differences in quality is likely to be significant when fertility is high. This is the rationale for using NGC in paper II, III and IV.

To record the number of grandchildren we needed data on the number of children for all second-generation women. One problem with the approach was that some second-generation females moved out of the area and were "lost" from the dataset and therefore significantly reduced the dataset. In addition, by explicitly including women with full information on NGC it would be easier to track those with few NGC compared to those with many NGC. To avoid this reduction and bias in the data we estimated NGC in cases where less than 50% of second-generation females were "lost." To use information from the "lost" females, we assumed that their average fertility value was equal to the average fertility of the group to which they belonged. Under this assumption, we thus calculated an approximate number of grandchildren for the first-generation females.

Chapter 6. Concluding remarks and further perspectives

This thesis demonstrates the importance of intrinsic constraints (I and III), and extrinsic environment (II, III, IV, V and IV) for life history strategies in humans, a typical long-lived mammalian species. In addition, we have made suggestions about the proximate mechanisms behind the strategies studied. Given that some of our best evidence on mechanisms comes from humans (Flatt and Heyland, 2011; Monaghan, 2014), and based on the findings provided in this thesis, humans seems to be an ideal study species to test BE models. Below I will present some ideas and new predictions arising from this research.

In paper II we found that the fitness effect of status was highly dependent on the ecology – these factors can thus interact and create fitness differences between individuals in a group. We suggest that these differences may be mediated by differences in diet. Research on animal foraging behavior, however, have traditionally been carried out within an ecological framework, and have rarely focused on how environment and social pressures interact on foraging patterns (Finestone et al., 2014). Thus, the interaction studied in this thesis should be included in future animal foraging studies in order to fully understand such behavior among animals in both wild and captive environments. Furthermore, there are reasons to suspect that humans are adapted to a diet consisting of roughly equal amounts of carbohydrates, proteins and fat (Cordain et al., 2005; Eaton, 2006; van Elst et al., 2014). As such, the low fertility and long-term fitness of the poor agricultural women were most likely affected by an unbalanced diet (II). This finding highlights the long-term effects of diet on fertility in women.

There is mounting evidence that most social and health problems are worse in unequal societies (Wilkinson and Pickett, 2010). Given the growing gap between rich and poor in modern societies and that inequality of access to high-quality food increases (Wang et al., 2014), an important task for future investigations will be to evaluate whether detrimental effects of under- or malnutrition (both before and after birth) on fertility can span generations in contemporary women.

Other environmental conditions before birth that were found to have effects on fitness that spanned generations was maternal parity (i.e. level of testosterone in uterus) and high solar activity the year born (i.e. maternal exposure to UV radiation during pregnancy). I acknowledge that the proxies used here for these early factors are indirect (maternal parity and sun spot numbers the year born). Nonetheless, maternal effects can have important evolutionary consequences (Lummaa and Clutton-Brock, 2002), and future studies should further investigate the relationship between maternal parity and testosterone in uterus and its potential long-term effects on for instance divorce. We found that the most successful couples were formed by low-parity boys (masculine) and high-parity girls (feminine). These couples had high fitness because they had long reproductive lives. It would be interesting to investigate if such pairs had low chances of divorce in contemporary humans. Another prediction from the same work (Paper IV) is that these couples may be highly compatible and thus have healthier children compared to couples consisting of high-parity boys and low-parity girls. The predictions regarding the effects of both diet and parity could be tested with data from The Norwegian Mother and Child Cohort Study (MoBa), run by The Norwegian Institute of Public Health (Magnus et al., 2006). MoBa is a unique study that has collected biological material and questionnaire data from mothers, fathers and children from 100 000 pregnancies (from 17th week of pregnancy to the child is 8 years old).

It has already been noted that high solar activity at birth may be a potential determinant of individual fitness, due to both increased infant mortality and decreased fertility. Based on our findings in paper VI, I strongly encourage future studies on animals and, in particular, contemporary humans to evaluate both long- and short-term effect of solar activity on fitness related traits. It seems like an interesting question whether children born of light skinned pregnant women living in temperate latitudes high in solar activity experience the same effects in a similar way as children born in years of high solar activity in this thesis. Furthermore, future studies are needed to evaluate whether folate degradation (Borradale et al., 2014; Lucock et al., 2014; Osterhues et al., 2013) could be the link between high solar activity during pregnancy and infant mortality found in this thesis.

The finding that co-breeding benefited women of both younger and older generations (Paper IV) highlights the importance of other group members during the evolution of cooperatively breeding animals (Hrdy, 2009). This underlines the role of copying or imitation (how to be a good parent) as a mechanism that can be selected for, and strongly emphasizes the need for further research on potential negative fitness effects with single generation breeding among females (e.g. captive animals and women in industrialized societies) of cooperative breeders.

In paper V we present indications that wealth increased sexual selection on the ability to remarry (mate with several partners) in both genders. Further investigations on this topic from other human populations would be needed to confirm this result. In the context of remarriage for women, the age of 35 years was crucial for a successful reproduction in a second marriage. This finding gives rise to two predictions that would be interesting to test in contemporary humans. Firstly, women should tend to change partner at that age, which could be reflected in relatively high divorce rate at the age of 35 in women. Secondly, women who divorce after the age of 35 should have a relatively low probability of succeeding in finding a new partner.

To conclude, the focus of my thesis research was to test models within behavior ecology with human demographic data from historical Norway, and to understand the variation in reproductive behavior and life histories in animals, in addition to provide insight into the selective pressures affecting evolutionary processes. As with any investigation on few populations, further work involving other human populations is needed to confirm the generality of the results and conclusions. Nevertheless, in this thesis I have focused on fundamental paradigms within BE and demonstrated how their theoretical predictions can be tested within two human populations. As this procedure was successful, it may inspire future research on data from other contemporary and historical human populations.

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PAPER I

My father’s ancestors at a funeral at Brattgjer,
Sør-Trøndelag in 1903.
Photo Credit: Unknown

PAPER II

View of Reine in Lofoten. The village where my mother's father grew up.
Photo Credit: Stein Roll (2013)

Evolution and Human Behavior 32 (2011) 305 – 314

Evolution and Human Behavior

Original Article

Wealth, status, and fitness: a historical study of Norwegians in variable environments

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Abstract

Wealth and status covary with lifetime reproductive success in preindustrial human populations. Local ecology is likely to modify this association, but details of this presumed relationship are not yet known. We sought to determine whether local ecology modifies the relationship between status and fitness (number of grandchildren). Our approach to the problem was to measure variation in fitness relative to status (landless or with land) and to local ecology (inland versus coastal communities). We also analyzed life history traits that might explain observed variations in fitness. Our results confirm previous findings that both status (landless=9.9 vs. with land=16.5) and ecology (inland=12.3 vs. coast=14.1) affect the number of grandchildren produced by a female in pre-industrial society. We also found that the differences in number of children between the status groups were less pronounced on the coast (landless=12.0 vs. with land=16.1) than inland (landless=7.8 vs. with land=16.8). Our findings are novel because they suggest that the fitness consequences of human status may depend on details of local ecology. We discuss four different mechanisms that could account for these fitness differences: (1) differential reproductive rate of mothers, (2) differential marriage rate of children (3) differential survival rate of children, and (4) different social practices (breastfeeding, inheritance of property and diet).
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Keywords: Human life history; Fitness; Grandchildren; Reproductive success; Diet; Social status and wealth

1. Introduction

Life history traits such as age at first reproduction, number of offspring born, offspring survival, reproductive period, interval between births, and age of death are all components of variation in reproductive success (Roff, 2002; Stearns, 1992). Resources are essential for an individual's survival and reproduction and therefore affect fitness (Roff, 2002; Stearns, 1992). Because resources (wealth) covary with social status (individuals with greater/lesser resource availability) (Ellis, 1995), status can also explain variations in different reproductive strategies between individuals and in the fitness that they gain (Roff, 2002; Stearns, 1976). Male reproductive success is influenced by status and wealth (Trivers, 1972), whereas the ability to gain sufficient resources is particularly important for a female (Low, 2000).

Associations between resource availability and reproductive success are reported from birds (review in Boutin, 1990; Martin, 1987) and from mammals (review in Boutin, 1990). Food is an important resource. The effects of food on individual mammalian reproductive effort have been observed in the laboratory and in the field. For example, food provision accelerates breeding in snowshoe hare (*Lepus americanus*) (Odonoghue & Krebs, 1992) and increases female fertility in hispid cotton rats (*Sigmodon hispidus*) (Doonan & Slade, 1995) and in red squirrels (*Sciurus vulgaris*) (Wauters & Lens, 1995). Provisioning increases weaning success in bank voles (*Clethrionomys glareolus*) (Koskela, Jonsson, Hartikainen, & Mappes, 1998). Food availability is an important determinant of interbirth intervals across 14 baboon populations (genus *Papio*) (Hill, Lycett, & Dunbar, 2000). Food quality may also be important for individual reproductive success (Maynard, 1979).

Dominance appears to be associated with food availability in a variety of taxa. In mammals, for example, dominant

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individuals have preferential access to greater amounts of food (Gende & Quinn, 2004; Vogel, 2005) and to higher quality food resources (Murray, Eberly, & Pusey, 2006). Status and diet may also affect life history. High-ranking primate females were well fed because they often displaced others from resources (Ellis, 1995). They had higher fecundity and offspring survival, and they began their reproductive careers earlier than low-ranking females. Local ecology may also modify the relationship between status and reproductive success. If resources are locally limiting, then the relationship between status and reproductive success may be stronger than it would be if resources are locally abundant and difficult to monopolize (Ellis, 1995).

Human families with dissimilar access to resources (high or low status) are expected to follow different life-history strategies (Mcnamara & Houston, 1996). Indeed, in many pre-industrial human populations, social status (access to resources) and wealth (individuals with greater/lesser resources) covary with reproductive success. Richer individuals had more children (Clarke & Low, 1992; Dribe, 2004; Ellis, 1995; review in Hopcroft, 2006; Low & Clarke, 1992; Low, Simon, & Anderson, 2002; Lycett, Dunbar, & Voland, 2000; Pettay, Helle, Jokela, & Lummaa, 2007; Røskaft, Wara, & Viken, 1992; Voland, 1998). These studies have often used the number of offspring that survive to reproductive age as a measure of reproductive success (except for Pettay et al., 2007). However, the number of grandchildren produced is a longer-term measure of fitness (Gillespie, Russell, & Lummaa, 2008). No previous study has examined the possible local ecological impact on the association between status and reproductive success (number of grandchildren) in humans.

The present study examines how status (an assessment of personal access to recourses divided to groups of landless or with land) and ecology may affect fitness (measured as number of grandchildren) under different ecological circumstances (inland or coastal). We also wanted to investigate the proximate mechanisms that might mediate a relationship among status, ecology, and fitness. We analyzed possible effects (both primary and interactions) of status and ecology on a number of key female life-history traits. We classified 1551 preindustrial Norwegian females according to status (high or low) and ecology (inland or coast). We analyzed these females' complete reproductive histories. Our data have four important features. First, the number of grandchildren of each woman is known and represents a longer-term measure of fitness. Second, the study period covers the years from 1700 to 1900 CE, before industrialization and improved health care associated with the demographic transition began to affect survivorship and family size (Coale & Watkins, 1986; Low & Clarke, 1992). Third, data include the status and wealth of each woman based on her husband's socioeconomic status in a farming community. In these data, status is a surrogate for differences in resource availability. Such differences have previously been shown to influence family size in our study (inland) population (Røskaft et al., 1992). Finally, we wanted to investigate potential pathways other than life-history traits. Such additional factors (climate, social conventions like breast-feeding, inheritance practices and diet) might mediate any observed differences. We include these factors (see also Materials and methods) in our analyses.

2. Materials and methods

2.1. Preindustrial Norway

Preindustrial Norwegian society was largely agricultural and highly monogamous. Both men and women married late. Half of the brides became pregnant during their engagement. Pregnant women who failed to marry tended to be cottagers, belonged to the working class, and were often penalized. Illegitimacy was high; for example, in 1851, 9.1% of Norwegian children were born out of wedlock (Eliassen & Sogner, 1981). Between 1801 and 1865, Norway's population growth rate, 1.3% per year, was one of the highest in Europe (Moseng, 2003).

2.2. Study area

We studied inland and coastal populations in central Norway (see Skjærvø, Stokke, & Røskaft, 2009). The Soknedal area (63° N, 10° E, 435 km^2) has a typical inland ecology with mountains and valleys between 200 and 600 m above sea level. Throughout the study period, the majority of residents were farmers (oats, barley, cattle, sheep, and pigs). The population was 1367 in 1801 and increased to 2035 by 1865 (Haukdal, 1971), a population growth rate of 48.5% (0.74% per year). The island of Smøla (63° N, 8° E, 275 km^2) has a typical coastal ecology and a maximum altitude of 70 m above sea level. Some land clearing took place on the island during the 16th and 17th centuries. The typical Smøla man became both a farmer (oats, barley, cattle, sheep and pigs) and a fisherman. Fishing benefited both low-status and high-status people. The coastal population increased from 1166 to 2366 from 1801 to 1865 (Berg 1981). The equivalent population growth rate is 102.9% (1.5% per year). In general, the northern climate limits farming in Norway. Farms in the communities varied in size, but none was particularly large (Haukdal 1971). The two areas are located 100 km apart at the same latitude (63° N) and have similar climates (Nordli & Grimenes, 2004; Nordli, Lie, Nesje, & Dahl, 2003).

2.3. Demographic data

We used demographic data collected from local history books (Berg, 1981; Haukdal, 1971). Data are based on primary sources such as church registers, local tax lists, land registers, population censuses, and electoral registers. Data are of high quality and consist of complete information on all family members in most families. We recorded life-history traits for women (N=1551) who married before 1850 because emigration began to increase soon after 1850. Variables recorded were number of children born, number of adult children (reaching the age of 20), reproductive period, number of children married, number of grandchildren, age of mother when last child was born, mother's age of first reproduction, mother's age at death, birth intervals, status, and area. Individuals who migrated out of the area were excluded. A source of bias is that females of high status tended to marry within their own area and were therefore far more likely to remain under observation (87%) than were females of low status, who tended to marry outside the area (78%). We analyzed individual variation in female lifetime reproductive success according to the number of a female's grandchildren. This approach requires data on the number of children for all second-generation females. One difficulty with the approach was that some second-generation females moved out of the area and were "lost" from the data set. This loss reduced our usable sample to 307 grandmothers. To use information from the lost females, we assumed that their average fertility value was equal to the average fertility of the group to which they belonged. These average values for the number of children born to females were as follows: on the coast, with high status=5.4; with low status=4.6; inland, with high status=5.3; with low status=3.8. Under this assumption, we can calculate an approximate number of grandchildren for the first-generation females. The calculations were limited to cases where less than 50% of second-generation females were lost. By making this approximation, we obtained a dataset consisting of 1551 grandmothers. The two methods of recording the number of grandchildren were highly and statistically significantly correlated (r=0.722, N=307, p<.001). A reproductive history was considered to be completely known if the beginning (marriage) and the end (death) of all marriages of a person were documented in the church registers. Table 1 presents descriptive statistics of life-history traits, including the number of grandchildren. The average age of marriage was higher than the average age of first reproduction in all groups of females. This was because married mothers of illegitimate first children were included in the data. When we excluded data from these females the average age of marriage became lower than the age of first reproduction (Table 1).

Table 1
Descriptive statistics for life history variables according to group of women

Variables	Coast		Inland	
	High status	Low status	High status	Low status
	Mean±S.D.			
	N			
Age of marriage[c]	26.1±5.2	26.8±5.9	27.0±5.8	29.8±6.5
	327	140	673	368
Age of marriage[a,c]	25.6±4.5	26.0±5.9	26.1±4.7	28.2±5.1
	309	123	605	290
Age of first reproduction[c]	26.6±4.8	26.6±5.6	26.8±4.8	28.5±5.4
	352	151	675	373
No. children born	5.4±2.6	4.6±2.8	5.3±3.0	3.8±2.6
	352	151	675	373
Birth interval[b]	36±15	40±23	38±17	43±20
	324	127	576	289
Age of last reproduction[c]	39.2±5.6	37.6±6.2	39.9±5.6	38.9±5.9
	342	146	623	334
No. adult children	3.7±2.0	3.2±2.1	4.4±2.3	3.4±2.1
	351	149	631	343
No. children married	3.1±1.9	2.7±1.9	3.3±2.0	2.1±1.5
	349	147	615	323
Age of death[c]	65.3±17.6	66.2±16.1	68.2±17.1	69.6±16.5
	334	142	662	357
No. grandchildren	16.1±7.8	12.0±7.4	16.8±9.5	7.8±5.3
	352	151	675	373

[a] Married mothers of illegitimate first children were excluded from the data.
[b] Values are in months.
[c] Values are in years.

2.4. Status

We classified families and their members as either high or low status based on their socioeconomic position in the farm community. We assumed that such status was associated with stable access to food resources. Most people belonged to one of four different social groups (Røskaft et al., 1992): (1) "Bønder": farmers who owned their farms, (2) "Leilendinger": farmers who leased their farm from landowners, (3) "Husmenn": cottagers who rented a house in exchange for an agreed amount of working days on the landowner's farm, and (4) "Inderst": farm servants and other people who worked on and off for farmers. We considered Bønder and Leilendinger to be high status and assumed that they enjoyed relatively stable access to resources. Inderst and Husmenn owned no land. We considered them to be low-status groups and assumed that they enjoyed less access to resources (Dyrvik, 1990; Haukdal, 1971). The social status groups were based on male characteristics. We assumed that women's access to resources depended on the social status of their husbands (Røskaft et al., 1992). We looked for differences in farm size between areas by measuring differences in the number of animals kept (cattle, sheep and pigs). We selected 20 inland (Soknedal) farms at random and 20 coastal (Smøla) farms at random. We then counted the number of animals recorded in 1865 (Berg 1981; Haukdal 1971).

2.5. Statistical methods

We used multiple linear regressions to investigate the possible influences of area, status and the interaction of area and status on a female's overall fitness (number of grandchildren) and on each reproductive trait [age at first marriage (none of the females were excluded), age at first reproduction, number of children born, number of adult children, inter-birth interval, age at last reproduction, age at death, and number of married children]. We controlled all regressions for the female's birth year and the method for entering the predictors in the model was enter. We also investigated possible between-area fitness differences for females who married upwards or downwards in the social hierarchy. We used one-way parametric analysis of variance (ANOVA) for this analysis. We compared differences in number of grandchildren among four groups of females: (1) females marrying upwards in the social hierarchy, (2) females whose social status remained low after marriage, (3) females who grew up in the high-status group and remained in this group as adult, and (4) females marrying down in the social hierarchy. If any significant differences were found between the groups in the ANOVA, we compared individual groups of mothers with a post hoc (Tukey's honestly significant difference [HSD]) test. The distribution of the number of grandchildren appeared to deviate only slightly from the normal distribution. We could find no transformation that produced better agreement with a normal curve. We therefore used untransformed data in all subsequent analyses. All tests are two-tailed unless otherwise stated. The size of the farm on which a female resided could in principle affect her reproductive success. However, we found no statistically significant difference between the two areas in the mean number of animals per farm ($F_{1,39}$=1.91, *df*=1, *p*=.18). All data analyses were carried out in SPSS for Windows (SPSS Inc.) version 15.0.

3. Results

3.1. Main and interactional effects of status and area on fitness

Our study, like previous studies, showed that both status (landless=9.9 vs. with land=16.5) and ecology (inland=12.3 vs. coast=14.1) have significant positive main effects on the number of grandchildren produced by females in a pre-industrial society. The differences between the status groups in the number of grandchildren were smaller on the coast (landless=12.0 vs. with land=16.1) than inland (landless=7.8 vs. with land=16.8). These findings indicate that the fitness consequences of human social status may vary in ways that depend on the local ecology. Fig. 1 illustrates these results. Our linear statistical (regression) model for the data explained 20% of the variance in female fitness. In the model, status (β=0.81) had the largest slope and appeared to be the most important predictor in the regression. The status x area interaction (β=0.53) was the second largest predictor. Area (β=0.36) was less important (Table 2).

3.2. Main and interaction effects of status and area on life-history traits

When we controlled for year of birth, we found significant positive main effects of status on all life-history traits other than age at last reproduction and age at death (Table 2). When we controlled for year of birth, geographical area predicted age at marriage, age at first reproduction, number of adult and married children and inter-birth intervals. When we controlled for year of birth, area did not predict number of children born or age at last reproduction (Table 2). The status x area interaction had significant effects on a female's age at marriage (β=0.29), on age at first reproduction (β=0.29), on the number of children born (β=0.19) and on the number of her children who married (β=0.34). When we controlled for birth year, this interaction did not predict interbirth intervals, age at last reproduction or the number of adult children (Table 2). Together, the main and interactional effects of status and area accounted for between 2.7–5.9% of the variance in each life-history trait analyzed (Table 2).

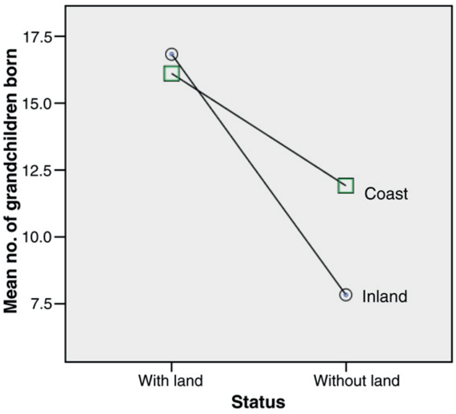

Fig. 1. Interaction between area and status in predicting number of grandchildren, when adjusting for year born.

3.3. Fitness differences between the two areas among females marrying up or down in the social hierarchy

Our results indicate that poor agricultural females marrying upwards in the social hierarchy still had impaired fitness. In the inland area, but not in the coastal area, we found that females marrying upwards as well as downwards in the social hierarchy, as well as females whose social status remained low after marriage; all had significantly lower numbers of grandchildren relative to females who remained in the high-status group after marriage (Fig. 2).

4. Discussion

Our study confirms the finding of previous studies that both ecology (Low & Clarke, 1991, 1992) and status (reviewed in Hopcroft, 2006; Low, 2000) affect female life-history traits, including fitness (Gillespie et al., 2008; Lummaa, Jokela, & Haukioja, 2001; Pettay et al., 2007) in preindustrial societies. We analyzed fitness in terms of social status and also in geographical terms. We feel that by adding a spatial-geographical-ecological dimension to previous analyses of social status and fitness, we have shed new

Table 2
Results of multiple regressions using area, status, and area´status (independent variables) to explain the variation in each life history trait (dependent variable)

Independent variable	Adjusted R^2	Status[a]		Area[b]		Status x area	
		β	t	β	t	β	t
Dependent variable							
Age of first marriage	.051***	.39	5.17***	.09	1.25	.29	-3.03**
Age of first reproduction	.048***	.32	4.01***	.19	2.00	.29	-2.80**
No. children born	.043***	-.33	-4.40***	-.09	-1.08	.19	2.12*
Birth-interval	.030***	-.18	2.17*	-.02	-0.02	-.10	-0.94
Age of last reproduction	.018***	-.03	-0.32	.01	0.16	-.08	-0.78
No. adult children	.045***	-.32	-4.19***	-.26	-3.40**	.17	1.85
No. children married	.059***	-.48	-6.23***	-.21	-3.12**	.34	3.41***
Age of death[c]	.019***	.05	0.52	-.09	-1.23	-.03	-0.28
No. grandchildren	.203***	-.81	-11.39***	-.36	-5.17***	.53	5.61***

All models control for year of birth.

[a] High=reference.

[b] Coast=reference.

* $p<.05$.

** $p<.010$.

*** $p<.001$.

light on possible ways in which local ecology might modify previously hypothesized relationships between social status and individual fitness. We also analyzed a number of underlying variables that might explain variation in fitness. We found that fitness differences between the status groups were less significant on the coast than in the inland area. Our novel findings show that the fitness consequences of social status in humans may vary depending on the local ecology, as is the case in other species (Ellis, 1995). Compared both with rich females from both environments and with poor females on the coast, poor mothers from the inland area had the fewest grandchildren born. We also found that four out of seven life history variables investigated were associated with these apparent differences in individual fitness (female's age at marriage, age at first reproduction, number of children born and the number of children married, while it did not predict the interbirth intervals, age at last reproduction, or number of adult children), and that out of these four traits, number of married children was the most important predictor.

The number of grandchildren a woman produces will depend on various life-history traits: age at marriage, age at

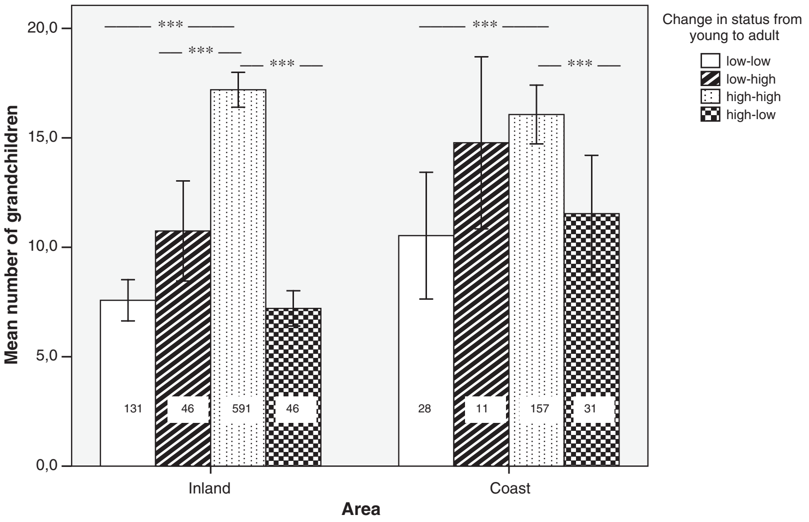

Fig. 2. Number of grandchildren (±S.D.) of females remaining in the low social class after marrying (low-low), females marrying upwards in the social hierarchy (low-high), females who spent their entire lives in the high-status group (high-high) and females marrying down in the social hierarchy (high-low). The results from an agricultural society and from a fishing society. Symbols indicate significance of differences between groups: *$p<.05$; **$p<.01$; ***$p<.001$. Numbers within the bars indicate sample sizes.

first reproduction, the number of children born, birth interval, the number of children who survive to adulthood and who marry, age at last reproduction, age at death, and offspring fertility (Røskaft et al., 1992). We showed that age at marriage, age at first reproduction, the number of children born, and the number of married children were all affected by the interaction between status and area. In other words, compared with the other women in the study, poor inland women had fewer grandchildren in part because they had lower fertility because they began reproduction later and because their children married at a lower rate. These life-history variables important to individual fitness mediate the effect of the status x area interaction. Other historical studies have shown that fecundity as well as age at first reproduction (Helle, Lummaa, & Jokela, 2005; Käär, Jokela, Helle, & Kojola, 1996) are the best predictors of female fitness and that poor females tend to start reproduction later and have lower fertility than rich females (Pettay et al., 2007). High extrinsic adult mortality may have decreased the age at first birth (Hill & Hurtado, 1996) in females of both status groups in the fishing society. The mortality rate of females of both status groups in the fishing society was higher than the corresponding mortality rate in the inland. This difference likely resulted from accidents (Anonymous, 1868) and from disease (Moseng, 2003). Both of these mortality factors were more common along the coast, the principal historical location of travel and transport in Norway (Sogner, 1979). However, we found little evidence to suggest that the observed differences in fitness were likely to be caused by differences in survival during adulthood, with interaction effects of status and area having no significant effect on age at death. High age at marriage can also explain the delayed reproduction in poor inland women. Our data show (mothers of illegitimate first children were excluded from the data) that there were no differences in the time after marriage and first reproduction between the groups ($F_{3,1327}$=0.30, p=.83), indicating that there were social constraints in the delay of the reproduction to poor mothers from the inland compared with the other women. Instead, the age of reproduction was high because age at marriage was high, likely because their future spouses needed more time to accumulate sufficient resources to establish an independent household (Low, 2000; Pettay et al., 2007). However, Røskaft et al. (1992) showed no difference in first age of marriage between females marrying upward (30.4) and those remaining in the low class (30.3) in the inland population. This suggests that other factors like mate quality (Gettler, Agustin, & Kuzawa, 2010; Phillips et al., 2001) might also account for the high age at marriage in poor inland women. The most important life-history variable that influenced the differences found in this study was the marriage probability of the children of poor inland women. These individuals could appear less attractive as mates if (1) their early rearing environment was relatively poor (Lummaa & Clutton-Brock, 2002) and if (2) bad early condition reduced (subjective) attractiveness at marriageable ages (Gettler et al., 2010; Phillips et al., 2001) and/or anticipated poor reproductive performance (Lummaa & Tremblay, 2003). We showed that the main and interaction effects of status and of ecology explained more variance (20%) in the number of grandchildren than in any other life-history trait (3–6% of variance). This result indicates that the effects in question tended to span generations. Consistent with this finding, we showed that poor agricultural females marrying upwards in the social hierarchy still had impaired fitness. We found that females inland, but not on the coast, whether they married upwards or downwards in the social hierarchy, had significantly fewer grandchildren than females whose social status was high all their lives. Similarly, females whose social class remained low after marriage had significantly fewer grandchildren than females whose social status was permanently high.

If offspring mortality were higher among poor people in inland areas than among poor people on the coast, then this difference could account for the fitness differences that we found. However, the survival rate of children (up to 20 years) born on the coast was actually lower than the corresponding survival rate in the inland, likely caused by accidents (Anonymous, 1868) and by disease (Moseng, 2003). High infant mortality could result if women's high workloads allowed them insufficient time to breastfeed their children (Ågren & Erickson, 2005). These plausible suggestions seem at least generally consistent with the circumstances faced by females of both status groups in the fishing society. One possible consequence of fishermen's absence from home might be increased workloads for mothers and for grandmothers. In our analyses, the status x area interaction did not explain the variation in the number of children who survived to adulthood. In all, these arguments suggest that the observed differences may not result from differences in offspring survival.

Infant mortality in Norway during the epoch of the study averaged 13%, the lowest in Europe. Regional differences within the country resulted in part from differing breastfeeding practices (Moseng, 2003). Nursing practices did not tend to vary with status within a society and therefore could not explain our results. In one population, for example, high-status mothers were no more likely to breastfeed their children than were low-status mothers (Moseng, 2003). We assumed that these traits followed similar patterns in our study areas. Communities in both areas practiced primogeniture (Røskaft et al., 1992). Land saturation and restrictive inheritance rules may have decreased the marriage rates (Boone, 1988) in the inland. The population density was higher in the inland (8.6 persons/km^2) than at the coast (4.6 persons/km^2). However, this would principally affect the marriage rate among the rich people with heritable wealth and not landless people. Thus, land saturation and inheritance practices could not explain the differences that we found.

Dietary patterns may in part explain our results. Suppose that the diet of poor inland women was of lower quality than the diet of other women in the sample. A high-carbohydrate diet, for example, could affect female fertility (Chavarro, Rich-Edwards, Rosner, & Willett, 2009; Cordain, 1999; Jokela, Elovainio, & Kivimaki, 2008; Jokela et al., 2007). Such a low-quality diet could also exert prenatal influence on that female's children by interfering with the development of reproductive organs. This defect would impact the children's subsequent attractiveness (Gettler et al., 2010), marital status (Phillips et al., 2001) and, finally, the female's fitness (Lummaa & Clutton-Brock, 2002). The healthiest human diets have roughly equal amounts of carbohydrate (27%), fat (43%) and protein (30%) (Cordain et al., 2005; Eaton, 2006; Mysterud, 2006). A female whose diet during pregnancy was high in carbohydrates might ultimately have fewer grandchildren than would an otherwise comparable female whose diet during pregnancy was low in carbohydrates. Literature on dietary patterns in the status classes and areas included in our study suggests that poor inland women's diets were less adequate than those of the other women in the sample. In light of this assumption, we propose that a diet high in carbohydrates may account, at least in part, for our finding that poor inland mothers from the inland had the lowest fertility, the lowest reproductive success and the lowest number of grandchildren born. We also showed that marrying upwards in the social hierarchy (and therefore, presumably, acquiring a balanced diet) failed to improve female fitness. This finding supports the idea that insufficient diet may influence human fitness across several generations.

Evolved strategies that serve to monopolize resources depend on resource availability and on the level of competition for these resources. The diets of individuals who monopolize food resources successfully and the diets of individuals who are displaced from food resources are therefore expected to differ (Allen, 1997). It has been suggested (Summers, 2005) that agriculture in harsh environments differentially benefits high-status individuals. These individuals may then control surplus foods and communal storage facilities to retain power over subordinates. Our study found precisely this pattern in the social system of cottagers (Dyrvik, 1990). Farmers had complete control of the fate of food resources and of individuals lower in the hierarchy. Individuals of low socioeconomic status traded their labor for low-quality food in order to survive famines (Supphellen, Kjelland, & Imsen, 1984).

Increasing evidence emphasizes the importance of natural diet for fertility (Chavarro et al., 2009; Cordain et al., 2005; Douglas et al., 2006; Jokela et al., 2007, 2008). Our findings suggest that diet may have long-term fitness effects. There is need for future research whose focus is the possible association between diet and fitness.

We should point out two limitations of our study. First, we studied only two populations. We need to be cautious about generalizing these effects. Second, we had no individual information on diet. We had to use known or assumed group differences as a diet measure. However, the diet in the coastal area was indeed different from the inland diet. Different status groups in the coastal area had different diets. We may reasonably suppose that the diet of poor inland women was less adequate nutritionally than the diets of the other women in the sample.

Our conclusions are consistent with those of other human studies that reveal fitness consequences of status and hence of resources. Different local environments (local geographies) modify this relationship. We found that rich females from both environments had higher fitness than those who were landless and that differences between the status groups were greater in the agricultural area than in the fishing area. Landless agricultural mothers had fewer grandchildren than did mothers in the other three groups. These fitness differences reflected variation in life-history traits, including fertility, age of first reproduction and the number of married children. These differences may be due in part to differences in diet. Diet affects both maternal fertility and offspring fertility. Additionally, diets for the two social classes differed across environments. The diets of poor inland women were less balanced than were the diets of the other women in the sample.

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Table 3
Food consumption characteristics of the women studied

Group	Diet type	Characteristic food types consumed		
		High quantities	Moderate quantities	Low quantities
CH	M-Carb.	Cod (dried and fresh), herring (salted), vegetables and whole milk	Barley meal, beef, lamb meat (fresh and salted/dried) and oatmeal	Cod liver, cod's roe and fruits
CL	M-Carb.	Cod (dried and fresh), herring (salted) and whole milk	Barley meal, oatmeal, herring (fat)	Cod liver, cod's roe, dried pea, lamb meat (salted/dried), beef and vegetables
IH	M-Carb.	Lamb meat (fresh), beef, vegetables and salmon	Barley meal, oatmeal, cod (dried), herring (salted), lamb meat (fresh and salted/dried)	Fruits
IL	H-Carb.	Barley meal, oatmeal and whole milk	Dried pea, lard and salted herring	Lamb meat (salted/dried), beef and vegetables

CH, from the coast with high status; CL, from the coast with low status; IH, inland with high status; IL, inland with low status.
Diet types are unbalanced diet high in carbohydrates (H-Carb) and balanced diet moderate in carbohydrates (M-Carb).

Appendix A. Diet

We found information on diets in 16th and 17th century Norway in a scientific review written by a medical historian (Grøn, 1942), in historical records (Dyrvik et al., 1979) and in books of recipes (Bakkevig, 2004; Notaker, 2000; Ulltveit, 2000). Grøn was one of the first researchers to work with medical history on a scientific basis. His research, particularly on Norwegian nutrition and medicine, is still cited today (Arntzen & Helle, 1999). The literature provides reliable information on the food consumption patterns of subgroups (i.e., high-status vs. low-status people and agricultural vs. fishing societies). We will address Norwegian diet in a broad sense and will then examine differences in diet according to social status and area. The sources cited above indicate that the diet consisted mainly of grain (oat and barley), milk, dried peas, fish, and meat (Table 3). Grain, consumed as soup, porridge, and bread, was the primary source of energy. Norway imported approximately 30% of its total grain consumption. Imported grain was of generally poor quality (Grøn, 1942), particularly during famines (Dyrvik et al., 1979). Meat, primarily from sheep and cattle, represented only a small portion (6 kg/year) of an average person's diet (Grøn, 1942). According to the literature, a variety of fish, including salmon (*Salmo salar*), herring (*Clupea harengus*), and cod (*Gadus morhua*) were part of the diet. Most marine fish caught were dried and/or salted and consumed by people of all status groups along the Norwegian coast. Freshwater fish were usually consumed by people of high status (Grøn, 1942). Milk, the main source of dietary fat, was used in almost every dish and meal. Cheese made from cow's milk was a popular food item (Bakkevig, 2004). Cultivation and consumption of potatoes was limited prior to 1850 in our study areas but increased in Norway by the end of the 18th century (Berg, 1981).

Quality and quantity of food consumed varied both with social status and with area (inland or coast) (Table 3). Landless inland people had a diet relying heavily on grain and milk. Marginal amounts of salted/dried herring and meat, sometimes as much as 10–20 years old, accompanied these staples (Table 3). Thus, the diet was high in carbohydrates (Table 4). We characterize this group in terms of its unbalanced, high-carbohydrate diet (H-Carb, Table 3). Coastal people of low social status consumed relatively greater amounts of fresh fish and relatively smaller amounts of bread (Table 3) (Grøn, 1942; Ulltveit, 2000), thus they had a more nutritionally balanced diet (Table 4). Wealthy individuals in both areas had a more nutritionally (Table 4) varied diet: fresh fish and meat, grain, milk, vegetables and imported fruits (Table 4).We characterize the latter 3 groups in terms of their balanced diet, a diet that included only moderate amounts of carbohydrates (M-Carb, Table 3). The correlation between undernourishment and child mortality in human populations is strong (Caulfield, De Onis, Blossner, & Black, 2004). However, we found no differences in survival rates between offspring from different status groups residing inland (c^2=0.19, *df*=1, 5644, *p*<.1). We therefore find it unlikely that individuals of low social status were underfed.

Table 4
Nutrient content per 100 g edible portion

Food type	Nutrient			
	Energy	Protein	Fat	Carbohydrate
	kcal	g	g	g
Barley meal	302	8.6	1.1	60.6
Beef	212	28.9	10.7	0
Cod (boiled)	94	22.6	0.4	0
Cod (dried)	327	78.5	1.4	0
Cod liver	630	6.9	66.9	0
Cod's roe	125	27	1.9	0
Herring (fat)	367	21.3	31.3	0
Herring (salted)	210	16.5	16	0
Lard	900	0	100	0
Lamb meat (fresh)	213	27.9	11.3	0
Lamb meat (salted/dried)	313	26.2	23.1	0
Oatmeal	373	11.7	7	61.7
Pea (dried)	287	22	2.1	41.4
Salmon (boiled)	215	23.2	13.6	0
Whole milk	66	3.2	3.9	4.6

Data adapted from Widdowson and McCance (2002).

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PAPER III

My father as a child with his family
Photo Credit: Unknown

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Original Article

Editor's choice

Early conditions and fitness: effect of maternal parity on human life-history traits

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Stable pair bonds are widespread in humans and reproductive success varies greatly among pairs. Determinants of fitness may be based on testosterone-dependent sexually dimorphic traits. Prenatal condition is a critical period of physical development, and fetal testosterone has a profound effect on adult behavior and reproduction. Maternal parity (the number of previous births) might be a proxy for fetal testosterone because the prenatal level of male sex hormone, testosterone, is previously shown to decrease across parities. Offspring reproductive potential may, therefore, be positively associated with low parity in sons and high in daughters, by different masculinization by testosterone. In this study, we explored the effects of maternal parity on offspring's subsequent (individual and pair-specific) life histories including number of grandchildren (controlling for age at marriage, number of siblings, social status, and year of birth) in a Norwegian preindustrial society. We found that parity was a positive predictor of daughters' and negative (but not significantly; $P = 0.058$) predictor of sons' subsequent fitness. Furthermore, within the mated pairs, the difference between the parity of their 2 mothers was a strong predictor of each couple's fitness. Sons born to mothers of low parity married to daughters from mothers with high parity had much higher number of grandchildren than, for example, sons of mothers with high parity married to daughters of mothers with low parity. The result highlights the importance of early prenatal condition on human life histories, particularly pair-bond duration and fitness, and that parity may have an impact on offspring pair-specific fitness in the studied population. *Key words:* early condition, grandchildren, pair bond, parity, reproductive success, testosterone. *[Behav Ecol]*

INTRODUCTION

Many species reproduce within long-term pair bonds, such as a majority of birds (Cockburn 2006) and some mammals, including humans (Clutton-Brock 1991; Reichard and Boesch 2003). Stable mating relationships are widespread in humans and reproductive success varies considerably among pairs (Hawkes 2004). Variations in reproductive success have been associated with a range of individual, social, life-history, and phenotypic characteristics, such as access to resources (Røskaft et al. 1992), age at first reproduction (Skjærvø et al. 2011), and the reproductive potential (Apicella et al. 2007; Jokela 2009; Fraccaro et al. 2010). Fitness is not only determined by individual qualities but may also be affected by the compatibility between partners in various testosterone-dependent sexually dimorphic traits (Trivers 1972; Havlicek and Roberts 2009), including reproductive potential (Bereczkei and Csanaky 1996). Thus, the initial formation of pair bonds is extremely important to both female and male fitness, and there is evidence for mate choice–based reproductive potential (e.g., masculinity for men and femininity for women) (Little et al. 2001; Manning 2002; Penton-Voak et al. 2004; Saino et al. 2006; Lummaa et al. 2007; van Straaten et al. 2009; Fraccaro et al. 2010; Vukovic et al. 2010).

Previous studies have suggested the importance of early condition on reproductive success (Lindstrom 1999; Lummaa and Clutton-Brock 2002). The effects of maternal parity (the number of previous live births and stillbirths) could be a potential source of variation in the mate quality of the offspring because individuals born to mothers of different parity have different prenatal environments that may influence growth, health, and survival (Bai et al. 2002; Fessler et al. 2005). A number of human studies indicate that the level of testosterone decreases with maternal parity or age (Zumoff et al. 1995; Carlsen et al. 2003; Rohrmann et al. 2009; Toriola et al. 2011). Consistent with this, 2 other lines of evidence indicate that parity can be used as a proxy for prenatal levels of testosterone. First, parity effects on birth weight are well known among mammals, including humans (reviewed in Fessler et al. 2005): low-parity offspring tend to have lower birth weight than high-parity offspring (Magnus et al. 1985; Seidman et al. 1988; Wilcox et al. 1996; Carlsen et al. 2006; Nordtveit et al. 2009). Second, elevated levels of testosterone in the uterus decrease birth weight (Wolf et al. 2002; Carlsen et al. 2006; Recabarren et al. 2009). Thus, low-parity children have low birth weight because they may be exposed to relatively higher levels of testosterone than those born to mothers of high parity (Zumoff et al. 1995; Carlsen et al. 2003; Rohrmann et al. 2009; Toriola et al. 2011).

Fetal testosterone is essential for sexual differentiation and has a profound effect on adult behavior and reproduction (of both the sexes) in mammals (Wallen and Baum 2002), including humans (Ryan and Vandenbergh 2002; Cohen-Bendahan et al. 2005; Abbott et al. 2006). More precisely, regardless of the exact mechanism, female fetuses exposed to high levels of testosterone mature at a later age, have a shorter reproductive period and lower fertility, are less attractive to males, and have weaker (less feminine) mate preferences (Ryan and Vandenbergh 2002; Wallen and Baum 2002). Likewise, mammal males exposed to low testosterone

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levels during prenatal development show feminine sexual behavior and are less attractive as mates to the opposite sex (Ryan and Vandenbergh 2002; Wallen and Baum 2002). In humans, the more feminine females (i.e., female offspring of high-parity mothers) are preferred as mates by males (Manning 2002; Penton-Voak et al. 2004; Saino et al. 2006; Lummaa et al. 2007), whereas the more masculine males (i.e., male offspring of low-parity mothers) are more sexually attractive to females (Manning 2002; Penton-Voak et al. 2004; Saino et al. 2006). Ultimately, fetal testosterone, and thus maternal parity, may affect fitness. This hypothesis is in line with the findings that female fetuses exposed to high levels of testosterone have both reduced fertility (Homburg et al. 1988; Franks 1995; Abbott et al. 2006) and breastfeeding rate (Vanky et al. 2008). To our knowledge, the effects of maternal parity on offspring's subsequent (individual and pair-specific) life histories and fitness have not yet been studied.

The present study had 3 aims, using maternal parity as a surrogate of early condition (fetal testosterone). First, we hypothesized that the reproductive potential and thus the mate quality is positively associated with high parity in female offspring (highly feminine) and low parity in male offspring (highly masculine). We, therefore, investigated whether maternal parity could influence offspring's (sons and daughters) fitness (measured as the number of grandchildren). Second, if mate choice–based on reproductive potential has fitness benefits, we predicted that the effects of maternal parity could influence a pair's reproductive outcome: couples formed by a low-parity boy and high-parity girl (the difference of their mother's parities had a high value) had higher fitness than pairs consisting of high-parity boy and low-parity girl (the difference of their mother's parities had a low value, see Figure 1 for explanation). We, therefore, tested if the value of the difference of parity between the partners' mothers within mated pairs were predictors of pair-specific fitness. Third, we analyzed the possible effect of such early conditions on key life-history traits (number of children born, number of adult children, age at last reproduction, and number of married children) within mated pairs to understand the underlying pathways that might mediate the fitness differences found.

Our data and study design have several benefits addressing these aims. First, the number of grandchildren of each couple is known and represents a long-term measure of fitness. Second, the study period covers the years from 1700 to 1900 CE, before industrialization and improved healthcare associated with the demographic transition began to affect survivorship and family size (Coale and Watkins 1986; Low and Clarke 1992). Third, the data include the status and wealth of each couple based on the husband's socioeconomic status in a farming community. In these data, status is a surrogate for differences in resource availability. Such differences have previously been shown to influence family size in our study population (Røskaft et al. 1992). Fourth, in all the analyses, we have paid particular attention to the task of separating "before birth" and "after birth" explanations. There are at least 2 important "after birth" factors that can be used in the analysis of biased parental investment: birth order and sibship size. Life-history theory predicts that when parents have limited energy and resources, they should strategically distribute their resources to maximize the total success of their offspring

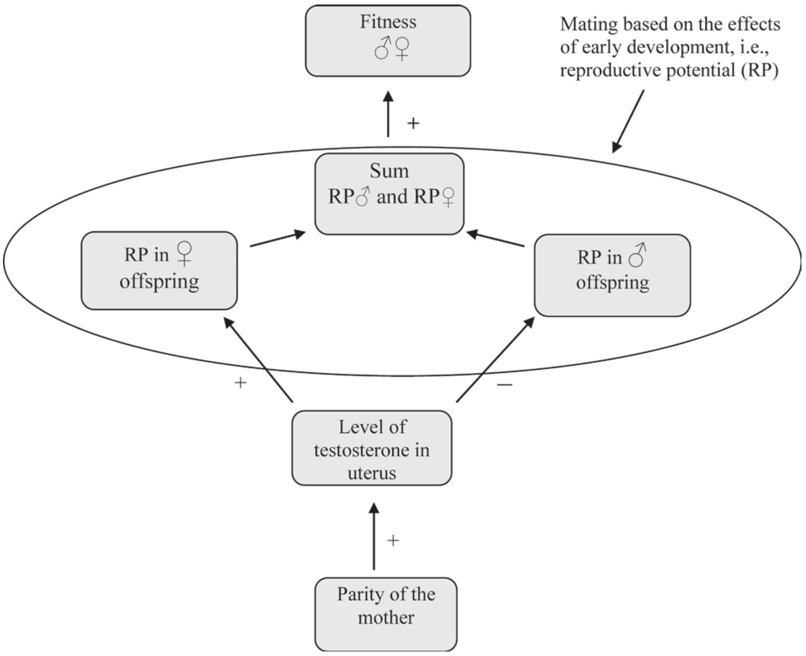

Figure 1
A schematic representation of the consequences of maternal parity effects on offspring's subsequent fitness by means of the effects of early development on RP (reproductive potential). Environmental conditions, such as testosterone level in uterus, may affect the RP of male and female offspring in opposite directions. The sum of each RP to both the individuals in a couple (tot-RP) may influence the fitness of that couple.

(Trivers and Willard 1973; Clutton-Brock 1991). This helps in explaining why parents bias their investment by birth order (e.g., Faurie et al. 2009) and sibship size (e.g., Mace 1996). These 2 factors may confound our results. However, by sampling all individuals in the present study from different families, we reduced the effect of biased postnatal parental investment among children within families (Michalski and Shackelford 2001) and we collected data on sibship size to control for variation in sibling competition (Michalski and Shackelford 2001).

MATERIALS AND METHODS

Participants

We used demographic data from a Norwegian patriarchal farming society (Soknedal, 63°N, 10°E), collected from local history books (see Røskaft et al. 1992; Skjærvø et al. 2009). The study sample included complete life-history data of 89 married couples, consisting of men and women (F1 generation) born to 180 mothers (P generation). Mating system was monogamous with practically no divorce. Marriages were not arranged and both sexes were free to choose their spouses, though parents' consents were often required (Eliassen and Sogner 1981).

Measures

We recorded full life-history data for all F1 individuals (number of children born [F2 generation], number of adult children [20 years], reproductive period, and number of married children), including the number of grandchildren (F3 generation), which is the ultimate measure of fitness. We were interested in the variable effect of early condition before birth. Parity of the P mothers was, therefore, used to build the variable of interest, comprising 2 categories: Pf, parity of the mothers to the F1 women and Pm, parity of the mothers to the F1 men. From the records, several F1 individuals between couples came from same families. In order to avoid pseudoreplication of the data (see Hurlbert 1984) (same family environment), we randomly picked only one of these same family F1 individuals to be included in the data. This procedure reduced the sample size and the degrees of freedom but enabled us to reduce the postnatal effects. For all F1 individuals, we also collected data on female and male sibship size to control for variation in sibling competition (Michalski and Shackelford 2001). We also had data on female age of marriage, male age of marriage, and year when female was born, which all have already been associated with variation in fertility in these populations (Røskaft et al. 1992). We classified couples as either high or low status based on their socioeconomic position in the farm community. In these data, status is a surrogate for differences in resource availability. Such differences have previously been shown to influence fitness in our study population (Skjærvø et al. 2011).

We hypothesized that girls born to mothers of high parity and boys born to mothers of low parity are both positively related to reproductive potential and pair-specific fitness. We, therefore, calculated a predicted correlate of fitness within each couple: parity of the mothers to the F1 females − parity of the mothers to the F1 men (P (f − m)). Table 1 presents the descriptive statistics of the variables studied.

Table 1
Descriptive statistics of study variables

	Mean (±1 SD)
Reproductive period (years)	13.1 (6.9)
Number of children born	5.3 (2.9)
Number of adult children	4.0 (2.3)
Number of married children	2.8 (1.8)
Number of grandchildren	14.8 (10.0)
Male number of siblings	4.7 (2.2)
Female number of siblings	5.6 (2.4)
Male age at marriage	29.5 (5.8)
Female age at marriage	26.5 (5.3)
Pf	3.8 (2.3)
Pm	3.1 (2.1)
P (f − m)	0.90 (2.9)

Pf: parity of the mothers to the F1 women and Pm: parity of the mothers to the F1 men. P (f − m): parity of the mothers to the F1 females − parity of the mothers to the F1 men.

Statistical analysis

First, we wanted to explore the effect of both Pm and Pf (in the same model) on the number of grandchildren produced by each couple while controlling for the confounding variables mentioned above. Second, we investigated the possible influences of P (f − m) on each reproductive trait (number of children born, number of adult children, reproductive period, and number of married children) including number of grandchildren.

Prior to the statistical analyses, data exploration was applied following the protocol described in Zuur et al. (2012). We looked at the presence of outliers using Cleveland dotplots, collinearity (correlation between explanatory variables) using multipanel scatterplots and variance inflation factors (VIF), and relationships between the response variables and explanatory variables were visualized using multipanel scatterplots to see whether relationships were linear or nonlinear. Multiple linear regression was applied to model reproductive period as a function of the P (f − m), male number of siblings, female number of siblings, male age at marriage, female age at marriage, status, and year born.

Generalized linear models (GLMs) using a Poisson distribution were applied on the response variables, number of children born, number of adult children, number of married children, and number of grandchildren, as these variables are counts (Zuur et al. 2009). The same explanatory variables were used. Various GLMs were slightly underdispersed or overdispersed and in such cases a quasi-Poisson GLM was used to correct the standard errors (SEs) (Zuur et al. 2009). Once models were fitted, a model validation was applied on the residuals (Pearson residuals for the GLMs and standardized residuals for the multiple regression model); we inspected the residuals for the presence of outliers and influential observations (using Cooks distances), patterns (by plotting residuals vs. each covariate), normality, homogeneity, and independence (by making a sample variogram of the residuals vs. year).

Calculations were carried out in R Development Core Team (2012).

RESULTS

Cleveland dotplots (Supplementary Figures 1–5) suggested that there are no outliers and the multipanel scatterplots and VIF values (Supplementary Table 1) indicate that there is no strong collinearity.

Effect of Pm and Pf on fitness

The full GLM model, including estimate SE, *t*, and *P* values for all factors and covariates, is reported in Supplementary Table 2. The parity of P mothers was found to be a predictor

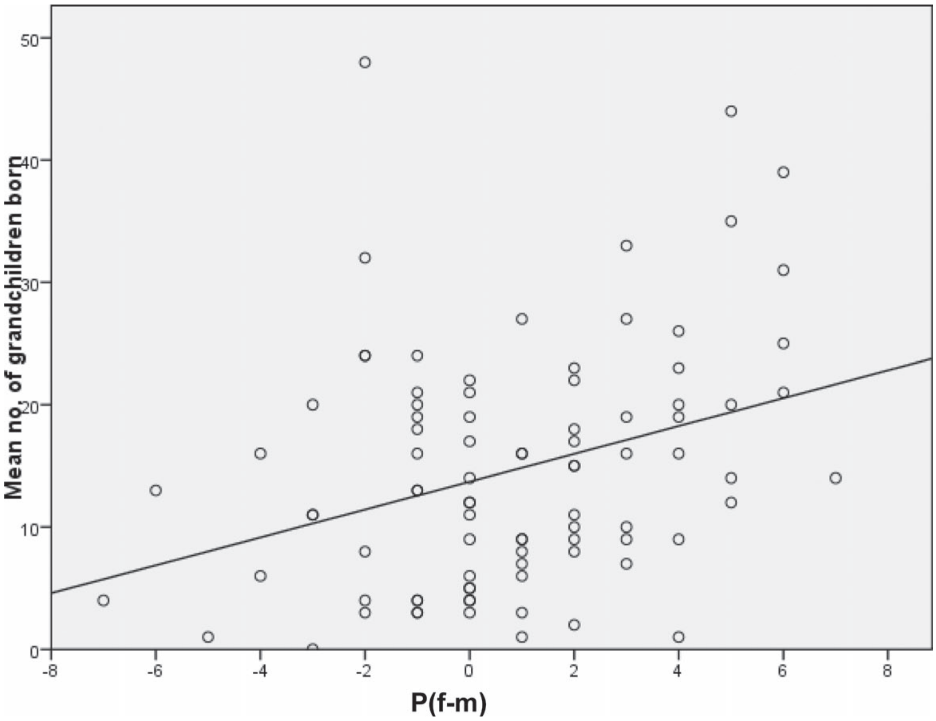

Figure 2
Mean number of grandchildren per couple (n=89) regressed on parity of the mother to the female partner minus parity of the mother to the male partner (P (f – m)).

of F1 women's number of grandchildren (GLM, $P = 0.011$), but not statistically significant for F1 men (GLM, $P = 0.058$), after controlling for male number of siblings, female number of siblings, male age at marriage, female age at marriage, status, and year born (Supplementary Table 2). The model explained approximately 32% of the F1 women's variance in number of grandchildren (Supplementary Table 2).

Effect of P (w – m) on fitness and key life-history traits

The value of the difference between Pf and Pm within the studied pairs (P (f – m)) had a significant effect on fitness (number of grandchildren) (Table 6 and Figure 2) including all life-history parameters (Tables 2–5). Number of siblings of males, but not females, also had a significant effect (positive) on pair-specific fitness and key life-history traits (Tables 2–6). Age of marriage (of both female and male) had significant effects on key life-history traits, but only female age of marriage had effect on number of grandchildren (Tables 2–6). Status had significant effect on 2 (reproductive period and number of children) of the 4 life-history variables investigated (Tables 2–5). After controlling for these confounders, we found that in partnerships in which the male was born of a mother of lower parity than his partner, the couple had higher number of grandchildren than when his mother's parity was higher than that of his partner's mother (high value of difference in parity) (Table 6). Couples with a high value of difference in parity had higher fitness, presumably because they had longer reproductive period and higher number of children born, surviving, and marrying (Tables 2–5). The GLMs explained approximately 39, 48, 37, 36, and 39% of the variance in couples' reproductive periods, number of children born, number of adult and married children, and number of grandchildren, respectively (Tables 2–6).

DISCUSSION

Previous studies have shown that stable mating relationships are widespread in humans (Reichard and Boesch 2003) and

Table 2
Factors explaining the variation in reproductive period among the couples studied

Factor	Estimate	SE	t	P
P (f – m)	0.64	0.2527	2.55	0.0127
Male number of siblings	0.73	0.2739	2.70	0.0085
Female number of siblings	−0.40	0.2982	−1.34	0.1830
Male age at marriage	−0.22	0.1089	−1.99	0.0502
Female age at marriage	−0.38	0.1213	−3.14	0.0023
Status	−2.55	0.3220	−1.93	0.0574
Year born	−0.02	0.0163	−1.09	0.2789
Intercept	6.104	29.3585	2.08	0.0408

Residual standard error: 5.578 on 81 degrees of freedom (df). Multiple R^2: 0.3932, F-statistic: 7.5 on 7 and 81 df, P-value: 6.055e-0. See text for explanation of variables. P (f – m): parity of the mothers to the F1 females – parity of the mothers to the F1 men. Model validation indicated homogeneity, normality, independence, and absence of influential observations.

Table 3

Factors explaining the variation in number of children among the couples studied

Factor	Estimate	SE	*t*	*P*
P (f − m)	0.06	0.0190	3.25	0.0017
Male number of siblings	0.07	0.0196	3.42	0.0009
Female number of siblings	−0.02	0.0190	−0.85	0.3995
Male age at marriage	−0.02	0.0184	−1.84	0.0697
Female age at marriage	−0.04	0.0108	−3.28	0.0015
Status	−0.25	0.1043	−2.45	0.0179
Year born	0.00	0.0012	−1.85	0.0677
Intercept	6.90	2.1568	3.20	0.0019

General linear model analysis, estimate, SE, and *t* values for variables explaining number of children born. See text and Table 2 for explanation of variables. A quasi-Poisson GLM was applied as the Poisson GLM was slightly underdispersed with 0.88. Dispersion parameter for quasi-Poisson family taken to be 0.8893. Null deviance: 145.40 on 88 df. Residual deviance: 75.52 on 81 df. The generalized R^2 is 0.48. Model validation indicated homogeneity, normality, independence, and absence of influential observations.

Table 4

Factors explaining the variation in number of adult children among the couples studied

Factor	Estimate	SE	*t*	*P*
P (f − m)	0.06	0.0212	2.71	0.0089
Male number of siblings	0.07	0.0220	2.95	0.0042
Female number of siblings	−0.02	0.0239	−0.66	0.5109
Male age at marriage	−0.02	0.01	−1.87	0.0654
Female age at marriage	−0.03	0.0118	−2.68	0.0089
Status	−0.16	0.1153	−1.41	0.01627
Year born	0.00	0.0014	−1.19	0.02346
Intercept	5.47	2.4341	2.25	0.0272

General linear model analysis, estimate, SE, and *t* values for variables explaining number of adult children. See text and Table 2 for explanation of variables. A quasi-Poisson GLM was applied as the Poisson GLM was slightly underdispersed with 0.88. Dispersion parameter for quasi-Poisson family taken to be 0.8605. Null deviance: 117.48 on 88 df. Residual deviance: 74.44 on 81 df. The generalized R^2 is 0.37. Model validation indicated homogeneity, normality, independence, and absence of influential observations.

Table 5

Factors explaining the variation in number of married children among the couples studied

Factor	Estimate	SE	*t*	*P*
P (f − m)	0.06	0.0241	2.45	0.0017
Male number of siblings	0.08	0.0252	3.01	0.0035
Female number of siblings	−0.02	0.0272	−0.87	0.3859
Male age at marriage	−0.02	0.011	−1.52	0.1322
Female age at marriage	−0.05	0.0139	−3.45	0.0009
Status	−0.13	0.1311	−0.99	0.3239
Year born	0.00	0.0016	−1.04	0.2995
Intercept	5.45	2.7749	1.96	0.0532

General linear model analysis, estimate, SE, and *t* values for variables explaining number of married children. See text and Table 2 for explanation of variables. A quasi-Poisson GLM was applied as the Poisson GLM was slightly underdispersed with 0.76. Dispersion parameter for quasi-Poisson family taken to be 0.7697. Null deviance: 103.88 on 88 df. Residual deviance: 66.13 on 81 df. The generalized R^2 is 0.36. Model validation indicated homogeneity, normality, independence, and absence of influential observations.

Table 6

Factors explaining the variation in number of grandchildren among the couples studied

Factor	**Estimate**	**SE**	*t*	*P*
P (w − m)	0.07	0.0263	2.61	0.0109
Male number of siblings	0.10	0.0267	3.75	0.0003
Female number of siblings	0.00	0.0291	−0.05	0.9569
Male age at marriage	0.00	0.0113	−0.35	0.7279
Female age at marriage	−0.04	0.0151	−2.56	0.0124
Status	−0.16	0.1423	−1.13	0.2620
Year born	0.00	0.0017	−2.29	0.0243
Intercept	10.22	2.9603	3.46	0.0009

General linear model analysis, estimate, SE, and *t* values for variables explaining number of children born. See text and Table 2 for explanation of variables. A quasi-Poisson GLM was applied as the Poisson GLM was slightly overdispersed with 4.69. Dispersion parameter for quasi-Poisson family taken to be 4.6981. Null deviance: 593.10 on 88 df. Residual deviance: 363.49 on 81 df. The generalized R^2 is 0.39. Model validation indicated homogeneity, normality, independence, and absence of influential observations.

that reproductive success may vary among pairs according to pair-specific reproductive potential (Apicella et al. 2007; Jokela 2009; Fraccaro et al. 2010). Parity may have an effect on offspring reproductive potential because individuals born to mothers of different parity have different prenatal environments (e.g., levels of testosterone) that may influence growth, survival, and fertility. However, it is unknown whether such a condition affects both individual and pair-specific fitness (measured based on the number of grandchildren).

Our results suggest that maternal parity has an effect on individual offspring's subsequent fitness among preindustrial Norwegians. We also analyzed life-history variables, including fitness among couples in terms of the value of difference between the parity of their mothers (couples with a high value are more compatible than those with a low value). We presume that by adding pair-specific quality based on the effect of maternal parity on both the partners to previous analyses of fitness, we have shed light on the possible ways in which the effects of early development modify previously hypothesized relationships between mate quality and fitness. We found that within mated pairs, P (f − m) was a strong predictor of each couple's fitness. As we had predicted, couples formed by a low-parity boy and high-parity girl (high value of difference of parity) had, on average, at least 4 more grandchildren than pairs consisting of high-parity boy and low-parity girl. Thus, P (f − m) can be considered as an indicator of pair quality.

Obviously, the final choice of a partner is based on a number of preferences that signal partner quality (Gangestad and Simpson 2000). It is important to note that we have not tested mate choice in this population, but only the association between the effect of parity on pair-specific quality (presumably important in mate choice) and fitness. If maternal parity effects due to fetal testosterone could affect the children's subsequent attractiveness, then these effects may be important in mate choice. Our results are in line with this idea and earlier studies that found an association between attractiveness and reproductive success (Manning et al. 2000; Apicella et al. 2007; Pawlowski et al. 2008; Jokela 2009), by showing that partnership formed by low-parity sons and high-parity daughters had the highest number of grandchildren. This fitness benefit arises because these pairs had both higher number of children born as well as surviving and more married children, partly because they had a longer reproductive period. Thus, this indicates a link between compatibility between partners in sexual dimorphic traits, pair-bond duration (Käär et al. 1996; Manning et al. 2000), and fitness. In accordance, sociological studies have shown that couples formed by spouses with different birth orders (e.g., an older brother of sisters with a younger sister of brothers) have lower divorce rates and their marriages are likely to last longer than that of, for example, 2 youngest children, because of factors including marital stability, relationship commitment, and quality and satisfaction (Kemper 1966; Toman 1970, 1971; Weller et al. 1974).

At the proximate level, the relation between parity and fitness in our results may in part reflect 2 processes. First, prenatal birth-order effects, such as exposure to fetal testosterone (Carlsen et al. 2006; Nordtveit et al. 2009) may affect the reproductive potential of an individual. Low-parity masculinized sons and high-parity feminized daughters may both have higher reproductive potential (Ryan and Vandenbergh 2002; Wallen and Baum 2002; Abbott et al. 2006), and thus higher reproductive success (Franks 1995; Abbott et al. 2006; Lummaa et al. 2007) than both early-born masculinized females and later-born feminized males. Second, postnatal birth-order effects of early family environment, including sibling competition (number of siblings) (Low 1991; Mace 1996; Gillespie et al. 2008) and different parental investments (Voland 1998; Draper and Hames 2000; Pettay et al. 2007; Rickard et al. 2007; Faurie et al. 2009) may be an alternative explanation. However, we found little evidence to suggest that the patterns observed were likely to solely be explained by the differences in sibling competition and postnatal parental investment. First, after controlling for a number of competing siblings, we still found that the value of difference between the parity of each couple's mothers was a significant factor explaining the fitness differences found. Second, we collected data on parity from different families. Using such a between-family design reduces the effects of biased parental investment among children within families (Michalski and Shackelford 2001). A number of studies support the predictions from the theory that having more siblings has negative consequences for individual development, survival, and reproductive success (Low 1991; Mace 1996; Gillespie et al. 2008), but some studies have also found the opposite, which is in line with our findings that boys' numbers of siblings had a significant positive effect on fitness (Draper and Hames 2000). The mechanisms of the association are unclear although they may result from the support from the kin within a patriarchal society. The greater the number of siblings a boy has, the more economic or social support that he and his family might get, which could be converted to enhancement of reproductive success (Draper and Hames 2000).

Biased parental investment strategies, such as primogeniture, where first-born sons have higher reproductive success, when compared with their younger siblings, because they are favored as the inheritors of land or "helping-at-the-nest" (Hrdy and Judge 1993). Furthermore, the first-born daughters marry late because they help parents in rearing younger siblings (Bereczkei and Dunbar 2002). Both strategies may benefit parent's inclusive fitness. Although we have no data on how parental investment was allocated among different children within families, we assume that first-born males were favored because people followed the rule of primogeniture (Røskaft et al. 1992). First-born females were not favored because as shown earlier, they had lower probability of marriage than later-born females (Bongard 2005). Such practices may intensify the effects of fetal testosterone that "naturally" favor both low-parity sons and high-parity daughters and are probably adaptive because parents provide extra resources to those children with greatest reproductive potential (Trivers and Willard 1973; Clutton-Brock 1991; Faurie et al. 2009).

Previous studies on traditional (reviewed in Draper and Hames 2000), preindustrial (Faurie et al. 2009), and contemporary (Goodman and Koupil 2009; Milne and Judge 2009) humans concerning the relationships between birth order, reproductive behavior, and reproductive success all contradict each other. Let us consider that there is a connection between parity and parental treatment of offspring, as mentioned earlier. Thus, the effect of birth order on reproductive behavior including fitness could also, similar to our results, work in the opposite direction between the 2 sexes. We suggest that these contradictions may be minimized by taking into account the combination of spouse's birth order, rather than individual birth order when investigating the association between birth order and fitness in the future.

The main strength of our study includes full life-history data on 4 generations for both the female and male lines within the pairs. However, one constraint is certainly the number of couples. Yet, it is difficult to collect adequate complete data for each couple over 4 generations because data from individuals who migrated out of the area were lost from the sample. However, the significant findings indicate that the sample size was not detrimental.

In conclusion, the present results highlight the importance of early condition on human life histories, particularly pair-bond duration and fitness, and that maternal parity may in part have an impact on offspring's pair-specific fitness in the studied population.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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PAPER IV

Four generations. The first generation is my maternal grandparents.
Photo Credit: Unknown

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Menopause: No support for an evolutionary explanation among historical Norwegians

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ABSTRACT

Life history theory proposes that menopause is either an epiphenomenon or an adaptation. The most recent adaptive hypothesis proposes that menopause in humans has evolved because of conflict between reproducing generations (RCH). Overlapping reproduction between generations may impose fitness costs to older and younger females who co-breed. However, it has yet to be demonstrated by using a measure of evolutionary fitness (i.e. grandchildren). Here, we tested the RCH by using multigenerational life-history data of historical Norwegian women. Our results indicate that both generations seem to experience some fitness benefits with co-breeding (i.e. reproductive overlap and cohabit). This was because both younger and older females who co-bred had more grandchildren than those who did not co-breed. We suggest that younger females may partly had enhanced fitness because they copied behaviour of females of the older generation. Our results do not support the hypothesis that reproductive conflict between generations explains the evolution of menopause in women. Our results, taken together with the growing evidence against several assumptions of the RCH, indicate that 1) the decline in follicle number has no marked increase in women as they reach the age of 38 years; 2) humans do not have an abrupt decline in fertility at mean age of 38 years; 3) menopause is not unique to humans; and 4) there are not high numbers of individuals surviving to older adulthood during our evolutionary past. Finally, we discuss an alternative point of view suggesting that menopause might be understood in the light of both ageing in general as well as our increased lifespan.

1. Introduction

Menopause is an evolutionary enigma because theory predicts that natural selection should act to synchronise the senescence of reproductive and somatic systems (Hamilton, 1966; Williams, 1957). Both non-adaptive (reviewed in Peccei, 2001b) and adaptive (reviewed in Lahdenpera et al., 2011b) explanations have been proposed to explain why females stop reproducing long before they die. The most recent adaptive hypothesis (RCH) states that reproductive conflict between generations explains the evolution of menopause (Cant and Johnstone, 2008). However, as this hypothesis has not been tested adequately (Johnstone and Cant, 2010; Mace and Alvergne, 2012) by considering a measure of evolutionary fitness in populations with natural fertility and mortality, we still do not have the complete picture.

Life-history theory predicts that evolutionary forces should shape the timing of life events such as development, maturation, reproduction and death (Stearns, 1992). Compared with other primates, human lifetimes are often described as unusual in many respects: long period of infant dependence, late age at maturation, female menopause and long lifespan (Low, 2000) (however, see Bronikowski et al., 2011; Ricklefs, 2010). Females experience a gradual decline in reproductive performance and cease natural fertility at a mean age of 38 years, followed by complete sterility after 10 years, which is called menopause (Velde and Pearson, 2002). In contrast, males have the ability to reproduce until old age, with only a slight decrease in fertility (Perheentupa and Huhtaniemi, 2009).

RCH proposes that menopause is adaptive and has evolved as a result from reproductive competition between generations (Cant and Johnstone, 2008). Cant and Johnstone (2008) argue that the onset of menopause coincides with the age females can become grandmothers and might face reproductive competition from the younger generation, thus there is a minimal reproductive overlap between generations. Younger ancestral females tend to join the kin groups of their mates. Under such circumstances, younger females are only related to their own children and there is no genetic profit for younger females to help their mothers-in-law bear more offspring because they will not share any genes with those children. However, older females who help their sons' wives breed will benefit by passing 25% of their genes to their grandchildren. Therefore, the best strategy for older women might be to stop breeding, avoid competition and allow the younger women to breed and help them with their parental care (Cant and Johnstone, 2008; Johnstone and Cant, 2010). Cant and Johnstone (2008) supported this view with a mathematical model. In addition, they proposed that because menopause reflects “the ghost of reproductive competitions past”, there will be a cost to both daughters and daughters-in-law of breeding alongside a reproductive grandmother. A recent study claims to support the RCH by studying the effect of

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reproductive competition on child survival and fertility (Mace and Alvergne, 2012). This is despite the fact that the evolution of menopause should be manifested in long term reproduction (e.g. grandchildren) (Williams, 1957). Thus, there is a lack of a rigorous test of the RCH. The main prediction of this hypothesis (RCH) is that there should be fitness costs to both 1) the younger generation (daughters and daughters-in-law) and 2) older females who co-breed.

The aim of this study was to provide the first comprehensive test of the predictions outlined above using a four-generational life-history dataset of historical Norwegians. We had information on whether or not females of the younger generation were living in the same household (or in close vicinity) with females of older generation (Berg, 1981; Haukdal, 1971). We first examined the effect of this reproductive overlap between generations on both P and F1 females (where P is the parental generation and F1 is the first filial generation) using fitness correlates (number of children born, number of adult and married children and number of grandchildren) while controlling for a large number of confounding effects. These effects included socioeconomic status, relatedness asymmetry between P and F1 females, age difference between wife and husband, ecological differences, temporal differences in living conditions (birth cohort) and individual phenotypic quality (captured as age at first reproduction and death) (Van de Pol and Verhulst, 2006).

2. Material and methods

2.1. Demographic data

The data are of high quality and were collected from local history books (Berg, 1981; Haukdal, 1971) based on primary sources, such as church registers, local tax lists, land registers, population censuses, and electoral registers from two geographically distinct areas. One of these locations was coastal (Smøla, 63° N, 8° E, 275 km^2) and one was mainland (Soknedal, 63° N, 10° E, 435 km^2). The two areas are located 100 km apart at the same latitude (63° N) and have similar climates (Nordli and Grimenes, 2004; Nordli et al., 2003). From the records, we first compiled life-long marriage and reproductive details of 160 randomly selected P females (born 1676–1840). We also recorded full life-history data for those offspring (daughters: $n = 49$; sons: $n = 111$) born to them who married and produced the first grandchild. For those of the offspring who were sons, we collected data on their wives (females of the F1 generation born 1704–1876). We also classified families and their members as of either high or low status according to whether they were landowners. Thus, we were able to control for both ecology and access to resources (such as food), which was previously found to be important to fitness-related life-history traits in these populations (Røskaft et al., 1992; Skjærvø et al., 2011). Because our first aim was to investigate whether it is a reproductive competition between generations, we included information on cohabitation and reproductive overlap. The term ‘cohabit’ is when P and F1 females (both daughters and daughters-in-law) are living in the same household or in close vicinity to each other, and ‘no cohabit’ is when they do not live in the same household or in close vicinity to one another. Reproductive overlap (henceforward termed as ‘overlap’) is when P females are still reproductive during the time that F1 females start to reproduce, and ‘no overlap’ is when P females have ceased reproduction when F1 females started to reproduce. Thus, both overlap and no overlap are proxies for P females' reproductive behaviour (reproductive or ceased reproduction, respectively). We defined reproductive overlap as when P females had offspring younger than 15 years at the time the F1 females first started to reproduce. We chose these definitions because it has been shown that offspring are dependent on their mother for sustenance up to 15 years (Sear and Mace, 2008; Yusuf and Atrash, 2010); therefore, women can be regarded as reproductive up to 15 years after their last delivery. Consequently, older females were grouped into four breeding categories: 1) cohabit and overlap, 2) cohabit and no overlap, 3) no cohabit and overlap and 4) no cohabit and no overlap.

To test the first prediction of the RCH, we investigated both the main and interaction influences of cohabit and overlap on the fitness correlates of P females. Importantly, the interaction of cohabit and overlap was the measurement of co-breeding from the point of view of P females. The duration of co-breeding was on average 8.8 years ($SD = 3.2$; range 5–18). To determine the predicted fitness costs to F1 females, they were grouped into three breeding categories: 1) co-breeding (F1 cohabit with an overlapping P); 2) no co-breeding (F1 cohabit with a non-overlapping P); and 3) no cohabit (F1 not cohabit with P, regardless of whether P was ‘overlap’ or ‘no overlap’). The latter group serves as a control group because no F1 cohabits with P females. This allowed us to investigate the possibility that the results are a consequence of factors other than co-breeding.

Previous studies have shown that post-reproductive females (grandmothers) have a positive effect on the survival of their grandchildren (when they are between two and 15 years of age) and that the benefits start to diminish when grandmothers are over 60 years of age (Lahdenpera et al., 2004). Because we wanted to capture the potential fitness effects of a cohabit grandmother, we only included women in the P generation who reached an age of at least 60 years (mean 78.4 years, $SD = 9.2$ years). We noted the potential problem that females vary in inherent phenotypic quality, which results in superior individuals systematically having different values for life history variables than individuals of lower quality. To avoid such confounding effects, we controlled for any inherent differences in phenotypic quality, which is suggested to be captured by variation in the ages of first reproduction and lifespan (Van de Pol and Verhulst, 2006). It should also be noted that we collected data on the age difference between spouses that were previously found to be important to the reproductive success of both sexes (Røskaft et al., 1992). The study period ended before industrialism and improved health care had an impact on survival and family size (Coale and Watkins, 1986; Low and Clarke, 1992). In general, the northern climate limits farming in Norway, and the standards of living were low. Both men and women married late (29.5 and 27.3 years respectively), and the mating system was monogamous, with practically no divorce. Finally, communities in both areas practised primogeniture (Røskaft et al., 1992), and the pattern of dispersal was highly female-biased because females were more likely to disperse to their spouse's place of origin than were men (Anonymous, 1865; Sogner, 1979). The life-history variables recorded were the number of children born, number of adult children (reaching the age of 20 years), reproductive period, number of children married, number of grandchildren, age of mother when the first and the last child were born, age of mother at death and age of the husband. Table 1 presents descriptive statistics of life-history traits, including the number of grandchildren.

2.2. Statistical analysis

We analysed the effects of the breeding categories described above on fitness correlates such as the number of children born, number of adult children, number of married children and number of grandchildren of both F1 and P females. We used general linear models in which the fitness correlates were fitted as the response terms to a normal error structure. The main fixed effects were the breeding categories. Residuals of all GLMs were normally distributed, and the variances were homogeneous (Levene's test, $P > 0.05$). Where appropriate, we controlled for the confounding effects of socioeconomic status, relatedness asymmetry between P and F1 females, ecological differences and temporal differences in living conditions (birth cohort) and inherent phenotypic quality (age at first reproduction and age at death). All tests are two-tailed unless otherwise stated.

Table 1
Descriptive statistics for life-history variables according to the group of women studied.

	Females of the P generation				Females of the F1 generation		
	Cohabit		No cohabit		Cohabit		No cohabit
	Overlap	No overlap	Overlap	No overlap	Overlap	No overlap	
	Mean ± SD n						
Age of first reproduction[a]	24.3 ± 4.0 52	28.5 ± 5.8 73	25.3 ± 3.5 14	28.8 ± 9.0 21	25.6 ± 4.8 52	26.3 ± 4.8 73	26.4 ± 4.8 35
No. of children born	7.4 ± 2.6 52	4.6 ± 2.6 73	6.6 ± 1.8 14	5.3 ± 2.2 21	6.0 ± 2.8 52	5.4 ± 3.0 73	5.4 ± 3.0 35
Birth interval[b]	30 ± 15 52	29 ± 15 73	35 ± 15 14	32 ± 15 21	40 ± 23 52	38 ± 17 73	38 ± 17 35
Age of last reproduction[a]	42.2 ± 3.8 52	39.4 ± 6.8 73	43.5 ± 1.9 14	42.3 ± 3.4 21	40.0 ± 6.2 52	39.1 ± 7.0 73	39.4 ± 5.3 35
Reproductive period	18.1 ± 4.4 52	11.2 ± 6.1 73	18.6 ± 3.7 14	13.8 ± 5.6 21	14.7 ± 6.9 46	13.67 ± 6.2 73	12.2 ± 5.6 35
No. of adult children	5.6 ± 2.1 52	3.9 ± 2.0 73	5.4 ± 1.5 14	3.9 ± 2.0 21	4.9 ± 2.4 52	4.1 ± 2.2 73	4.2 ± 2.0 35
Survival of children	0.77 ± 0.17 52	0.87 ± 0.17 73	0.84 ± 0.19 14	0.75 ± 0.24 21	0.83 ± 0.17 52	0.77 ± 0.22 73	0.84 ± 0.21 35
No. of children married	4.2 ± 1.9 52	3.0 ± 1.9 73	4.3 ± 1.9 14	2.5 ± 1.9 21	4.1 ± 2.3 46	3.1 ± 2.0 68	3.2 ± 1.7 35
Age of becoming a grandmother	50.3 ± 5.1 52	60.3 ± 5.0 73	49.3 ± 7.2 14	62.1 ± 7.4 21			
No. of grandchildren	22.8 ± 9.1 52	13.2 ± 8.0 73	18.7 ± 7.2 14	13.9 ± 7.4 21	19.4 ± 11.0 46	14.6 ± 8.9 68	14.8 ± 8.4 35
Age of death[a]	77.8 ± 9.1 52	79.5 ± 9.2 73	74.5 ± 10.2 14	78.7 ± 8.4 21	74.7 ± 13.9 52	75.2 ± 13.5 73	73.7 ± 12.3 35

Values are in: [a]years and [b]months.

All data analyses were performed in SPSS for Windows (SPSS Inc.) version 17.0.

3. Results

3.1. Effects of co-breeding on fitness correlates of younger (F1) females

We found no indication that co-breeding with P females incurred fitness-related costs to F1 females in these populations. First, women of the F1 generation gave birth to 5.9 children on average (range 1–11; SD = 2.5). Status, age at first reproduction and lifespan significantly influenced fertility (electronic Supplementary material, Table S1). After controlling for such effects, we found no evidence that the breeding category influenced the number of children born (GLM: $F_{1,\ 150} = 0.77$, P = 0.465). Second, on average, 81% (range 0–100; SD = 21%) of the offspring of the F1 generation survived (up to 20 years). Neither breeding category nor any of the covariates affected the children's survival (Full GLM: $F_{9,\ 150} = 0.76$, P = 0.656; electronic Supplementary material, Table S2). Third, the mean number of children who later married was 3.5 (range 1–10; SD = 2.1) and was greater among high-status women (those who started to reproduce early and were paternal grandmothers) (electronic Supplementary material, Table S3). After controlling for the confounding variables above, we still found an effect of breeding category (GLM: $F_{1,\ 139} = 2.40$, P = 0.026) on the number of married children. Females of the first generation that co-bred with P females had 0.9 more married children than those who either cohabited with post-reproductive P females or did not cohabit with P females (electronic Supplementary material, Table S3). Finally, the mean number of grandchildren was 17.3 (range 0–44; SD = 9.9) and increased with both socio-economic status and life span and decreased with the age of first reproduction (Table 2). After accounting for such effects, the grand-offspring number of the F1s was highly affected by breeding category (GLM: $F_{1,\ 139} = 3.09$, P = 0.048; Table 2). F1 females co-breeding with the older generation had more grandchildren as compared to both F1 females who cohabited with post-reproductive P females and those that did not cohabit with P females (Fig. 1).

3.2. Effects of overlap, cohabitation and their interaction on fitness correlates of older (P) females

P females, on average, gave birth to 5.8 children (range 1–12; SD = 2.7). The fertility was higher among wealthier females who started to reproduce earlier, were paternal grandmothers to F1 females' offspring and had longer lifespans (electronic Supplementary material, Table S1). After controlling for these factors, we found an effect of reproductive overlap (GLM: $F_{1,\ 150} = 14.62$, P = 0.000) but no effect of co-breeding (GLM: $F_{1,\ 150} = 1.44$, P = 0.233) on the number of children born to P females. The average survival rate of offspring

Table 2
Factors explaining the variation in number of grandchildren of the women studied.

	Females of the P1 generation			Females of the F1 generation		
	F	η^2	P	F	η^2	P
Model	15.98	0.519	0.000	5.65	0.337	0.000
Status[a]	47.87	0.244	0.000	6.42	0.060	0.013
Area[b]	22.56	0.003	0.475	1.13	0.012	0.273
AFR	9.22	0.059	0.003	12.30	0.144	0.000
Age at death	−0.002	0.040	0.015	7.65	0.060	0.006
Age difference of spouses	1.27	0.008	0.262	1.55	0.020	0.161
Birth cohort	0.04	0.000	0.850	2.12	0.026	0.108
Overlap	14.23	0.088	0.000			
Cohabit	1.10	0.007	0.296			
Co-breeding (overlap × cohabit)	2.36	0.016	0.127	3.09	0.058	0.048

General linear model analysis, F and Partial eta squared for variables explaining the number of grandchildren born. See the text for a description of the variables.

[a] Low = reference.

[b] Unstable Resource Access = reference.

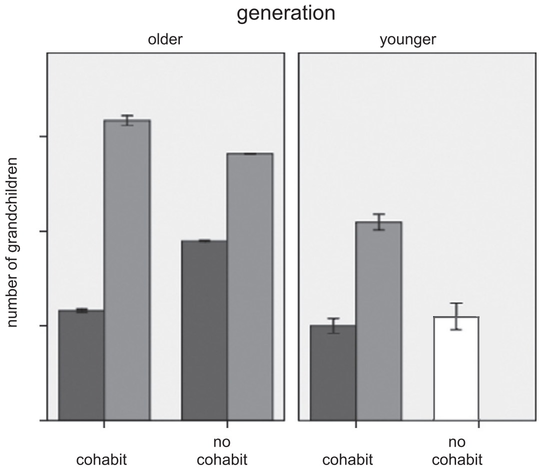

Fig. 1. Effects of reproductive overlap and cohabit on number of grandchildren for females of two generations (older (P) and younger (F1)). We found no evidence to suggest that co-breeding (reproductive overlap × cohabit) had any negative fitness consequences for females of either generation. Co-breeding was associated with higher number of grandchildren of both generations. Dark bars indicate no reproductive overlap: P females had finished their reproduction at the time when the F1 females started to reproduce. Pale bars represent reproductive overlap: P females had offspring younger than 15 years at the time when the F1 female started to reproduce. The white bar represents the control group for F1 females not cohabiting with P. Results are shown as predicted mean ± 1 s.e. from the GLM after controlling for confounding effects illustrated in Table 2.

was 81% (range 0–100; SD = 19%) and varied across cohorts. After controlling for the year P women were born in, we did not find a main effect of either cohabit or overlap (electronic Supplementary material, Table S2). However, we found an interaction effect between these variables on the survival rate of children (GLM: $F_{1,\ 150} = 0.76$, $P = 0.011$). Among P females who lived (cohabit) with F1 females, overlapping P females had lower offspring survival relative to those who did not overlap (77 vs. 87%). Conversely, P females who did not cohabit had higher child survival rates than those who overlapped (87 vs. 77%). The mean number of the children who married was 3.5 (range 3–9; SD = 1.8) and was greater among females from wealthy social classes as well as those who started to reproduce early in life and were paternal grandmothers (electronic Supplementary material, Table S3). After controlling for significant effects of these variables, we still found that the number of children who married was modified by overlap (GLM: $F_{1,\ 150} = 1.68$, $P = 0.000$), and this was not affected by cohabit factor or the overlap × cohabit interaction (electronic Supplementary material, Table S3). P females that overlapped with F1 females had 0.9 more married children than those who did not overlap with the younger generation. Finally, the mean number of grandchildren in all groups was 16.9 (range 2–44; SD = 9.3). Social status, age at first reproduction and lifespan all had significant effects on the number of grandchildren of P females (Table 2). After controlling for these effects, the number of grandchildren of P females was greatly affected by reproductive overlap (GLM: $F_{1,\ 150} = 14.23$, $P = 0.000$; Table 2). P females that had a reproductive overlap with the younger generation had more grandchildren than those who did not overlap, regardless of cohabitation status (Fig. 1).

4. Discussion

The Reproductive Conflict Hypothesis predicts that menopause evolves when reproductive conflict between generations has significant negative fitness consequences to females of both the younger (F1) and older (P) generations (Cant and Johnstone, 2008). None of these predictions are supported by the results of this analysis, which used a multigenerational life-history dataset from pre-industrial Norway. We found no evidence to suggest that co-breeding had any negative fitness consequences for women of either generation. Younger females breeding with reproductive P females had a higher number of grandchildren than those who bred with post-reproductive P females. Although we found that child survival was higher among older females who co-bred with younger females (Mace and Alvergne, 2012), we found no evidence to suggest that co-breeding has negative long-term consequences on the number of grandchildren. Thus, co-breeding is not associated with any fitness costs to either of the generations. However, younger females seem to experience some fitness benefits of co-breeding. We also analysed a number of underlying life-history traits that might explain the variation in fitness. Compared with the non-overlapping P females, we found that females of the older generation that had reproductive overlap with the younger generation, regardless of whether they were cohabiting, had lower age of first reproduction. Low age of first reproduction indicates that these females were probably of high quality (see: Lahdenpera et al., 2011a; Nussey et al., 2008; Skjærvø et al., 2009; Van de Pol and Verhulst, 2006). The present study provides the first critical test of the Reproductive Conflict Hypothesis, and based on our results, we consider it unlikely that reproductive conflict between generations can explain menopause in human females in these populations.

In contrast with the predictions of the RCH (Cant and Johnstone, 2008), our results indicate that younger females who were co-breeding with older females experienced fitness benefits. Two different forms of helping behaviour of the older females could explain our results, although we find them both unlikely. First, the "Grandmother Hypothesis" (GH) states that post-reproductive females actively enhance the fitness of their own offspring (Hawkes et al., 1997; Lahdenpera et al., 2004; reviewed in Sear and Mace, 2008). The GH predicts that cohabit P females increase their inclusive fitness by assisting their daughters or daughters-in-law in childcare after they have finished rearing their own offspring. The GH does not explain the evolution of menopause but it more directly addresses why women continue to live past menopause (Cant and Johnstone, 2008). Second, P females may be more prone to helping their own offspring with reproduction when the cost of helping is low, such as when they are reproductively active themselves (Pusey and Packer, 1994). This hypothesis was supported by another study showing that reproductive female lions (*Panthera leo*) increased the survival of their grand-offspring only when they were breeding themselves (Packer et al., 1998). However, both methods of assistance only had short-term benefits because these females did not have significantly more grandchildren as compared to those who were not living with their own grandchildren. Instead, we suggest that copying behaviour among younger females may partly explain our results. Individuals often face decisions that have consequences on fitness. To make the best choice, a person can use public information (copying) by monitoring how conspecifics interact with each other or the environment (for review, see Danchin et al., 2004). The use of public information can be based on cues that other individuals provide when engaged in their normal activities (e.g., rearing children). The benefit of copying may be that individuals can assess the quality of a resource faster and more accurately and, hence, enhance their own fitness without investing in costly direct information gathering (Boyd et al., 2011; Rendell et al., 2010). This result is also experimentally supported (Fletcher and Miller, 2008; Kameda and Nakanishi, 2003). Based on this, we argue that co-breeding F1 females had enhanced fitness because they copied the behaviour of P females, who are experienced, high-quality reproductive females of the older generation. Therefore, this copying behaviour made them better mothers. The adaptation is to copy an older and more experienced female in the way she raises her child.

The RHC and the adaptive theory have troubling features. The first aspect of the RHC is the assumption that the decline in follicle number (atresia) has a marked increase (biphasic model) in women as they reach the age of 38 years (Faddy et al., 1992). However, growing literature show that there probably is no abrupt decline in atresia

(Chang et al., 1998; La Marca et al., 2011; Leidy et al., 1998; Ng et al., 2003; Rosen et al., 2010a; Rosen et al., 2010b; Ruess et al., 1996). The age-dependent loss of fertility is due to the decline in both quality and quantity of ovarian follicles (Velde and Pearson, 2002). Several statistical models have been developed to describe the pattern of human ovarian follicle loss (Coxworth and Hawkes, 2010), and the most cited is the biphasic model (Faddy et al., 1992). This model suggests that the decline in follicle number has a marked increase in women as they reach the age of 38 years (Faddy et al., 1992). This increase might indicate an evolutionary shift to earlier menopause. Cant and Johnstone (2008) used this inference to support the RCH because it may coincide with the age at which ancestral human females first experienced reproductive competition from the younger generation. However, several authors, even the inventor of the biphasic model (Faddy and Gosden, 1996), propose that follicular atresia rates do not accelerate in the above-described manner (Chang et al., 1998; La Marca et al., 2011; Leidy et al., 1998; Ng et al., 2003; Rosen et al., 2010a; Rosen et al., 2010b; Ruess et al., 1996) and that there is nothing special about the decline in fertility in humans (Coxworth and Hawkes, 2010; Finch and Holmes, 2010; Hawkes and Smith, 2010; La Marca et al., 2011; Leidy et al., 1998).

The second aspect of the adaptive theory suggests an abrupt decline in human fertility. In this theory, reproductive cessation increases inclusive fitness more than continued reproduction. Pavard et al. (2008) suggested that this may be caused by an age-related decline in offspring quality that undermines the fitness contribution of later-born children (Pavard et al., 2008). Therefore, one prediction from this hypothesis is that the maternal age at delivery is negatively correlated with subsequent offspring fertility, with an abrupt decline in fitness above a maternal age of 38 years (Cant and Johnstone, 2008). However, we found that performing two multiple linear regressions with maternal age and the conditions of 1) lower than 38 years and 2) higher than 38 years, using available data on maternal ages at delivery and offspring subsequent fitness (number of adult children), the slopes did not differ (Regression 1. $\beta = -0.116$, $P = 0.001$, $n = 1273$; Regression 2. $\beta = -0.025$, $P = 0.627$, $n = 373$). We controlled for the females' birth year, status, family size, and sex of offspring in both regressions. Thus, we did not find any evidence to suggest that menopause is adaptive in response to an abrupt decline in fitness after a maternal age of 38 years. Instead, this indicates a monotone decline in fertility throughout the reproductive period and that the deterioration in fertility and menopause can be understood in the light of ageing in general. The non-adaptive view of menopause is the idea that menopause is a recent epiphenomenon of our increased lifespan. Evolutionary theories of ageing suggest that fitness-related traits, including fertility, will senesce because the strength of selection declines with age (Hamilton, 1966; Williams, 1957) and the difference between menopause and the female lifespan would be approximately equal to the time necessary for a female to raise her last offspring (Packer et al., 1998). Menopause becomes a by-product of this process (Pavard et al., 2008; Peccei, 2001b). Further, menopause is more evident when selection acts to increase longevity, increasing the difference between the lifespans of the reproductive and somatic systems (Austad, 1994; Finch and Holmes, 2010; Hawkes and Smith, 2010; Peccei, 2001a; van Bodegom et al., 2010).

A third aspect of the adaptive theories of menopause is longevity (number of individuals surviving to older adulthood), which relies on the assumption that humans have lived sufficiently long to commonly exhibit menopause during our evolutionary past. New Palaeodemographic data refute this assumption and indicate that few individuals lived long enough (Acsádi and Nemeskéri, 1970; Austad, 1994; Smith et al., 2010; Trinkaus, 2011) to undergo menopause and that older individuals became frequent only in modern human societies (Caspari and Lee, 2004; Hill et al., 2007; Peccei, 2001a). In addition, several adaptive studies have used populations of modern hunter-gatherers (Gurven and Kaplan, 2007). However, these studies may not satisfy the assumption because observed data on longevity on modern hunter-gatherers may not (Hill et al., 2007) represent Palaeolithic human longevity.

A fourth aspect of the adaptive theory suggests that menopause is unique to primate life history (e.g. Peccei, 1995). However, menopause (Hodgen et al., 1977; Pavelka and Fedigan, 1991) and survival after the end of reproduction (Cohen, 2004; Packer et al., 1998) in nonhuman primates seem to be widespread in mammals in the wild as well as in mammals in captivity (Packer et al., 1998). The post-reproductive lifespan in animals other than humans is shorter, except in killer whales (*Orcinus orca*) and short-finned pilot whales (*Globicephala macrorhynchus*). They have been reported to experience full reproductive cessation and post-reproductive lifespans that can be longer than in humans (Foote, 2008; Ward et al., 2009).

Some of the limitations of our study include the family structure of our populations and the lack of data from more than two communities. In addition, there was a strong correlation between 1) paternal grandmothers and high status (i.e., paternal grandmothers were most likely of high status) and 2) long reproductive periods and overlapping reproductive periods (i.e., women of the older generation with longer reproductive periods had higher change of having overlapping reproductive periods with the younger generation); therefore, we cannot distinguish between the effects of these correlating variables on variation in fitness. There are some difficulties with testing the evolution of menopause, because it is impossible to test the predictions of the RCH in the context in which it evolved. However, these problems are alleviated in this study, because it is conducted on a population before the demographic transition (Coale and Watkins, 1986), without access to medical care and where life in general was very harsh (Haukdal, 1971). Although child mortality was quite low, the Norwegian population had a life-expectancy (which is the average of the age of mortality) at birth between 35 and 40 years (Drake, 1969) which is in line with modern hunter gatherers (Gurven and Kaplan, 2007). Future studies on the evolution on menopause should focus on explanations with a combination of factors (Shanley and Kirkwood, 2001; Shanley et al., 2007) and communities with family structure other than monogamy, because the family structure in our evolutionary past was polygynous consisting of several kin-members (van Bodegom et al., 2010). The presence of grandmothers in such a setting would have been less likely to provide advantages to offspring survival, which is supported by studies from contemporary Ghana (Meij et al., 2009; van Bodegom et al., 2009).

5. Conclusions

We did not find support for the predicted fitness cost of reproductive overlap between generations among the Norwegian women in this study. Rather, reproductive overlap was associated with higher fitness in both generations. The reason for this benefit might be that grandmothers who were breeding alongside a reproductive daughter or daughter-in-law were of high quality and that younger females enhanced fitness by copying the reproductive behaviour of these high-quality females. Our findings contribute to the growing literature that uses the life history data of historical human populations to test hypotheses on the origin of menopause. Many of the apparent discrepancies in reports regarding menopause in humans may be accounted for by novel environmental and social factors (different from those of the Palaeolithic era), such as life expectancies and pair-bond strategy. Our findings suggest that menopause might be understood in the light of both ageing in general as well as our increased lifespan and that the human life history is not so unique in the animal world.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.exger.2013.02.001.

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PAPER V

Grandmother and grandfather with three grandchildren.
Photo Credit: Fotograf Schrøder, Trondheim (1986)

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Original Article

Wealth and the opportunity for sexual selection in men and women

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Sexual selection theory suggests that males benefit more than females from multiple mates and that sexual selection is weak in monogamous mating systems. However, little research on sexual selection has been conducted simultaneously in men and women, and we lack a detailed understanding of the socioecological factors that can influence it. Here, we examined the effects of wealth and sex on 2 distinct episodes of human sexual selection (marry once and remarry) in historical Norwegian populations with imposed monogamy, where remarriage was only possible after widowhood. We quantified sexual selection using the Bateman gradient. We also examined the underlying proximate factors that might influence the odds of remarriage and reproduction after widowhood. We found that the intensity of sexual selection corresponds well with Bateman gradients measured in other monogamous populations and was stronger for those who married once than for those who remarried. The selection gradients on "marry once" were affected by neither sex nor wealth. However, when we measured the gradients on "remarry," sexual selection was stronger on wealthy men and women compared with those who were poor. Remarriage age was the most important underlying factor explaining how widows increased reproductive success. For widowers, it was to remarry a younger woman than themselves. In conclusion, we show that sexual selection can operate on both sexes in a monogamous population and suggest that under certain circumstances (when very wealthy), women can benefit as much as men can by remarriage.

Key words: **Bateman, human evolution, monogamy, remarriage, sexual selection, wealth.**

INTRODUCTION

In sexually reproducing species, individuals must obtain one or more mates to reproduce (Darwin 1859). Each sex may use different strategies to optimize their reproductive success (RS) and maximize fitness. In species with conventional sex roles, females invest more than males in gametes (Wallace et al. 1996) and parental care (Trivers 1972). Because of this difference, male RS is primarily limited by access to fertile mates, whereas female RS is primarily limited by access to resources that affect fecundity; as such, RS and mating success (MS) are expected to vary more among males than among females (Bateman 1948). Consequently, sexual selection (competition for mates) is thought to act more strongly on males than on females (Bateman 1948; but see Trivers 1972; Gowaty et al. 2012). The correlation between MS and RS is the key aspect of sexual selection and is characterized by the regression slope, known as the Bateman gradient (also termed Bateman's third principle) (Arnold 1994). The slope of this gradient is an indicator of the fitness benefits gained from multiple mating, and it measures the strength of sexual selection on traits related to the competition for mates (Arnold and Duvall 1994; Andersson and Iwasa 1996; Jones 2009). Such traits may include competition for resources that directly affect the probability of acquiring or becoming a mate (Rosvall 2011). As such, socioecological factors that cause inequalities in the distribution of resources among individuals in a society can, therefore, impact the strength and direction of sexual selection (Emlen and Oring 1977).

Several empirical studies on animals have provided support for the universal expectation of sexual selection theory by measuring steeper Bateman gradients in males than in females (Andersson 1994). However, new theoretical developments (Kokko and Jennions 2008) and empirical evidence (Clutton-Brock 2007; Gerlach et al. 2012; Kvarnemo and Simmons 2013) suggest that multiple mating can also influence female RS and that females are also subject to sexual selection. Thus, the pattern predicted by Bateman's third principle is not universal. Therefore, identifying the potential socioecological factors that may contribute to the variation in the opportunity for sexual selection in both sexes is very important (Webster et al. 2007). To understand the processes of sexual selection, it is important to appropriately measure the Bateman gradient according to the selection episode considered. Many studies consider only a limited set of selection episodes and subgroups of individuals (discussed in Wade and Shulter 2004; Klug et al. 2010), potentially affecting estimates of the Bateman gradient. For

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example, excluding all nonreproducing individuals inflates estimates of the average RS and underestimates its variation, leading to underestimates of the Bateman gradient. Therefore, when comparing Bateman's third principle across populations, it is important to ensure consistency among the sample groups (Klug et al. 2010).

In humans, predictions from sexual selection theory have been tested in a variety of populations (historical, traditional, and contemporary) characterized by a range of mating systems (monogamous, polygynous, and serially monogamous), and they have received mixed support (reviewed in Brown et al. 2009; Jokela et al. 2010; Moorad et al. 2011; Courtiol et al. 2012; Pettay et al. 2014). Thus, human mating strategies are unlikely to exhibit a universal pattern (Brown et al. 2009). The majority of these studies focus solely on males in polygynous populations, excluding important data on women and precluding simultaneous comparisons of the strength of sexual selection experienced by each sex. Bateman's third principle, that is, that the gradient should be steeper in males than in females, is supported by 3 studies: one in the serial monogamous population of the contemporary United States (Jokela et al. 2010), one of a monogamous historical population of Finns (Courtiol et al. 2012), and one of a preindustrial, serially monogamous/polygynous population in Utah, USA (Moorad et al. 2011). These studies also support the prediction of sexual selection theory that the degree of polygyny influences the magnitude of sex differences in Bateman gradients (Wade and Shulter 2004). However, in a serially monogamous Pimbe population in Tanzania, women were found to exhibit a positive gradient, whereas men showed a negative gradient (Borgerhoff Mulder 2009), demonstrating that women, but not men, increased their RS through multiple mating. Little research has been conducted on the fitness benefits of multiple mating arising simultaneously in men and women, and a detailed understanding of the socioecological factors that may directly or indirectly influence MS and RS is lacking (Brown et al. 2009; but see Courtiol et al. 2012). For example, possessing resources that directly affect the probability of acquiring a mate may be an important influence on the strength of sexual selection in both males (Andersson 1994; Ahnesjo et al. 2001) and females (Rosvall 2011; Kvarnemo and Simmons 2013). Theory predicts that sexual selection is weaker in monogamous than polygamous mating systems (Wade and Shulter 2004). Empirical data indicate that the differences in the sex-specific benefits with multiple mating are small within restricted monogamous societies (Brown et al. 2009). Furthermore, monogamy is associated with low levels of extrapair paternities and, thus, low levels of multiple mating (Simmons et al. 2004; Anderson 2006). However, with the possibility of remarriage after the death of a spouse, both men and women can have multiple mates in monogamous societies. Furthermore, such serial monogamy may benefit both sexes if some men and women are in possession of resources (e.g., through inherited wealth accumulation) that can increase their probability of acquiring a mate. The main prediction of this hypothesis is that among married individuals, the Bateman gradient should be higher for rich than for poor individuals of either sex. Hence, despite the cultural constraints on mating strategies, the opportunity for sexual selection can be high in a monogamous mating system.

The aim of this article is to test this prediction. First, we examined the effects of resources (wealth) in each sex on 2 distinct episodes of selection (married once vs. married at least twice) by comparing the sex-specific Bateman gradients among different subpopulations varying in the degree of wealth accumulation. To do so, we analyzed the life-history data of men and women from 2 monogamous preindustrial societies that follow different methods of subsistence (agricultural and fishing) (see Skjærvø et al. 2011). Sexual selection in these populations includes at least 2 selection episodes: 1) marry once and 2) remarry (i.e., where men or women remarry after being widowed). To distinguish between these selection episodes, we measured the Bateman gradients in 2 different subgroups: 1) one in which both nonreproducing and reproducing individuals were included and 2) one in which only reproducing individuals were included. Within each subgroup, men and women were classified into 1 of 2 different status groups: high status (landowners whose livelihoods relied on wealth inheritance) and low status (landless individuals whose livelihoods did not rely on transmitted wealth). In general, wealth inequalities are known to be larger in agricultural societies than in fishing societies (Diamond 1992; Summers 2005). Based on this knowledge and previous life-history studies on these populations (Røskaft et al. 1992; Skjærvø et al. 2011), we assumed that 1) high-status individuals of the inland agricultural population were more wealthy than those along the coast and 2) low-status individuals were poorer in the agricultural population than in the fishing population. Consequently, our data consist of 4 categories of individuals that vary in the degree of wealth. This data set enables us to examine whether an individual's resources (wealth) could influence the degree of sexual selection. Importantly, in the study populations, men and women inherit wealth from their dead spouses and, therefore, have control over these resources when widowed (Dupaquier 1981). Hence, the rich widows and widowers from the agricultural area were the wealthiest individuals in the sample.

Second, we examined variation in RS and MS among widowers by investigating the factors that might influence 1) the odds of remarriage after widowhood in both men and women and 2) the odds of reproduction in both men and women in the second marriage.

The main strength of this study is that the life-history data include information on region (i.e., agricultural or fishing) and wealth (based on the first husband's status), allowing us to investigate how these factors enhance or constrain individual RS. Finally, the data come from societies preceding the industrialization and improvements in health care that are associated with demographic transition and changes in family size (Coale and Watkins 1986; Low and Clarke 1992).

MATERIALS AND METHODS

Study populations

We collected demographic data from history books (Haukdal 1971; Berg 1981) on 2 geographically separated Norwegian populations (Soknedal, 63°N, 10°E, 435 km^2 and Smøla, 63°N, 8°E, 275 km^2). The Smøla community was in a coastal area, where fishing was the primary livelihood (Skjærvø et al. 2011), whereas the Soknedal community was in an inland area, where most individuals were farmers (Røskaft et al. 1992). The marriage system was strictly monogamous with almost no divorce, and remarriage was only possible after widowhood; adultery was punishable by law (Berg 1981; Eliassen and Sogner 1981). The rate of extrapair paternity was likely lower than that reported in contemporary European populations (lower than 3%) (Simmons et al. 2004; Anderson 2006). Consequently, this social constraint led to low levels of multiple mating, and the only possible mating strategies was to marry or remarry when widowed. Therefore, we used an individual's number of marriages as a proxy for their MS. There were formal rules dictating the minimum period of mourning (i.e., the timespan between the death of a spouse until remarriage) in Norway: 9 months for women and 3 months for men (Dupaquier 1981). During the time under study, population densities were low (inland area: 5.0–8.6 persons/km^2; coastal area: 2.7–4.7 persons/km^2) and longevity was similar between the parishes: 68.8 (standard deviation [SD] = 15.9) years inland and 64.8 (SD = 17.0) years on the coast. In addition, emigration was higher (23%) in the agricultural area than in the fishing area (14%).

First, we classified individuals by selection episodes: 1) married once or 2) remarry. To measure the Bateman gradient for the marry once stage, we included all married and unmarried individuals in the population who reached 20 years of age. For the remarrying stage, we included individuals who had married at least once (categorized as "Married once" and "Remarried"). In total, we obtained life-history data for 2270 men (435 had never married, although 1.6% of these produced children) and 2378 women (489 of which never married) born between 1704 and 1876. We found that 592 individuals were widowed (301 men and 291 women) before the woman reached 55 years of age (see below for an explanation of this age criterion). Of these individuals, 158 women and 226 men remarried after widowhood. Ten men and 3 women married 3 times; as these individuals were so few, they were pooled into the "Married more than once" group. Second, to investigate the factors that might influence the odds of remarriage after widowhood in both men and women, widowers who remained single after the loss of a spouse were categorized as "Not remarried." Third, to explore the factors that might affect the odds of reproduction in the second marriage, we divided remarrying individuals into 2 groups: "RemarriedNoCh" (those with no children via the second marriage) and "RemarriedCh" (those with children via 2 or more partners). The presence or absence of lifelong marriage and several measures of reproduction were recorded for each married individual: 1) the age at first reproduction, 2) the age at last reproduction, 3) the number of children, 4) the reproductive period, 5) the age of each partner at the first marriage and, if applicable, at the second marriage, 6) the spouse's life span, 7) the time elapsed between widowhood and remarriage, and 8) the age difference between the spouses (calculated as the partner's age minus the focal individual's age). We used 55 years of age and under as a selection criterion for the "Remarried" group because we wanted to study the factors that affect the probability of having children in a second marriage; therefore, we selected individuals who were still of reproductive age (caring for dependent offspring). We defined women as reproductive up to the age of 55 because the average age at last birth is 40 in these populations (Skjærvø et al. 2011) and children are dependent on their mother for sustenance for up to 15 years (Sear and Mace 2008; Yusuf and Atrash 2010). The populations did not have access to medical care, and life was harsh (Haukdal 1971). Finally, we recorded the birth year of each individual to control for birth-year cohort effects in our analyses (Røskaft et al. 1992). Table 1 presents the descriptive statistics of the studied variables in the different study groups (unmarried individuals are not included).

Statistical analysis

Bateman gradients (β_{ss}) were calculated as the linear regression slopes of the relative values (dividing each individual's value by the population mean) of MS (number of marriages) and RS (number of children born) (Arnold and Duvall 1994). We use single-generation rather than multigeneration (e.g., grandchildren) measure of fitness because using the number of grandchildren may conflate traits and fitness across generations (Moorad 2013). The 2 selection episodes (married once and married more than once) were examined separately. For each selection episode, we investigated differences in the Bateman gradients among the 4 subpopulations (ranked in order of wealth, from highest to lowest: IH, inland with high status; CH, coastal with high status; CL, coastal with low status; IL, inland with low status) for each sex separately, and then we tested for sex differences within each group. We initially included birth cohort as a fixed factor in this analysis; however, as it was not statistically significant, we removed it from subsequent analysis. The gradients may be influenced by female age of remarriage (cutoff age of 55 years) because female fertility declines with age.

Table 1

Mean (±SD) for studied life-history traits by sex and marriage status

	Men					Women				
		Widowed					Widowed			
	Married once	Single	Remarried			Married once	Single	Remarried		
			All	NoCh	Ch			All	NoCh	Ch
	N = 1534	*N* = 75	*N* = 226	*N* = 78	*N* = 148	*N* = 1598	*N* = 133	*N* = 158	*N* = 60	*N* = 98
Age of first reproduction	29.8 (5.6)	30.5 (5.1)	29.5 (6.7)	28.6 (5.7)	30.1 (7.1)	27.3 (4.5)	26.6 (4.5)	25.3 (5.5)	28.1 (5.3)	26.3 (5.1)
No. of children born	4.7 (2.9)	5.3 (2.7)	5.8 (3.4)	3.7 (2.9)	6.8 (3.1)	4.7 (2.4)	4.9 (2.4)	5.6 (3.0)	4.0 (3.0)	6.6 (2.5)
Age of last reproduction	41.7 (13.2)	42.3 (7.0)	45.8 (9.8)	38.2 (8.0)	49.4 (8.3)	38.8 (5.9)	37.9 (6.0)	40.8 (5.3)	37.6 (6.3)	42.5 (4.0)
Reproductive period	11.9 (13.0)	11.8 (6.1)	16.3 (10.1)	9.6 (8.3)	19.3 (9.3)	11.5 (6.9)	11.3 (6.0)	14.5 (7.2)	9.5 (6.5)	17.2 (6.0)
Age difference in the first marriage[a]	2.0 (6.8)	4.5 (6.1)	0.5 (7.3)	0.1 (7.3)	0.6 (7.4)	−3.2 (6.9)	−2.0 (6.8)	−3.6 (8.0)	−3.6 (8.0)	−5.6 (7.3)
Age of death[a]	66.4 (16.0)	70.2 (13.8)	70.7 (12.6)	72.4 (12.0)	69.7 (12.9)	67.6 (17.3)	70.5 (14.1)	71.8 (13.)	70.7 (13.3)	72.5 (14.0)
Spouse age when dead		45.7 (6.4)	40.1 (10.7)	45.3 (10.8)	36.8 (9.3)		45.8 (8.2)	41.1 (9.9)	45.6 (9.8)	38.5 (8.8)
Timespan widowed			2.7 (3.0)	2.5 (3.0)	2.7 (3.0)			2.5 (3.0)	4.6 (4.0)	2.5 (2.0)
Age at second marriage			43.5 (8.9)	48.2 (9.3)	40.9 (7.8)			39.7 (7.8)	46.6 (6.1)	35.4 (5.3)
Age difference in the second marriage[a]			8.5 (10.4)	5.4 (11.4)	10.1 (9.1)			4.5 (10.5)	6.6 (12.7)	2.7 (8.7)

[a] The value is negative when the focal individual is younger than his/hers spouse. There were 435 and 489 unmarried men and women registered in the populations.

Therefore, we tested the robustness of these analyses against the use of 45 years of age as selection criterion for the "Remarried" group. To do this, we reanalyzed the gradients using a restricted sample that included 1) women that remarried before they had reached an age of 45 years and 2) men who remarried women younger than 45 (Supplementary Table S1).

Men and women were examined separately in the following analyses. To investigate the odds of remarriage following the death of a spouse, we used Pearson chi-square tests. Logistic regression was used to analyze the probabilities of remarriage and having additional children after widowhood. The independent variables in the remarriage model were spouse's life span, the age difference between spouses in the first marriage, status, region, and the interaction of status and region. The independent variables used in the model of having children by 2 partners were the age differences between spouses in first and second marriages, the age at the death of the spouse from first marriage, the time elapsed between widowing and remarriage, status, and area. Potential confounders, such as the age at first reproduction and the focal subject's age at death and birth cohort, were included in both models. All tests were 2-tailed unless otherwise stated. We used the statistical software program SPSS for Windows (SPSS Inc.) version 21.0.

RESULTS

Factors contributing to the probability of remarriage among widowed men and women

Supplementary Table S2 shows the results from the logistic regression modeling the probability of remarriage. Men (226/301; 75%) were significantly more likely to remarry than were women (158/291; 54%, $\chi^2 = 28.1$, degrees of freedom = 1, 592, $P < 0.000$) after widowhood. In the total population, the frequencies of being married twice were 13.6% for men and 9.7% for women. The logistic regressions revealed both similarities and differences in remarriage between the sexes. Wealthy men from both areas had the same (0.76) probability of remarrying, whereas low-status men on the coast had a lower (0.56) probability of remarrying than did those inland (0.73) (Figure 1). However, there was no significant interaction of area and status on remarrying in men. For women, on the other hand, there was a significant interactional effect of status and area on the probability of remarrying. Women from the inland community had a 0.69 probability of remarriage when they were of high status but only 0.25 when they were of low status. In contrast, the probability of remarriage in women was similar (0.49) in both status groups on the coast (Figure 1). For all women, the odds of remarriage decreased with increasing spousal age at death. Furthermore, the odds of remarriage decreased for men who were older than their first wife was and increased for women who were younger than their first husband was. For men and women who remarried, the average spousal age at death was approximately 40 years old (Table 1). Men who remarried were less than a year older than their first wife, whereas women who remarried were almost 4 years younger than their first husband (Table 1). In other words, a person's age at widowhood strongly affected their odds of remarriage. Women who remarried were 4 years younger, on average, than those that did not remarry (34 vs. 38), whereas men were 10 years younger, on average, than those who failed to remarry (40 vs. 50; these numbers were calculated by adding the spousal age of death to the age difference in the first marriage from Table 1). Both confounding variables, age at first reproduction and life span, had significant positive effects on women, whereas only life span had a positive effect on men. In both men and women, there was a weak but significant negative effect of cohort on the probability of remarriage, showing that the probability of remarriage decreased over time.

Factors contributing to the probability of having additional children in a second marriage

Of the 226 men and 158 women who remarried after widowhood, 65% and 60%, respectively, produced at least 1 child during the second marriage. There were independent effects of the spousal age at death, the age difference in the first marriage and the duration of widowhood on the probability of reproducing in a second marriage in both men and women (Supplementary Table S2). Consequently, a person's age at second marriage had a strong effect on the odds of reproducing in that marriage (Figure 2); the optimal age was 41 years in men and 35 years in women (Supplementary Table S2). The odds of having children in a second marriage also depended on the age difference in the second marriage for men, but not for women. It was, therefore, important for men, but not women, to remarry a younger spouse (younger by at least 10 years). These results were not affected by age at first reproduction, status, birth cohort, life span, or region.

Selection for marrying

The mean ± standard error (SE) of all measures of MS and RS including β_{ss} are reported in Table 2.

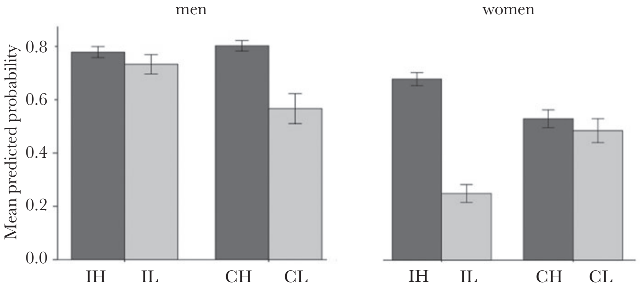

Figure 1
The predicted probability of remarriage among widowed women and widowed men according to status (dark bars for high status and gray bars for low status) and area (inland and coast): IH, inland with high status; IL, inland with low status; CH, coastal with high status; CL, coastal with low status. The probability was acquired with logistic regression presented in Supplementary Table S2.

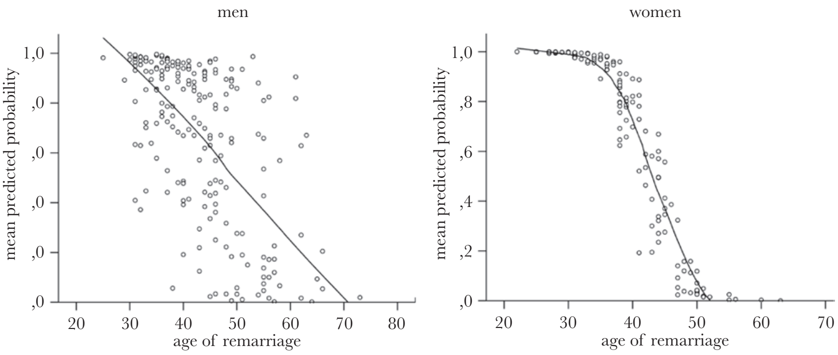

Figure 2
The predicted probability of having additional children in a second marriage for women and men in the studied populations as a function of age of remarriage. The probability was acquired with logistic regression presented in Supplementary Table S2.

Table 2

Mean ± SE of MS, RS, and Bateman gradients (βss) for men and women across the 4 wealth groups (ranked in order of wealth, from highest to lowest: IH, inland with high status; CH, coastal with high status; CL, coastal with low status; IL, inland with low status), for 2 episodes of selection

		Episode of selection											
		Married once						Remarried					
					t-Test						*t*-Test		
Wealth group	Sex	MS	RS	β_{ss}	*t*	df	*P*	MS	RS	β_{ss}	*t*	df	*P*
IH	Men	0.87 ± 0.55	4.0 ± 3.4	**0.57** ± 0.04***	−0.236	2019.1	0.814	1.12 ± 0.36	5.2 ± 3.0	**0.07** ± 0.04*	−0.016	1551.1	0.539
	Women	0.84 ± 0.53	3.9 ± 3.4	**0.61** ± 0.03***				1.10 ± 0.30	5.0 ± 3.0	**0.14** ± 0.04***			
CH	Men	0.95 ± 0.55	4.6 ± 3.3	**0.59** ± 0.04***	0.034	1115.1	0.973	1.15 ± 0.36	5.5 ± 2.8	**0.17** ± 0.05***	−0.657	920.1	0.511
	Women	0.91 ± 0.49	4.4 ± 3.2	**0.57** ± 0.05***				1.10 ± 0.30	5.3 ± 2.7	**0.09** ± 0.04**			
CL	Men	0.94 ± 0.49	3.7 ± 3.1	**0.46** ± 0.09***	−0.191	507.1	0.985	1.10 ± 0.30	4.3 ± 2.8	0.10 ± 0.09	0.035	441.1	0.972
	Women	0.97 ± 0.45	3.8 ± 2.8	**0.35** ± 0.09***				1.10 ± 0.30	4.2 ± 2.6	−0.04 ± 0.09			
IL	Men	0.93 ± 0.49	3.4 ± 2.9	**0.46** ± 0.07***	−0.281	1002.1	0.779	1.10 ± 0.33	4.0 ± 2.7	0.08 ± 0.06	−0.040	806.1	0.259
	Women	0.80 ± 0.47	2.9 ± 2.8	**0.51** ± 0.06***				1.04 ± 0.19	3.7 ± 2.4	−0.07 ± 0.06			

Bold β_{ss} values indicate gradients significantly different from 0 at *$P = 0.073$, **$P < 0.050$, and ***$P < 0.001$. *t*-Tests compare men and women β_{ss}. df, degrees of freedom.

All adult men and women were included in these analyses. The overall β_{ss} was 0.545 (SE ± 0.067), and the slopes were not different between men and women (Figure 3). The Bateman gradients were significantly positive for both sexes across all 4 subpopulations (all *P*-values < 0.0001), and the slopes of men and women did not differ significantly among the 4 subpopulations (all *P*-values > 0.843).

Selection for remarrying

We included men and women that married at least once in these analyses. The Bateman gradients were significantly positive in both high-status men and women on the coast including high-status women in the inland. High-status men in the inland had weakly positive Batman gradients that did not reach significance. In contrast, the gradients of poor men and women in both societies were not significantly different from 0. The slopes of men and women did not differ significantly among any of the 4 categories.

In the restricted data set (woman age <45 years), all female gradients were similar (Supplementary Table S1) as in the full data set. The male gradients were slightly different between the 2 data sets; the gradients of both wealthy and poor men in the inland were steeper and significantly different from 0 in the restricted sample (Supplementary Table S1). However, the gradients of men and women did not differ significantly among any of the subgroups in the restricted data set. Thus, this confirms that these results do

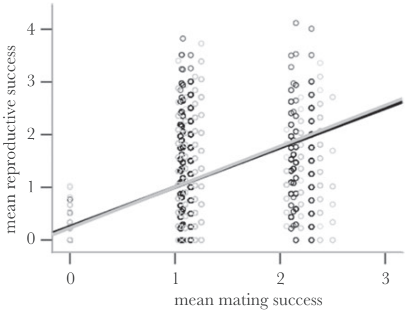

Figure 3
Bateman gradients for men (black) and women (gray) displaying the relationship between mean mating success and mean reproductive success including all individuals surviving to reproductive at a certain age (20 years). Male and female gradients almost exactly overlap.

not depend on the selection criterion (55 years) for the sample. Multiple partners significantly increased RS in landowner men (5.2 vs. 6.1) ($F_{1,1218}$ = 14.23, $P < 0.0001$) and women (5.0 vs. 6.2) ($F_{1,1244}$ = 19.59, $P < 0.0001$) including landless men (4.0 vs. 4.9) ($F_{1,608}$ = 5.41, $P = 0.020$), whereas landless women (3.9 vs. 3.5) did not increase RS with multiple partners (4.0 vs. 4.9) ($F_{1,621}$ = 6.26, $P = 0.429$).

DISCUSSION

A number of empirical studies on different animal species have provided support for the universal expectation of sexual selection theory by recording steeper Bateman gradients in males than in females (Andersson 1994). However, new theoretical developments (Kokko and Jennions 2008) and evidence (Clutton-Brock 2007; Gerlach et al. 2012; Kvarnemo and Simmons 2013) suggest that MS can also act on female RS. Thus, females, like males, are subject to sexual selection. Several authors have found that the strength of sexual selection may work simultaneously in men and women (Jokela et al. 2010; Moorad et al. 2011; Courtiol et al. 2012); however, we lack a detailed understanding of the effects of different socioecological factors that may influence sexual selection in both sexes. To date, it is not known whether different levels of wealth could be such a factor (Brown et al. 2009; Courtiol et al. 2012). We tested the effects of wealth in both sexes on 2 distinct episodes of selection (married once and remarried) by comparing sex-specific Bateman gradients between separate subpopulations varying in the degree of wealth accumulation. We found that the intensity of sexual selection in these 2 populations correspond well with Bateman gradients measured in other monogamous populations (Jokela et al. 2010; Moorad et al. 2011; Courtiol et al. 2012). The Bateman gradients were steeper when nonreproducing and reproducing individuals were included in the analyses compared with when only reproducing individuals were included. This difference was largely determined by the variation in RS between nonmarried and married individuals. Thus, the strength of sexual selection was stronger for those who married once than for those who remarried in these 2 populations, which is in line with 1 study estimating Bateman gradients on these 2 selection episodes (Courtiol et al. 2012, although they were using different terminology). Furthermore, the gradients for those individuals who married once were significantly positive for both sexes across all 4 subpopulations. The slopes for men and women were not significantly different from each other in any of the 4 subpopulations. This suggests that individuals who married once improved their RS at a similar degree independent of sex or degree of wealth in these populations. That sex did not influence Bateman gradients contradict previous studies in monogamous populations (Moorad et al. 2011; Courtiol et al. 2012) supporting the prediction derived from Bateman's third principle. We recall that it is important to measure the Bateman gradient correctly. For example, the omission of nulliparous individuals can lead to an underestimation of the gradient value (Brown et al. 2009). Thus, one explanation for the absence of differences in the "married once" gradients between the 2 sexes reported here may be that the proportion of nulliparous individuals differed between the sexes in our sample. However, this is not likely because the nulliparous fraction of men and women were quite similar (19% vs. 21%, respectively). Finally, social class did not influence our "married once" selection gradients despite the differences in the degree of wealth accumulation between the landowners and landless. Courtiol et al. (2012) reported a similar result in Finnish populations with relatively low stratification. Therefore, these findings suggest that wealth was not an important factor at first marriage due to high reproductive value (Low 2000).

We predicted that the selection gradients for individuals who remarried should be steeper for those who were rich than for the poor people, irrespective of sex. This prediction is supported by our results. The Bateman gradients for those who were remarried were all different from 0 for both men and women who were landowners (IH and CH), whereas the gradients for landless people (CL and IL) (except the gradient for IL men in the restricted sample) were not greater than 0 in both sexes. In all categories of individuals, the gradients for those who remarried (both sexes) were not significantly different from each other. These results suggest that accumulated wealth probably was an important factor for the probability of getting a new partner, ultimately influencing the strength of sexual selection on both men and women in these populations. Previous studies on preindustrial (Courtiol et al. 2012) and contemporary (Jokela et al. 2010) men and women concerning the reproductive benefits with multiple mating have supported Bateman's third principle (but see Pettay et al. 2014), that is, that the gradient should be steeper in males than in females and did not find any effect of wealth on the gradients (Courtiol et al. 2012). However, we found that when women were wealthy, they increased their number of children as much as men did by remarriage. Thus, a low degree of social stratification in Finland may be one explanation of the different results from the Finish populations (Courtiol et al. 2012). It should be noted, however, that there is another study (using preliminary data) that found a positive relationship between number of husbands and lifetime RS among economically independent women, but not men, in a horticultural population in Tanzania (Borgerhoff Mulder 2009).

A more detailed analysis demonstrated that the wealthiest widows were almost as likely to remarry as were widowers (69% vs. 76%) were. We tested for a significant interaction between status and region to determine whether the effect of status differed between the fishing and agricultural societies. Interestingly, women from the inland community had a much higher probability of remarriage if they were rich than if they were poor (0.69 vs. 0.25). In contrast, on the coast, the remarriage probability for widows was the same (0.49) between status groups. This indicates that status was more important for women in the inland agricultural area and less so in the coastal fishing area (Skjærvø et al. 2011). Thus, the differences in the accumulated wealth between rich and poor women were probably greater in the agricultural area compared with the fishing area. For men, the effect of wealth on remarriage was not so strong as for women (Forsberg and Tullberg 1995).

In addition, we found that the age at widowhood (i.e., spousal age at death plus the age difference in the first marriage) was the most important factor affecting the odds of remarriage in widows and that this probability declined rapidly after the age of 35 (Käär et al. 1998; Breschi et al. 2009; Lahdenperä et al. 2011), regardless of status, area, or resource control (status × area). The findings here converge with previous findings that have reported that it may be beneficial for women to have children with several men (Borgerhoff Mulder 2009). Further, it indicates that there might be some genotypic traits associated with female remarriage. Such traits may include a greater tendency to remarry (or divorce, in contemporary societies) in wealthy women near the age of 35. These women may have preferences for men of similar age (Waynforth and Dunbar 1995), and some men may have preferences for these women. For instance, studies show that women's preferences for men older than themselves shift with increasing resource control, and wealthier women prefer men of similar age as themselves (Eagly and Wood 1999; Moore et al. 2010). For men, the odds of remarriage first begin to decrease at an age of widowhood of 45 (Käär et al. 1998). The finding that the odds of remarriage start to decline at an earlier age in women than in men is consistent with the patterns of age-specific reproductive values for men and women (Røskaft et al. 1992), suggesting that reproductive value is important in mate choice (Low 2000).

A woman's odds of reproducing in her second marriage was highly dependent on both the age of her first spouse at death and the age difference in her first marriage, as well as the duration of widowhood. Consequently, a women's age at second marriage greatly influenced her odds of reproducing, which declined sharply after the age of 35; this pattern is consistent with the gradual decline in reproductive performance with increasing age (te Velde and Pearson 2002). A slightly different pattern was observed in men that had children with 2 partners. To reproduce successfully in the second marriage, the man's age was important, as was marrying a wife who was (on average) 10 years younger than himself. Thus, age-dependent reproduction in men was also highly dependent on the fecundity of their wives (i.e., their reproductive value), thereby producing greater reproductive variation in men than in women (Clutton-Brock 2007). At the proximate level, individuals that remarried had higher RS because they extended their reproductive period and because they replaced the dead spouse with a younger and more fertile one. The fertility of men (Crosnoe and Kim 2013) as well as women (te Velde and Pearson 2002) decrease with age. In addition, there tend to be a higher frequency of intercourse in newly formed unions (Klusmann 2002), potentially leading to higher fecundity. There are at least 2 limitations of our study. First, there was a strong correlation between long reproductive periods and having children with 2 partners; therefore, we cannot distinguish between the effect of these correlating factors and variation in fitness. It would be interesting to test if there were any remaining benefits with multipartner fertility after considering reproductive life span. Second, restricted monogamy is an important issue that needs to be considered when interpreting the findings regarding lack of differences in the sex-specific benefits with multiple mating. The present study is conducted to societies with restricted monogamy, where no alternative mating strategies (i.e., having illegitimate children or short-term mating) than remarriage after widowhood existed. Such social constraint may restrict the RS more in men than in women and may partly explain our results. Further, the paternity of illegitimate children is not known in these data. This may lead to an underestimation of male Bateman gradient values. However, the rate of extrapair paternities was most likely low and unlikely to bias our conclusion (Simmons et al. 2004; Anderson 2006).

In conclusion, we show that sexual selection can operate on both sexes in a monogamous population and indicates that under certain circumstances (a certain degree of wealth), women can benefit as much as men can by remarriage. We suggest that the large inconsistency in previous research on sex-specific benefits with multiple mating partly might arise from differences in socioecological factors and should be further investigated across and within populations.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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PAPER VI

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Solar activity at birth predicted infant survival and women's fertility in historical Norway

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Ultraviolet radiation (UVR) can suppress essential molecular and cellular mechanisms during early development in living organisms and variations in solar activity during early development may thus influence their health and reproduction. Although the ultimate consequences of UVR on aquatic organisms in early life are well known, similar studies on terrestrial vertebrates, including humans, have remained limited. Using data on temporal variation in sunspot numbers and individual-based demographic data ($N = 8662$ births) from Norway between 1676 and 1878, while controlling for maternal effects, socioeconomic status, cohort and ecology, we show that solar activity (total solar irradiance) at birth decreased the probability of survival to adulthood for both men and women. On average, the lifespans of individuals born in a solar maximum period were 5.2 years shorter, than those born in a solar minimum period. In addition, fertility and LRS were reduced among low-status women born in years with high solar activity. The proximate explanation for the relationship between solar activity and infant mortality may be an effect of folate degradation during pregnancy caused by UVR. Our results suggest that solar activity at birth may have consequences on human lifetime performance both within and between generations.

1. Introduction

Environmental factors during the early development of an organism can have downstream effects on the phenotypic quality and reproductive performance of that organism [1]. Several long-term studies on a wide variety of species [2], including humans [3–5], have revealed that the environment an organism is exposed to early in life may influence adult life-history traits, such as survival, fertility and lifetime reproductive success (LRS). Individuals may differ in their sensitivity to stressors during early development, which can be influenced by gender and life stage. First, it is generally accepted that males are more vulnerable to environmental stressors than females [6], and second, such effects may vary at different life stages, with greater vulnerability appearing during early development [6].

Exposure to high levels of ultraviolet radiation (UVR) is one such type of environmental stressor that can affect later survival and reproductive performance [7,8]. Levels of UVR vary with solar activity [9], latitude/altitude [10] and photoperiod [11]. The detrimental effects of high UVR exposure during development is unclear but may act via multiple molecular (degradation of folate and DNA damage) and cellular (membrane damage) mechanisms [10,12–14] in the developing organism. Such effects may lead to detrimental consequences later in life [15]. However, organisms can exhibit differential defences against UVR damage, including behaviour (avoidance), accumulation of photo-protective compounds (pigmentation, e.g. melanin and carotenoids) as well as cellular defence mechanisms (DNA-repair and antioxidants) [16,17], and specific genotypes [11]. Moreover, the presence of such UVR defence mechanisms is often costly and indicates that UVR represents a potential environmental factor in life-history evolution [13]. Indeed, a number of aquatic studies indicate that ambient UVR exposure during early development affects life-history traits later in life [7,8]. However, to our knowledge, such research with respect to terrestrial vertebrates is lacking (but see [18]). A few studies have focused on how periods of

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high solar activity (as a proxy for UVR) during gestation may adversely affect humans through fetal loss [19,20] and through the onset of diseases in adult life [21–23]. Furthermore, some studies have investigated how solar activity during embryonic development predicts lifespan. Whereas one study found that individuals born during years with high solar activity experienced a reduced lifespan [24], another study found there to be no effect [25]. While certain studies suggest stronger long-term effects in men than in women with respect to both lifespan and disease due to early life exposure to high UVR [9,24], no study has yet considered the effect on survival across the complete lifespan or captured changes in effects across age and gender. This approach makes it possible to identify the specific phases where selection occurs as such information would help determine the causal mechanism responsible for long-term consequences of high UVR during development. However, thus far, no human study has explored the fitness consequences of this association in terms of both survival and reproductive performance.

Herein, we use an individual-based dataset from two human populations in Norway that spans 160 years. The data include information regarding natural fertility and mortality and enable us to test the hypothesis that high solar activity during early development affects human life-history traits (survival, fertility and LRS) and that these associations are modified by gender and age. Specifically, we examine whether the solar activity at birth is (i) related to the probability of survival from birth to the age of 20 years; (ii) related to fertility, and (iii) related to reproductive success (LRS). We analyse each gender separately as UVR has been found to affect men and women differently [9,24]. In contrast to data used in previous studies, the longitudinal individual-based data enable us to control for factors known to affect survival and fitness, such as socioeconomic status, age of first reproduction and ecology [26].

2. Material and methods

(a) Study system and data collection

We used demographic data collected from Norwegian church records of two different populations in mid-Norway that included 9062 individuals born between 1676 and 1878 [26,27]. The two populations were located at similar latitudes (63°N) and experienced similar climatic conditions [28,29]. However, the Smøla population represented a coastal island population at low altitude (0 to 70 m.a.s.l), whereas the Soknedal population represented an inland population at a somewhat higher altitude (200 to 600 m.a.s.l) [30,31]. Both populations comprised two distinct socioeconomic groups and each individual belonged to either a low (poor) or high (wealthy) status group [26,27]. The chief demographic characteristics of both populations during the study period can be described as strictly monogamous where both men and women married late and experienced moderate infant mortality and natural fertility [32].

Solar activity, measured as the number of sunspots (SS) observed on the solar surface, varies in 11 years cycle with 8 years of low activity (solar minimum-SS_{min}) followed by 3 years of high activity (solar maximum-SS_{max}) [24]. The mean annual number of sunspots were downloaded from the Oceanic and Atmospheric Administration (NOAA), US Department of Commerce website (http://www.ngdc.noaa.gov/stp/SOLAR/ftpsunspotnumber). First, to capture UVR effects on early development, we divided all individuals into two groups based on whether they were born in a solar maximum or solar minimum period [9]. However, we categorized all children born between 1800 and 1825 as part of the solar minimum period as the sunspot peaks during this period were most of the time below (mean: 20.1, range (0–47.5) the mean number of sunspots for the entire study period (46.5, range: 0–154.4) [33]. This resulted in 1041 boys and 965 girls born in a solar maximum period (mean = 96.9, range: 47.7–154.4) and 3362 boys and 3294 girls born in a solar minimum period (mean = 34.0, range: 0–118.1). Second, we investigated the effects of UVR during early life on the probability of survival to adulthood (age 20). The age of each individual birth year and death year were used for calculation, because neither birth month nor death month was available. Q1

Of all the children (from both groups), 2006 (22.1%) died before the age of 20 years. Third, we analysed potential effects of solar activity during early life on adult survival and fitness by restricting our sample to individuals who survived to adulthood, got married and sired at least one child. Consequently, we excluded individuals who were either unmarried (925 individuals) or emigrated (1422 individuals). We also excluded individuals with incomplete data (1375 individuals), thus leaving full-life-history information on 1498 women and 1623 men.

We used two different measures to capture the variation in fitness: fertility (number of children born) and LRS (number of children surviving to the age of 20 years) (see electronic supplementary material, table S1, for descriptive data, including life expectancy at age 20). In all analyses, each gender was analysed separately. We controlled for confounding effects of socioeconomic status, ecology, age of first reproduction and year of birth, all of which have been found to be associated with variations in survival, fertility and LRS in these populations [26,27]. LRS may be a better estimate of fitness in these populations as high infant mortality can inflate any measure of fitness based on fertility and that LRS is a more suitable measure of fitness in this study [34].

(b) Statistical analysis

We used generalized linear mixed models (GLMM) to control for cohort effects and used year of birth as a random factor. The generalized mixed models were analysed with the statistical software R (R Core Team 2014) using the package 'lmerTest' [35]. The analyses were run separately for each gender. We always included the interaction between solar period (maximum/minimum) and socioeconomic status and the interaction between solar period and population. Non-significant interactions were sequentially excluded from the models, while significant interactions were further explored by rerunning the analyses for each group separately (i.e. low and high status, Smøla and Soknedal populations, respectively).

For the analyses of child survival rates, we fitted a binomial model of survival to the age of 20. In the survival analyses, we also included identity of the mother as a random factor in addition to year of birth to control for maternal effects. This was not possible, however, in the fitness analyses as doing so would require full information on four generations and hence diminish the sample size. Nonetheless, as including mother ID in the survival analysis only produced a minor change in the results, we assumed that it did not have a large effect in the fitness analysis. For the analyses of fertility (number of children born), we fitted the data to a Poisson distribution. For the analyses of LRS, we fitted a 'cbind' binomial GLMM with number of children born reaching the age of 20 as the nominator and number of children born *not* reaching the age of 20 as the denominator. We also analysed survival using Kaplan–Meier survival plots and Cox proportional hazard models controlling for socioeconomic status and population using the package 'survival' [36] in R.

3. Results

(a) Effects of early solar activity on child survival

Of all children, 2006 (22.1%) died before the age of 20 years. Mortality was very high (8.2% of live births) in the first year

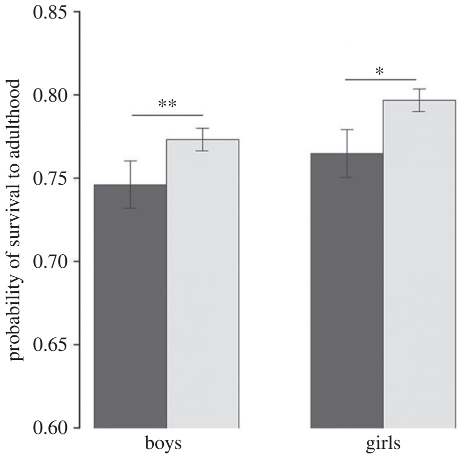

Figure 1. Probability (mean ± s.e.) of survival to adulthood in relation to solar activity for boys and girls. $^{**}p < 0.1$ and $^{*}p < 0.05$. Black bars denote SS_{max}, grey bars denote SS_{min}. Q2

Table 1. GLMM on the probability of survival to adulthood (age 20) in relation to solar activity at birth, status and population for each sex. Survival was fitted to the model using a binomial distribution. The interactions among solar activity and status and population, respectively, were not statistically significant for either sex and hence were removed from the analyses. Q4

	estimate ± s.e.	*Z*	*p*
(*a*) girls ($N = 4259$ inds, 1476 mothers, 200 years)			
intercept	1.08 ± 0.11	9.49	<0.001
SS_{min}	*0.27 ± 0.11*	*2.52*	*0.012*
$status_{low}$	−0.03 ± 0.09	−0.33	0.740
$population_{inland}$	0.21 ± 0.08	2.53	0.011
(*b*) boys ($N = 4403$ inds, 1526 mothers, 198 years)			
intercept	1.05 ± 0.11	9.19	<0.001
SS_{min}	*0.18 ± 0.10*	*1.71*	*0.087*
$status_{low}$	0.21 ± 0.10	2.15	0.032
$population_{inland}$	0.19 ± 0.09	2.11	0.035

of life and then declined in the second (3.3%) and third (1.7%) years. It then remained stable over the next 17 years (0.3–0.8%). There were no significant interactions between solar activity and status or population for either girls or boys (GLMM, results not shown). Models with main effects only revealed a strong significant effect of solar activity on survival for girls and a tendency for boys (table 1 and figure 1). Kaplan–Meier plots and Cox proportional hazard models corroborated the results in the GLMMs and showed a strong significant effect of solar activity on survival for girls and a strong tendency for boys (electronic supplementary material, table S2 and figure S1). The analyses also indicated that children from the coastal population, irrespective of sex, had lower survival probability than those from the inland population and that low-status boys had lower survival probability than high-status boys (table 1).

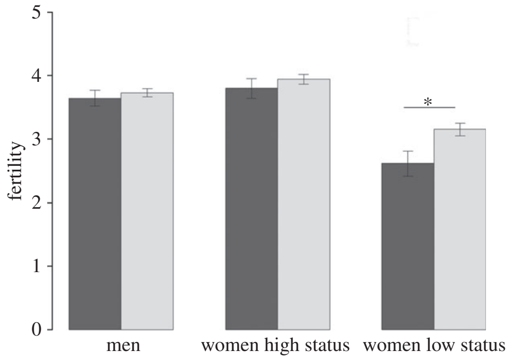

Figure 2. Fertility (mean ± s.e.) in relation to solar activity for men and for women in relation to socioeconomic status. $^{*}p < 0.05$. Black bars denote SS_{max}, grey bars denote SS_{min}.

Table 2. GLMM indicating the number of children born (fertility) in relation to solar activity at birth, status, population and age of marriage. Number of children was fitted to the model using a Poisson distribution. As there was a significant interaction between solar activity and status for women, Q4 separate models for each status group were analysed.

	estimate ± s.e.	*Z*	*p*
(*a*1) women, high-status ($N = 1222$ inds, 202 years)			
intercept	3.21 ± 0.08	41.30	<0.001
SS_{min}	0.00 ± 0.04	0.00	0.990
$population_{inland}$	0.00 ± 0.03	0.00	0.980
age of marriage	−0.06 ± 0.00	−22.00	<0.001
(*a*2) women, low-status ($N = 621$ inds, 162 years)			
intercept	3.03 ± 0.12	25.65	<0.001
SS_{min}	*0.14 ± 0.06*	*2.21*	*0.027*
$population_{inland}$	−0.01 ± 0.05	−0.16	0.871
age of marriage	−0.06 ± 0.00	−15.97	<0.001
(*b*) men ($N = 1718$ inds, 195 years)			
intercept	2.62 ± 0.07	36.40	<0.001
SS_{min}	0.03 ± 0.04	0.70	0.490
$status_{low}$	−0.20 ± 0.02	−7.90	<0.001
$population_{inland}$	0.00 ± 0.02	0.20	0.840
age of marriage	−0.03 ± 0.00	−15.20	<0.001

(b) Effects of solar activity on fertility

The mean number of children born across all women and men in the dataset was 4.8 (s.d. = 2.9, range 1–16). For women, there was a significant interaction between solar activity at birth and status (GLMM, SS × status: $F_{1,1843} = 0.13$, $p = 0.036$), but there was not a significant interaction between solar activity at birth and population ID (GLMM, SS × population: $F_{1,1843} = -0.02$, $p = 0.68$). Therefore, we reanalysed the data for each status group separately and found that high solar activity significantly reduced fertility in low-status but not high-status women (table 2 and figure 2). For men, none of the interactions were statistically significant (GLLM, SS × status: $F_{1,1718} = -0.07$,

Table 3. GLMM indicating the number of children reaching maturity (LRS) in relation to solar activity at birth, status, population and age at marriage. The data were fitted to the model using a 'cbind' binomial distribution with the number of children born reaching the age of 20 as the nominator and the number of children born *not* reaching the age of 20 as the denominator. The interactions among solar activity and status and Q4 population, respectively, were not statistically significant for either sex and hence were removed from the analyses.

	estimate ± s.e.	Z	p
(a) women ($N = 1498$ inds, 195 years)			
intercept	0.45 ± 0.18	2.50	0.013
SS_{min}	*0.16 ± 0.09*	*1.70*	*0.088*
$status_{low}$	0.01 ± 0.06	0.24	0.810
$population_{inland}$	0.60 ± 0.06	10.39	<0.001
age of marriage	0.01 ± 0.01	0.82	0.410
(b) men ($N = 1623$ inds, 194 years)			
intercept	0.50 ± 0.18	2.77	0.006
SS_{min}	0.05 ± 0.10	0.47	0.640
$status_{low}$	0.08 ± 0.061	1.25	0.210
$population_{inland}$	0.53 ± 0.057	9.34	<0.001
age of marriage	0.01 ± 0.006	1.80	0.072

$p = 0.27$; SS × population: $F_{1,1718} = 0.01$, $p = 0.49$), and the analysis of the main factors revealed no significant effect of solar activity on fertility (table 2).

(c) Effects of early solar activity on lifetime reproductive success

The mean LRS in the dataset was 3.6 (s.d. = 2.4, range 0–14) children. There were no significant interactions between solar activity at birth and status or population for either sex (data not shown). The GLMM with main effects showed a tendency for high solar activity to reduce LRS among women but not among men (table 3 and figure 3). Furthermore, while socio-economic status showed no effect on LRS, the inland population (Soknedal) had significantly higher LRS than the coastal population (Smøla). Age of marriage tended to be important in men with older age at marriage increasing LRS (table 3).

4. Discussion

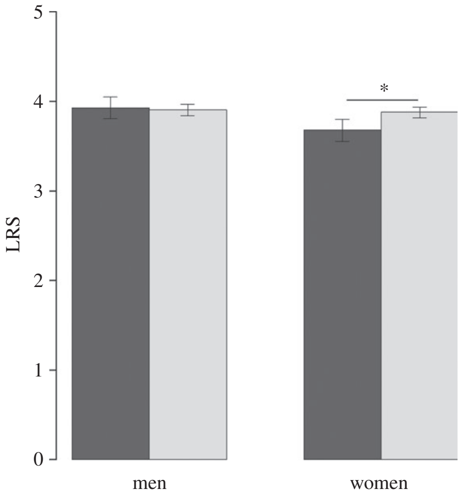

Figure 3. LRS (mean ± s.e.) in relation to solar activity for men and women. $*p < 0.1$. Black bars denote SS_{max}, grey bars denote SS_{min}. Q3

Previous studies have found that different environmental conditions experienced early in life may influence adult life-history traits [2–5]. Furthermore, solar activity during early development have been found to predict the onset of diseases later in life [21–23] that may reduce the lifespan by 1.5 years ([24], but see [25]). Such effects are most likely stronger in men [9,24] than in women. Herein, we show for the first time that not only infant survival and thus lifespan but also fertility is statistically associated with solar activity at birth in these two populations. Our findings support the hypothesis that high solar activity during early life affects subsequent survival and fitness. In addition, we tested whether these associations were modified by gender, and contrary to our predictions, the associations were stronger in females than in males.

Individuals born in years with high solar activity had a lower probability of surviving to adulthood than those born in years with low solar activity. On average, the lifespans of women and men born in a solar maximum period were 5.1 and 5.3 years shorter, respectively, than women and men born in a solar minimum period, a finding that is consistent with previous findings [24]. Importantly, we have taken this finding one step further by showing that the effect of early exposure of solar activity affects childhood survival, particularly during infancy. One proximate explanation for the relationship between solar activity and infant mortality may be an effect of folate degradation (vitamin B) caused by UVR [11,37,38]. Folate is needed for DNA synthesis and for the maintenance of the epigenome [39] and is thus essential for the development of healthy and fecund individuals during gestation [13]. Folate deficiency during pregnancy is associated with higher morbidity and mortality (reviewed in [40]), and hence, increased folate degradation in solar maximum periods could result in folate deficiency in pregnant women and, consequently, fetal loss [19,20] as well as reduced subsequent survival of children [13]. Another candidate explanation may be the selection for specific genotypes associated with folate loss and vitamin D biosynthesis at the time of conception or early pregnancy in relation to solar activity. While folate is UV labile, vitamin D biosynthesis is UV dependent. Previous studies have found that photoperiod can influence both vitamin D receptor and nuclear folate gene variants via differential embryo survival [11,19]. Importantly, the genotypes that influence embryo survival are also associated with late-life clinical phenotypes [11,19]. Thus, the selection of these vitamin D and folate-related gene variants could partly explain the association between mortality and solar activity found in this study.

Next, we tested whether solar activity at birth affected reproductive success. Our results revealed that low-status but not high-status mothers born in a solar maximum period had reduced fertility and that all mothers born in a solar maximum period had reduced LRS, although the latter did not reach statistical significance. Our findings suggest that maternal exposure to solar activity during gestation can affect the fitness of female children. The effect of socioeconomic status on the relationship between solar activity and fertility suggests that high-status pregnant women were better able to avoid the adverse effects of high solar activity. One possible explanation for this is that poor pregnant women were exposed to higher doses of UVR than rich women because low-status women were outdoor workers, while pregnant high-status women could spend more time indoors [30,31]. In addition, the quality of diet was better among the high-status women than it was for low-status women [26]. High-quality food, in contrast to low-quality food, is rich in antioxidants and carotenoids as well as coenzymes that are involved in both the protection of DNA and the reparation of damaged DNA. Consequently, individuals on a low-quality diet are expected to be more susceptible to UV-induced DNA damage [41]. However, the mechanism linking the exposure of pregnant women and DNA damage in the fetus is not entirely clear and requires further research.

A competing explanation for the relationships found in this study is that fluctuations in sunspot numbers also reflect other aspects of the environment other than the levels of UVR, such as periods with heavy workloads for pregnant women or famines, that could influence early development. These explanations, however, are not likely. First, pregnant women with heavy workloads tend to experience reduced fetal growth and abortion [42]; however, in our data, we did not find any differences in the total number of children born in the populations between SS_{max} (56.1) and SS_{min} (56.6) years. Second, the nutritional status of a pregnant women is important for the development of the fetus and the subsequent survival and reproductive success [6]. For example, infant mortality increases during years of famines [43]. However, SS_{max} years did not follow famine years in these populations [30,31]. Why, then, is the fitness of women more sensitive to high solar activity during early life than is the fitness of men? First, solar activity could differentially affect the abortion rate of male and female fetuses. If only the most robust male fetuses survive, while all female fetuses survive, male fertility could be less affected. Thus, a male-biased sex ratio at birth would reflect such a situation. However, this explanation is not likely because, in our data, the sex ratio at birth in SS_{max} years (1.08) was not significantly less male biased than in SS_{min} years (1.02) ($\chi^2 = 1.27$, d.f. $= 1$, $p = 0.26$), and the tendency is that more males are born in SS_{max} years. A more likely explanation for the observed gender differences is that the development of the reproductive organs are more costly in females than in males, and thus more at risk for developmental abnormalities when exposed to a stressor during organogenesis [44]. Concurrently, as the developmental period of the reproductive organs in the two sexes is different, testicular and ovarian organs most likely experience different hazards of in utero exposure [44] to, for example, UVR.

Our results contradict one study that did not find any reduction in the lifespan of individuals born in years of high solar activity when using a population-based dataset [25]. One reason for this discrepancy may be that the individual-based data have important advantages over population-based data. Our data allowed us to control for both socioeconomic status and ecology, factors affecting child survival in these populations [45]. Because status and ecology may conflate the effects of early life solar activity on lifespan, we avoid any probability of a type II error in our tests. Furthermore, our populations may be more susceptible to UVR damage with their high latitudinal position and less protective skin pigments. Variations in skin pigmentation (skin type) may be adaptive partly because melanized skin reduces the UVR-induced damage [13,46,47]. Natural populations at lower latitudes are thus better adapted to the detrimental effects of UVR on health and fitness. Future studies are required to test the variability/repeatability of our findings across latitudes and skin types. For example, among pregnant Caucasian females living near the equator, we might expect increased abortion rates and morbidity.

Our study also has some limitations. First, we lack exact timing of birth—those born early or late in the 3-year period of SS_{max} may not have intense UVR during the entire gestation. Furthermore, we cannot fully distinguish between pre- and postnatal exposure to UVR. Nonetheless, as the gestation period among mammals is the most vulnerable developmental stage, we assume that the effects evidenced in this study are due to high UVR during development in utero as such periods lasted for, on average, 3 years. Second, individuals who emigrated were not included, which could bias the results; however, it is unlikely that these individuals differ with respect to fertility, LRS and lifespans from those who were included in the data.

To conclude, this study is the first to emphasize the importance of UVR in early life and human life history in such populations. UVR is a global stressor with potential ecological impacts and the future levels of UVR are expected to increase due to climate change and variation in atmospheric ozone [48]. Our results are thus highly relevant and contribute to a deeper knowledge of the effects of UVR for animal life history, including human health.

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Data accessibility. The datasets supporting this article may be requested by contacting G.R.S. (gine.skjarvo@bio.ntnu.no).

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Doctoral theses in Biology
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1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
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1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
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1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
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1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient. Zoolog	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
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1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
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1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek

1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient	The sodium energy gradients in muscle cells of

		Zoology	*Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors
1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex

			(Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2

2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.

2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period

2005	Tonette Røstelien	ph.d Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	ph.d Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	ph.d Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	ph.d Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	ph.d Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor*

			- a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	ph.d Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	ph.d Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	ph.d Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	ph.d Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	ph.d Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (*Taeniopygia guttata*)
2008	Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes. - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr.Scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes

			and re-epithelialisation
2008	Tommy Jørstad	ph.d Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	ph.d Bilogy	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	ph.d Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches
2009	Zsolt Volent	ph.d Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	ph.d Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	ph.d Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	ph.d Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments -Focus on formulated diets
2010	Eli Kvingedal	ph.d Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	ph.d Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	ph.d Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. Tha Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	ph.d Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	ph.d Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	ph.d Biology	Impact of protective clothing on thermal and cognitive responses

2010	Ingerid Brænne Arbo	ph.d Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	ph.d Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	ph.d Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	ph.d Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	ph.d Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	ph.d Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	ph.d Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	ph.d Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in *Arabidopsis thaliana*
2011	Grethe Robertsen	ph.d Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	ph.d Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	ph.d Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	ph.d Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	ph.d Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	ph.d Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	ph.d Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	ph.d Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	ph.d Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	ph.d Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	ph.d Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	ph.d Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	ph.d Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	ph.d Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance

2012	Elin Noreen	ph.d Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	ph.d Biology	Theoretical and empirical approaches to studying foraging decisions: the past and future of behavioural ecology
2012	Aleksander Handå	ph.d Biology	Cultivation of mussels (*Mytilus edulis):*Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	ph.d Biology	Reproductive and migratory challenges inflicted on migrant brown trour (*Salmo trutta* L) in a heavily modified river
2012	Jisca Huisman	ph.d Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	ph.d Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	ph.d Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	ph.d Biology.	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	ph.d Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos.	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	ph.d Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	ph.d Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg Hovland	ph.d Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	ph.d Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	ph.d Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	ph.d Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	ph.d Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	ph.d Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	ph.d Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	ph.d Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	ph.d Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia

2013	Anders Foldvik	ph.d Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	ph.d Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	ph.d Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Ane Kjersti Vie	ph.d Biology	Molecular and functional characterisation of the IDA family of signalling peptides in ***Arabidopsis thaliana***
2013	Marianne Nymark	ph.d Biology	Light responses in the marine diatom ***Phaeodactylum tricornutum***
2014	Jannik Schultner	ph.d Biology	***Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird***
2014	Craig Ryan Jackson	ph.d Biology	Factors influencing African wild dog ***(Lycaon pictus***) habitat selection and ranging behaviour: conservation and management implications
2014	Michael Puffer	ph.d Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar L.*)”
2014	Gundula S. Bartzke	ph.d Biology	Effects of power lines on moose ***(Alces alces)*** habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	ph.d Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	ph.d Biology	The parasite ***Syngamus trachea*** in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	ph.d Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholipase A2
2014	Espen Lie Dahl	ph.d Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	ph.d Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	ph.d Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	ph.d Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: Calanus, little auks (alle alle) and black-legged kittiwakes (Rissa tridactyla)
2014	Kristin Møller Gabrielsen	Ph.d Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants