

## Original Article

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

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Initial receipt 29 November 2009; final revision received 5 November 2010

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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).

Published by Elsevier Inc.

**Keywords:** Human life history; Fitness; Grandchildren; Reproductive success; Diet; Social status and wealth

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**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, & Volland, 2000; Pettay, Helle, Jokela, & Lummaa, 2007; Røskft, Wara, & Viken, 1992; Volland, 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 resources 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

(Røskft 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, & Røskft, 2009). The Soknedal area (63° N, 10° E, 435 km<sup>2</sup>) 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<sup>2</sup>) 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).

#### 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

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 <sup>c</sup>	26.1±5.2	26.8±5.9	27.0±5.8	29.8±6.5
	327	140	673	368
Age of marriage <sup>a,c</sup>	25.6±4.5	26.0±5.9	26.1±4.7	28.2±5.1
	309	123	605	290
Age of first reproduction <sup>c</sup>	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 <sup>b</sup>	36±15	40±23	38±17	43±20
	324	127	576	289
Age of last reproduction <sup>c</sup>	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 <sup>c</sup>	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

<sup>a</sup> Married mothers of illegitimate first children were excluded from the data.

<sup>b</sup> Values are in months.

<sup>c</sup> Values are in years.

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 entered. 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 ( $\beta=0.81$ ) had the largest slope and appeared to be the most important predictor in the regression. The status  $\times$  area interaction ( $\beta=0.53$ ) was the second largest predictor. Area ( $\beta=0.36$ ) 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,

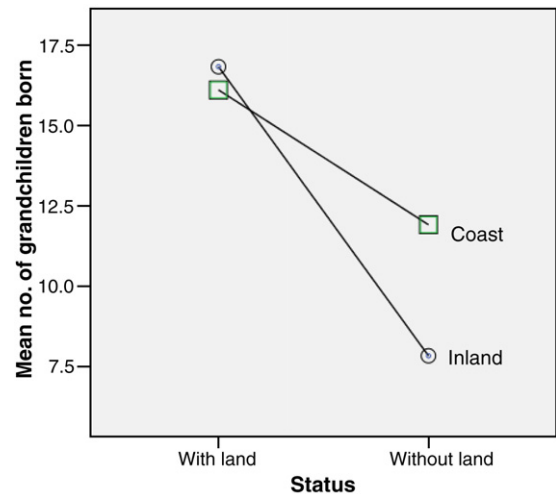


Fig. 1. Interaction between area and status in predicting number of grandchildren, when adjusting for year born.

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  $\times$  area interaction had significant effects on a female's age at marriage ( $\beta=0.29$ ), on age at first reproduction ( $\beta=0.29$ ), on the number of children born ( $\beta=0.19$ ) and on the number of her children who married ( $\beta=0.34$ ). 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).

#### 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 <sup>a</sup>		Area <sup>b</sup>		Status x area	
		$\beta$	t	$\beta$	t	$\beta$	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 <sup>c</sup>	.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.

<sup>a</sup> High=reference.<sup>b</sup> 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

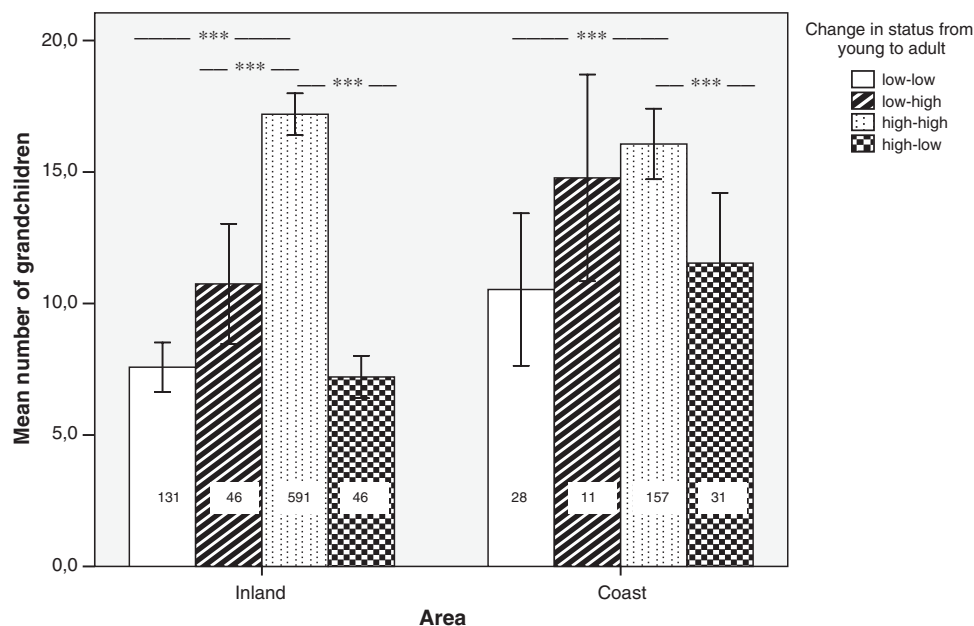


Fig. 2. Number of grandchildren ( $\pm$ S.D.) of females remaining in the low social class after marrying (low-low), females marrying upwards in the social hierarchy (low-high), females who spent their entire lives in the high-status group (high-high) and females marrying down in the social hierarchy (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  $\times$  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  $\times$  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<sup>2</sup>) than at the coast (4.6 persons/km<sup>2</sup>). 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, & Kivimäki, 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; Myerud, 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.

### Acknowledgments

We thank all the students who helped us collect data, and an anonymous reviewer for helpful comments on the manuscript.

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,

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).

we found no differences in survival rates between offspring from different status groups residing inland ( $\chi^2=0.19$ ,  $df=1$ , 5644,  $p<.1$ ). We therefore find it unlikely that individuals of low social status were underfed.

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