A tradeoff between reproduction and growth in contemporary Finnish women

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Abstract

Women have been suggested to trade growth in height for reproduction, as an earlier age at menarche and first birth seem to be related to shorter adult stature. Although women likely accrue fitness benefits by maturing and starting reproduction at young age, short adult stature may be selected against by natural and sexual selection later in their life. We studied how age at menarche and first reproduction affected adult height and whether adult height in turn was related to lifetime reproductive success in Finnish women born 1946–1958. Our results show that a delay of 1 year in age at menarche and first reproduction was related to a 0.43- and 0.20-cm increase in adult height, respectively. The sex of the first-born offspring was not related to adult height. Moreover, women gained fitness benefits by starting reproduction early but not by growing tall. These findings among Finnish women are thus compatible with tradeoffs between reproduction and growth, by showing a compromised adult height at the cost of early age at menarche and first birth. However, in these women, natural selection favored those women who traded their stature for young motherhood.
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1. Introduction

Tradeoffs between energetically costly functions of growth, reproduction, and survival are central tenets of life history theory, as they constrain the evolution of life history traits (Roff, 2002). These tradeoffs are generally expected to be mediated via the allocation of limited energetic resources because the resources allocated to one function cannot be allocated to other function(s). In humans, there is still relatively little evidence that, in women, i.e., the sex that pays the higher direct costs of reproduction, current reproductive effort impairs their future reproductive effort (Lummaa, 2001; Sear, Mace, & McGregor, 2003) or postreproductive lifespan (reviewed in Helle, Lummaa, & Jokela, 2005; Hurt, Ronsmans, & Thomas, 2006; Le Bourg, 2007).

Whether women trade their growth in height for reproduction has received considerably less attention among evolutionary biologists. In line with life history theory, the research conducted on the women of rural Gambia has found that younger age at first reproduction may be associated with shorter adult height (Allal, Sear, Prentice, & Mace, 2004; Sear, Allal, Mace, & McGregor, 2004). Furthermore, previous studies in epidemiology provide evidence that shorter adult height may also be related to earlier age at menarche (Georgiadis, 1997; Gigante, Horta, Lima, Barros, & Victora, 2006; Nettle, 2002; Okasha, McCarron, McEwen, & Smith, 2001; Onland-Moret et al., 2005) and that pregnancy in adolescent still-growing girls may impair their height gain (Gigante, Rasmussen, & Victora, 2005; Scholl & Hediger, 1993). In sum, the available data show associations compatible with the reproduction growth tradeoff in women.

But why should women sacrifice their stature for an early start of reproductive career? In humans, young age at first reproduction has shown to be strongly favoured by natural selection, as it is one of the most important components of female fitness in both historical and contemporary populations (Kirk et al., 2001; Helle et al., 2005; Pettay, Helle, Jokela, & Lummaa, 2007). However, compromising growth in height in favour of an early start of reproduction may bear

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adverse fitness consequences later in life, since taller women may accrue fitness benefits through increased offspring number and survival, higher probability of multiple births, and longer lifespan (Allal et al., 2004; Basso, Nohr, Christensen, & Olson, 2004; Kemkes-Grottenthaler, 2005; Liljestrand, Bergström, & Westman, 1985; Martorell, Delgado, Valverde, & Klein, 1981; Sear et al., 2004). However, an association between adult height and fitness in women may turn out to be rather complex and vary between populations living in diverse environmental conditions. For example, in Peru and India, short women had the highest fitness (Devi, Kumari, & Srikumari, 1985; Frisancho, Sanchez, Pallardel, & Yanez, 1973). In addition, several studies have reported the lowest offspring count for both very short and tall women (Brush, Boyce, & Harrison, 1983; Mueller, 1979; Nettle, 2002; Vetta, 1975).

The aim of this study was to examine the predicted tradeoff between reproduction and growth in women of contemporary Finland, by studying (i) whether a young age at menarche was related to shorter adult height, (ii) whether having a first birth at young age was further related to shorter adult stature, and (iii) whether adult height in turn was related to their fitness. In addition to investigating the effects of age at menarche and first birth on women's height, we also studied whether the sex of the first-born offspring was associated with adult height. A rationale for looking at the sex of the first-born offspring is that delivering a son instead of a daughter is energetically more demanding for the mother due to sons' faster intrauterine growth rate, heavier birth weight, and larger birth size (Bukowski et al., 2007; Hindmarsh, Geary, Rodeck, Kingdom, & Cole, 2002; Loos, Derom, Eeckels, Derom, & Vlietinck, 2001; Marsál et al., 1996). Therefore, delivering a son should further reduce maternal height.

2. Materials and methods

2.1. Data

Data on completed lifetime reproductive history, including age at menarche and first birth as well as lifetime reproductive success, and the self-reported adult height of women (reported to the nearest 0.5 cm) born in years 1946–1958 in Finland were collected by questionnaires during 2006. These women (n=314) are a random sample of ca. 50-, 55- and 60-year-old voluntaries that participated in Finnish national screening program of cervical cancer, ongoing since the 1960s. The relatedness of these women is unknown but must be rather negligible because these women represent a geographically diverse sample from Finland. The women studied were largely born during the "baby-boom" period that followed the end of the Second World War. After the war, Finland was in an economical depression due to war indemnities until the mid-1950s when the gross domestic product started to increase steadily (Ritamies, 2006). From the 1960s onward, when the earliest cohort of the women

studied started to reach sexual maturity, Finnish women generally practised contraceptive use available to them (e.g., 78% of the women included in this study reported that they have used contraceptives during their lifetime). Therefore, for example, age at first reproduction was determined mainly by family planning rather than by physiological factors, such as age at menarche (Ritamies, 2006). This is clearly demonstrated in these data by the low correlation between age at menarche and first reproduction (β=−0.004; 95% CI, −0.39 to 0.39).

2.2. Statistical analyses

To maximize our sample size, we analysed two separate data sets in order to investigate whether age at menarche and first reproduction were related to adult height in women. First, we investigated whether a woman's age at menarche was related to reduced adult height by considering all those women who reported these two measures (n=290), irrespective of whether they reproduced during their lifetime or not. Recalled age at menarche even decades later has been shown to correspond well with the true age at menarche, irrespective of actual age at menarche (Must et al., 2002). Second, we studied whether young age at first reproduction reduced a woman's adult height by including naturally those women who reproduced during their lifetime only (n=251). In order to examine whether delivering a son instead of a daughter was further related to female stature, this analysis also included the effect of the sex of the first-born offspring on adult height. As only four women (1.6%) reported the death of their first-born child, our estimate of early reproductive effort was unlikely biased by offspring mortality. In these analyses, a woman's birth cohort (three cohorts, see above) and birth area (South Finland, West Finland, or North Finland) were included to control for potential spatial and temporal variation in female stature. Furthermore, the number of siblings a woman had was used to control for the effects of intra-family competition for parental resources (Parker, Royle, & Hartley, 2002), as nutritional shortage should lead to a shorter adult stature (Silventoinen, 2003). No other variables describing early family conditions, such as the socioeconomic status of parents, which potentially might have affected female growth, were available for these data.

The effect of female stature on her fitness was examined by relating adult height to lifetime reproductive success (LRS, the number of offspring surviving to age 18 years), which is shown to be a good proxy of the long-term individual contribution to the future gene pool (Brommer, Gustafsson, Pietiäinen, & Merilä, 2004). Again, we analysed two data sets. First, we included all the mothers available, i.e., also those who remained childless (n=271). Second, we included ages at first and last reproduction into the analysis because reproductive timing has shown to be a major importance to female fitness (Helle et al., 2005; Kirk et al., 2001; Pettay et al., 2007). This excludes naturally the childless women from the sample, reducing our sample size

Table 1
Summary statistics of the variables studied

Trait	n	mean (±S.D.)	Min–max
Adult height (cm)	290	164.2 (±5.4)	149–177
Number of siblings	290	2.9 (±2.3)	0–13
Age at menarche (years)	290	13.2 (±1.5)	10–19
Age at first reproduction (years)	251	24.2 (±4.5)	16–43
Age at last reproduction (years)	251	29.1 (±5.1)	17–43
Lifetime reproductive success, LRS	271	1.8 (±1.0)	0–5

to 236 women. As an association between female height and reproductive success may be nonlinear (Brush et al., 1983; Mueller, 1979; Nettle, 2002; Vetta, 1975), we also included a second-order polynomial (quadratic) term of female height in these analyses. The analyses conducted also included birth cohort and birth area to control for potential spatial and temporal variation in female LRS. In addition, because the socioeconomic status of women likely affected their LRS, we also included a woman's educational level (elementary school, secondary school, or university/college degree) in the analyses. Summary statistics of the variables studied are given in Table 1.

As almost all of the data in humans, our data are purely correlative. Therefore, we did not apply traditional frequentist approach, such as stepwise model selection and excessive number of null hypothesis tests, to select a proper statistical model describing our data. Instead, we used an information theoretical approach, which avoids a large number of probability tests and enables a firm theory-based quantitative evaluation of the relative support of competing models (Burnham & Anderson, 2002). This approach is based on Akaike's information criteria (AIC) and its derived measures, Akaike weights (w_i, indicating the probability that the model is the best one from the set of models considered) and evidence ratios (the ratio of w_i of the best model to the w_i of the subsequent models), to rank and select the most appropriate model(s) representing the patterns in the data (Burnham & Anderson, 2002). The second-order AIC (AIC$_c$) was used here because the ratio of sample size to the number of parameters estimated in global models (i.e., saturated models including all the predictors considered) exceeded 40 (Burnham & Anderson, 2002). The best model of the set of models considered is the one with the lowest AIC$_c$ value. However, the models having an AIC$_c$ value within two AIC$_c$ units from the best model are considered to be equally well supported by the data. Moreover, a particular model has substantial support over the other models, if it has w_i>0.9. If it is concluded that the data do not support a single best model, this indicates model selection uncertainty, and multimodel inference should be applied (Burnham & Anderson, 2002). This means calculating the model-averaged parameter estimates and their 95% CIs by weighting each parameter estimate obtained from the models with the corresponding Akaike weight (w_i) of the model, including the parameter of interest. If the 95% CIs of the parameter excludes zero, the variable can be regarded to have

a statistical association with the response variable. In general, it is not recommended to contrast all possible models (Burnham & Anderson, 2002). Therefore, in the case of reproduction growth tradeoff, we considered models where the variables of main interest were compared to those including also and only intrafamily resource competition and/or spatial and temporal variation in female height. In the case of adult height and LRS, the models including the variables of main interest were compared to those including also and only reproductive timing, educational level, and/or spatial and temporal variation in female LRS.

Prior to model selection, the fit of the global models was assessed by Pearson's χ^2 statistics. If the global model shows a good fit to the data, then the more parsimonious

Table 2
The results of the model selection procedure on the effects of age at menarche, age at first reproduction, the sex of the first-born offspring, number of siblings, birth cohort, and birth area on female adult height

Model	K	AIC$_c$	Δ_i	w_i	Evidence ratio
Childless women included (n=290)					
Menarche+Sibs	4	1793.2	0	0.495	2.65
Menarche+Sibs+Bcoh+Area	8	1795.1	1.9	0.187	3.11
Sibs	3	1795.5	2.3	0.159	6.85
Menarche+Bcoh+Area	7	1797.1	3.9	0.072	9.27
Sibs+Bcoh+Area	7	1797.7	4.5	0.054	22.00
Bcoh+Area	6	1799.4	6.2	0.023	43.94
Menarche	3	1800.8	7.6	0.011	
Women who reproduced (n=251)					
Menarche+Afr+Sibs	5	1553.7	0	0.332	1.63
Afr+Sibs	4	1554.7	1	0.200	2.36
Afr+Sex+Sibs	5	1555.5	1.7	0.141	8.81
Menarche+Afr+Sex+Sibs+Bcoh+Area	10	1558.1	4.4	0.038	9.03
Menarche+Afr	4	1558.1	4.4	0.037	4.44
Menarche+Afr+Bcoh+Area	8	1558.2	4.5	0.037	13.22
Afr	3	1558.9	5.2	0.025	13.27
Menarche+Afr+Sex+Bcoh+Area	9	1558.9	5.2	0.025	15.86
Menarche+Afr+Sex	5	1559.3	5.5	0.021	16.13
Afr+Sex+Sibs+Bcoh+Area	8	1559.3	5.5	0.021	16.30
Afr+Bcoh+Area	7	1559.3	5.5	0.020	17.98
Menarche+Sex+Sibs	5	1559.5	5.8	0.018	19.43
Menarche+Sibs	4	1559.7	5.9	0.017	23.56
Afr+Sex	4	1560.1	6.3	0.014	24.75
Afr+Sex+Bcoh+Area	8	1560.2	6.4	0.013	29.41
Sex+Sibs	4	1560.5	6.8	0.011	30.66
Sibs	3	1560.6	6.9	0.011	65.17
Menarche+Sex+Sibs+Bcoh+Area	9	1562.1	8.4	0.005	143.55
Sex+Sibs+Bcoh+Area	8	1563.7	9.9	0.002	145.00

The model with the lowest AIC$_c$ is given at top row of each model selection procedure. K represents the number of estimated parameters in the model (including the intercept and error term), Δ_i represents the differences in AIC$_c$ between the best and the subsequent models, and w_i represent Akaike weight. Evidence ratio gives the ratio of w_i of the best model to the w_i of the subsequent models. The goodness-of-fit test of the global models showed good fit to the data (childless women included: Pearson's χ^2_{283}=290, p=.38; women who reproduced: χ^2_{242}=251, p=.33). Models having Δ_i>10 (i.e., clearly inferior models compared to the best one) were omitted from the table. Menarche indicates age at menarche; Afr, age at first reproduction; Sex, the sex of the first-born offspring; Sibs, number of siblings; Bcoh, birth cohort; Area, birth area.

Table 3
The results of the model selection procedure on the effects of adult height, its second-order polynomial term, educational level, age at first reproduction, age at last reproduction, birth cohort, and birth area on female LRS

Model	K	AIC_c	Δ_i	w_i	Evidence ratio
Childless women included ($n=271$)					
Educ	4	791.0	0	0.546	2.71
Height+Educ	5	793.0	2.0	0.202	5.00
Height	3	794.2	3.2	0.109	7.62
Height+Height^2+Educ	6	795.0	4.0	0.072	13.82
Height+Height^2	4	796.2	5.2	0.040	37.36
Educ+Bcoh+Area	8	798.2	7.2	0.015	82.85
Bcoh+Area	6	798.8	8.8	0.007	107.03
Height+Educ+Bcoh+Area	9	800.3	9.3	0.005	
Women who reproduced ($n=236$)					
Height+Afr+Alr	5	377.8	0	0.442	1.18
Afr+Alr	4	378.1	0.3	0.375	2.87
Height+Height^2+Afr+Alr	6	379.9	2.1	0.154	23.90
Height+Height^2+Afr+Alr+Educ	8	384.2	6.4	0.018	64.58
Height+Afr+Alr+Bcoh+Area	9	386.2	8.4	0.007	192.01

The model with the lowest AIC_c is given at top row of each model selection procedure. K represents the number of estimated parameters in the model (including the intercept and error term), Δ_i represents the differences in AIC_c between the best and the subsequent models, and w_i represent Akaike weight. Evidence ratio gives the ratio of w_i of the best model to the w_i of the subsequent models. The goodness-of-fit test of the global models showed good fit to the data (childless women included: Pearson's $\chi^2_{262}=271$, $p=.64$; women who reproduced only: $\chi^2_{225}=236$, $p=.68$). Models having $\Delta_i>10$ (i.e., clearly inferior models compared to the best one) were omitted from the table. Height indicates adult height; height^2, its second-order polynomial term; Educ, educational level; Alr, age at last reproduction.

models will also fit the data (Burnham & Anderson, 2002). Residuals of the global models were normally distributed (Kolmogorov–Smirnov test, $p>.12$). Multicollinearity among predictors was assessed with variance inflation factors and tolerance values. The largest variance inflation factor was 1.38, and the lowest tolerance value 0.73, showing no problematic bias in the standard errors of regression coefficients. Analyses were conducted with general linear models in SAS version 9.1 (compmix macro was used for AIC-based model selection), using maximum likelihood estimation (SAS Institute, Cary, NC, USA).

3. Results

3.1. Model selection based on AICc

In all of the four model selection procedures conducted, no single model proved superior from the set of models evaluated. This model selection uncertainty was indicated by no model having an Akaike weight value (w_i) exceeding 0.9, or AIC_c difference (Δ_i) clearly exceeding two units from the second best model (see Tables 2 and 3). Thus, in order to take the model selection uncertainty into account in parameter estimates, the magnitude of the effect of predictors was based on model-averaged parameter estimate and its 95% CIs. If the 95% CIs do not include zero, the predictor was considered to have a statistical effect on the response.

Model-averaged parameter estimates were calculated for the effects of a woman's age at menarche and first reproduction, the sex of her first-born offspring, and the number of siblings on adult height, and for the effects of adult height and its second-order polynomial and the ages of first and last reproduction on female LRS (see below). These model-averaged parameter estimates control for the adjustments made for the effects of spatial and temporal variation on female height as well as female educational level on her LRS.
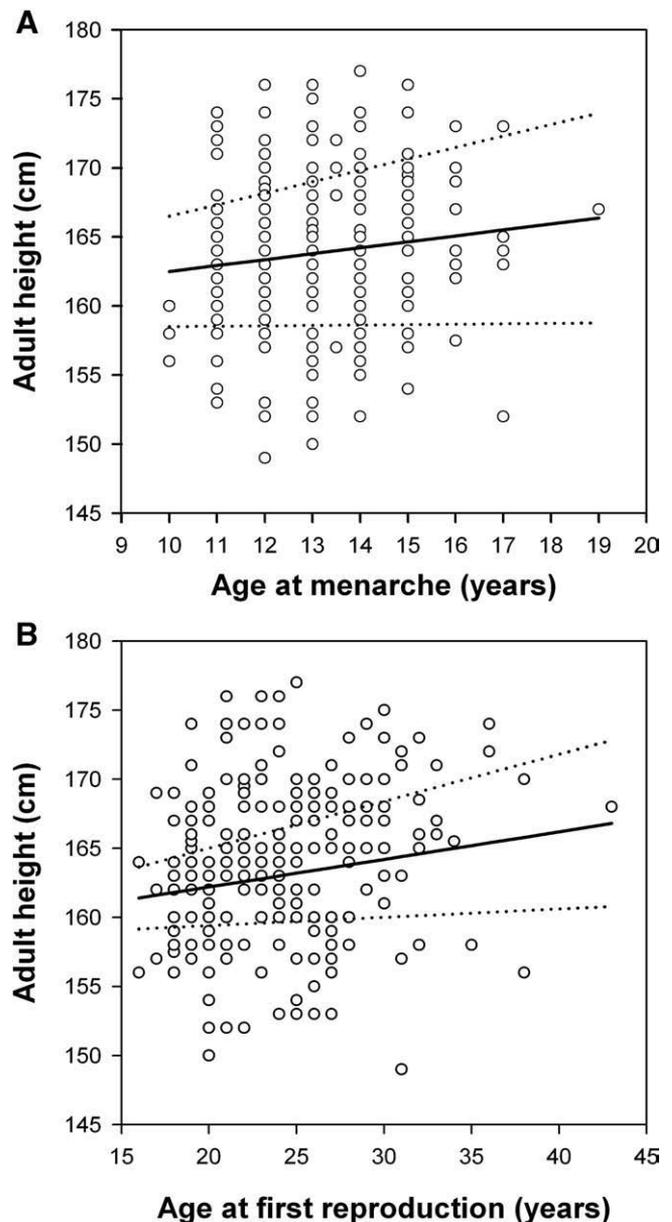

Fig. 1. The effect of a woman's age at menarche (A) and first reproduction (B) on her height at adulthood. Circles represent the original data points, solid line the model-averaged predicted linear association and dotted lines the 95% CIs of that estimate.

3.2. Age at menarche, age at first reproduction, and adult height

A delay of 1 year in age at menarche was related to a 0.43-cm (95% CI, 0.03–0.83) increase in adult height in women (Fig. 1A). The more siblings a woman had, the shorter she was as an adult. The magnitude of this effect corresponded to a 0.38 cm (95% CI, −0.09 to −0.67) reduction in adult height per one additional sibling born. Including those women who reproduced only, a delay of one year in age at first birth was related to a 0.20-cm (95% CI, 0.06–0.34) increase in adult height (Fig. 1B). Although women delivering a son instead of a daughter as their first-born were, on average, 0.25 cm (95% CI, −0.77 to 0.28) shorter as adults, this effect did not differ from zero.

3.3. Adult height, reproductive timing, and LRS

Including also childless women (i.e., those with zero LRS), adult height was not linearly (β=−0.002; 95% CI, −0.009 to 0.006) or quadratically (β=−0.0003; 95% CI, −0.0004 to 0.0004) related to LRS. Similar results were obtained when reproducing women only were included in the analysis (linear term: β=−0.005; 95% CI, −0.012 to 0.003; quadratic term: β=0.00002; 95% CI, −0.0005 to 0.0005). Moreover, those women who started reproducing early and ceased reproduction late had higher LRS. A delay of 1 year in age at first reproduction was related to a 0.12 (95% CI, −0.14 to −0.10) reduction in LRS, while postponing age at last reproduction by 1 year was related to a 0.14 (95% CI, 0.12–0.15) increase in LRS.

4. Discussion

Among the Finnish women studied, those who had an early age at menarche or first birth became shorter adults. A delay of 1 year in age at menarche and first reproduction was related to a 0.43- and 0.20-cm increase in adult height, respectively. The sex of the first-born offspring was not related to a woman's height at adulthood. Furthermore, having several siblings reduced a woman's adult height, suggesting that between-sibling competition for limited household resources might have impaired her growth. In addition, while ages at first and last reproduction were negatively and positively related to LRS, respectively, we found evidence for an association between adult height and LRS.

The finding that, in Finnish women, shorter adult height was related to an earlier age at menarche is in line with the previous results (Georgiadis, 1997; Gigante et al., 2006; Nettle, 2002; Okasha et al., 2001; Onland-Moret et al., 2005). The magnitude of this effect, on average, a 0.43-cm reduction in adult height per 1-year delay in age at menarche, is also in good accordance with previous reports from the other 20th century European women, ranging from 0.13 to 0.50 cm increase in height per 1-year delay in age at menarche (Onland-Moret et al., 2005). Life history tradeoffs

between growth and reproduction are not usually invoked to explain this association. Nevertheless, these findings are compatible with the interpretation that when women start to divert resources towards reproductive functions, fewer resources become available to somatic growth, and hence, these women are shorter as adults.

Further evidence for the reproduction growth tradeoff is provided by the finding that, in these women, young age at first reproduction was also related to shorter stature. Such an effect was found despite that these women used contraceptives, and late age at marriage with regard to age at menarche postponed their first birth, on average, into their mid twenties. This result supports the previous studies in the natural-fertility women of rural Gambia that show a tradeoff between age at first reproduction and adult height (Allal et al., 2004; Sear et al., 2004). In rural Gambia, a delay of 1 year in age at first reproduction was related to approximately a 0.33–0.41-cm increase in adult height, whereas in the contemporary Finns studied, the increase of adult height per 1-year delay in age at first reproduction was 0.20 cm only. The stronger effect of a woman's age at first birth on her adult height in rural Gambia compared to contemporary Finland is likely due to lower overall resource levels and, because of the lack of contraceptive use and an effective family planning, stronger dependence of age at first birth on age at menarche and marriage in rural Gambia. Note that neither this study nor those by Allal et al. (2004) and Sear et al. (2004) can answer the question whether the association between young age at first birth and short adult height was due to impaired or even halted growth among still-growing women or whether short women just started reproducing earlier. There is evidence that successful pregnancy among still-growing women does not end their growth (e.g., Scholl & Hediger, 1993), making perhaps the latter explanation more plausible. While there is clearly a need for more accurate individual-level data on age-specific growth rate and reproduction in women to answer this question, both of these scenarios are compatible with the life history tradeoff between reproduction and growth.

Although age at menarche and first birth were related to adult height in women in a manner predicted by the life history tradeoffs, the sex of the first-born offspring did not correlate with women's height at adulthood. This result was unexpected, given that having a son should be energetically more costly for the mother than having a daughter (Bukowski et al., 2007; Hindmarsh et al., 2002; Loos et al., 2001; Marsál et al., 1996). Since women delivering a son instead of a daughter as their first-born were slightly shorter as adults (on average 0.25 cm shorter), the surplus costs of delivering a son may not have been large enough to inflict (statistically observable) additional costs to maternal height. Alternatively, our results may not be fully consistent with the resource-based trade-offs between reproduction and growth. In line with this, the magnitude of the effect of age at menarche on adult height was estimated to be more than twice as high as the effect of age at first birth. From the

resource allocation perspective, this finding is somewhat unexpected, because gestation and lactation are energetically far more demanding for the mother than just being physiologically able to reproduce (i.e., maintaining ovarian function) (Jasienska, 2001). One likely explanation for this is the different timing of these events: menarche occurs while women are still rapidly gaining height, whereas first birth, at least in developed societies using contraceptives like the one studied here, is often postponed after the attainment of final adult height. On the other hand, an alternative interpretation to within-individual resource allocation may be that these kinds of associations are mediated mainly by steroids (Ketterson & Nolan, 1999; Williams, 2005). For example, in women, estrogens have a major and contrasting influence on both age at menarche and on the cessation of bone growth, which may explain why earlier age at menarche leads to shorter adult height (Ellison, 2001). Similar interpretation of human life histories has emerged from the studies of reproductive costs on the postreproductive lifespan of women, as the timing of reproduction seems to be more important to female longevity than total reproductive effort per se, measured as parity or lifetime reproductive success (Helle et al., 2005). In line with this, it was recently reported that among Norwegian women, an early age at menarche was related to increased all-cause mortality, irrespective of their age at first reproduction and total parity (Jacobsen, Heuch, & Kvåle, 2007). This is not to say that associations between ages at menarche and first birth and adult height were unrelated to within-individual allocation of resources (and potentially merely mediated by steroids) but just to note that they do not necessarily need to be and that phenotypic correlations provide only limited evidence for the underlying physiological mechanisms. Furthermore, one cannot exclude the possibility that both resource- and steroid-based mechanisms may be in action in humans.

Despite the extensive research efforts, previous studies investigating how a woman's adult height relates to her fitness have produced very mixed results. Some studies have reported higher fitness for tall women (Allal et al., 2004; Liljestrand et al., 1985; Martorell et al., 1981; Sear et al., 2004), whereas some studies have reported short women to have a fitness advantage (Devi et al., 1985; Frisancho et al., 1973). Several studies have also reported the lowest fitness for both very short and tall women (Brush et al., 1983; Mueller, 1979; Nettle, 2002; Vetta, 1975). We found neither a negative nor positive linear or quadratic selection for a woman's adult height in these Finnish women studied. Instead, these women accrued large fitness benefits by starting reproduction early and ceasing it late. Therefore, while becoming shorter adults, these Finnish women benefited in terms of fitness from sacrificing tallness for an early beginning of reproductive career.

As manipulative experiments are unavailable to study trade-offs in humans, one cannot overrule confounding due to phenotypic correlations that may result from an underlying variation in individual quality and/or resource acquisition.

However, at the present, those few studies being able to control for between-individual variation, for example, in health by direct physiological measurements, have failed to reveal trade-offs between female life histories (Sear et al., 2003; Sear, 2007). Here, we tried to control for between-individual variation in resource availability by including, (i) in the case of reproduction growth trade-off, the number of siblings representing the intra-family competition for household resources, and (ii) in the analysis of adult height and LRS, the educational level of a woman in our models. This was likely at least partly successful, as, for example, women having many siblings became shorter adults, indicating that these women might have been nutritionally constrained and, thus, might have experienced reduced growth (Silventoinen, 2003). It is, however, currently unclear whether one should assume more pronounced life history tradeoffs in the conditions of restricted resource availability (Roff & Fairbairn, 2007). This makes it hard to build a priori predictions of phenotypic correlations between life history traits based on resource allocation.

To conclude, we found evidence for a tradeoff between reproduction and growth in contemporary Finnish women: those who had an earlier age at menarche and first birth were shorter as adults. However, these women did not seem to suffer fitness costs by trading tallness for an early start of reproduction, because height at adulthood was irrelevant in terms of fitness while natural selection strongly favoured a young age at first birth.

Acknowledgments

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