Natural selection on anthropometric traits of Estonian girls

Markus Valge [a], Peeter Hõrak [a,*], Jonathan M. Henshaw [b,c]

[a] Department of Zoology, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia.
[b] Institute of Biology I (Zoology), University of Freiburg, Hauptstraße 1, 79104 Freiburg, Germany
[c] Department of Biological Sciences, University of Idaho, 875 Perimeter MS, 3051 Moscow, ID, USA

ARTICLE INFO

ABSTRACT

Natural selection is a key mechanism of evolution, which results from the differential reproduction of individuals due to differences in phenotype. We describe fecundity selection on 13 anthropometric traits in a sample of 4000–10,000 of Estonian girls, who were born between 1937 and 1962 and measured at around 13 years of age. Direct selection favoured shorter, slimmer and lighter girls with smaller heads, more masculine facial and body shapes and slower rates of sexual maturation. Selection was stabilizing for weight, body mass index and face roundness. Direct selection was absent on two markers of general health and viability – handgrip strength and vital lung capacity – although these traits experience negative indirect selection due to their association with educational attainment. Similarly, indirect selection, mediated by educational attainment, accounted for a significant portion of selection for girls with smaller heads, narrower faces, and higher shoulder/hip ratios. These traits are thus subject to gene-culture coevolution, in that selection on body dimensions arises via cultural and behavioural mechanisms.

1. Introduction

Natural selection occurs when individuals reproduce at different rates due to differences in their phenotypes. As well as having shaped our evolutionary inheritance, natural selection continues in contemporary human populations, where numerous studies have found selection on phenotypes, and sometimes evolutionary responses to such selection, involving a diverse range of life-history, physiological, and behavioural traits (reviewed by Stearns, Byars, Govindaraju, & Ewbank, 2010; Kong et al., 2017; Sanjak, Sidorenko, Robinson, Thornton, & Visscher, 2018; Meisenberg, 2019).

In contemporary Western societies, fecundity selection (i.e. selection on the number of children produced) typically favours shorter women (Stulp & Barrett, 2016; Stulp, Verhulst, Pollet, & Buunk, 2012), while a few studies have documented selection for increased weight or BMI (reviewed in Sanjak et al., 2018). However, the causes of such patterns are not well understood. One possible explanation is that selection does not act on height or weight directly, but rather indirectly via associations between these traits and the 'true' targets of selection (Stulp et al., 2012). The most obvious potential targets for such indirect selection are educational attainment and income, which typically correlate positively with height (Silventoinen, Posthuma, van Beijsterveldt, Bartels, & Boomsma, 2006; Tyrrell et al., 2016) and negatively with fecundity in women (Meisenberg, 2019; Skirbekk, 2008). However, studies of selection in Western women often still find negative effects of height on reproductive success, even after controlling for measures of socioeconomic status and education (Stulp et al., 2012). This suggests that at least some selection on height must arise via alternative causal pathways.

Socioeconomic factors can generate indirect selection on morphometric traits via two subtly different mechanisms. First, common social or genetic factors may underpin variation in both morphology and socioeconomic status (Silventoinen et al., 2006; Tyrrell et al., 2016). In this case, direct selection on socioeconomic traits leads to 'spurious selection' on morphometric traits, even when the latter have no causal effect on fitness. Second, morphometric traits may directly influence an individual's socioeconomic traits, especially later in life (e.g. if an individual's height influences their likelihood of attaining higher education). This leads to 'mediated selection' on morphometric traits via a two-step causal chain (i.e. morphometric traits influence socioeconomic traits, which in turn affect fitness). In this case, selection on morphometric traits is due (at least in part) to indirect causal effects of these traits on fitness. The causal structure of selection on height, weight and other morphometric traits is likely highly complex and remains

* Corresponding author.
    E-mail address: horak@ut.ee (P. Hõrak).

largely unresolved.

Here we examine fecundity selection on 13 anthropometric traits in a large sample (n = 4000–10,000) of Estonian schoolgirls born between 1937 and 1962, who were measured at an average age of 12.9 ± 3.12 (SD) years (see Hõrak & Valge, 2015; Hõrak, Valge, Fischer, Mägi, & Kaart, 2019 for descriptions of Juhan Aul's database). The demographic history of Estonia during the study period differs markedly from that of Western European countries and the United States. The post-war baby boom was absent in Estonia, which from the late 1940s to the mid-1960s had probably the lowest fertility rate in the world, alongside Latvia (Frejka & Sardon, 2004). Against the general trend in Europe, fertility in Estonia increased rather than decreased in the late 1960s, and by the late 1980s was higher than in any major region of the continent (Klesment, Puur, & Valge, 2010). Despite these major demographic differences, the social factors that are known to influence reproductive behaviour developed at similar or faster rates in Estonia as in many Western European countries. For instance, divorce rates started to rise already during the inter-war period (Sakkeus, Klesment, & Puur, 2016), equalling or exceeding those of Scandinavian countries from the 1970s onwards. Over the same period, non-married cohabitation began to prevail over marriage (Puur, Rahnu, Maslauskaitė, & Stankūnienė, 2016). Beginning with the birth cohorts of 1930s, women outnumbered men in secondary and tertiary education (Klesment, 2013), yet social mobility with respect to educational attainment remained low (Saar & Aimre, 2012). Throughout the 20th century, Estonian women with only primary education bore 0.5 to 0.75 more children on average than women with tertiary education (Tiit, 2013).

To our knowledge, this is the first study of multivariate selection on morphometric traits in growing children, and the richness of our dataset allows for a nuanced picture of natural selection on this human population. First, we consider whether fecundity selection favouring shorter women, which is typical of contemporary western societies, also acted on girls growing up in Estonia under the Soviet regime. Second, we provide the first ever measurements of selection on human cranial volume, which is known to correlate both phenotypically (Gignac & Bates, 2017; Hõrak & Valge, 2016) and genetically (Hagenaars et al., 2016) with cognitive abilities and educational attainment. Third, we quantify selection on breast development rate (a marker of the speed of sexual maturation) and various measures of face and body shape that are associated with perceived masculinity and testosterone exposure (Hodges-Simeon, Hanson Sobraske, Samore, Gurven, & Gaulin, 2016; Roosenboom et al., 2018; Sim, 2013). Lastly, we measure selection on two indices of physical ability – handgrip strength and lung capacity – which are predictive of short- and long-term morbidity and mortality in adult populations (Guerra et al., 2010; Norman, Stobäus, Gonzalez, Schulzke, & Pirlich, 2011). Grip strength is a testosterone-dependent general marker of upper body muscle strength, fat-free body mass and overall health and nutritional status (Gallup, White, & Gallup Jr., 2007; Żelaźniewicz & Pawłowski, 2018). Lung (vital) capacity is an indicator of pulmonary function that offers protection from respiratory (Batty et al., 2006) and cardiovascular (Sin, Wu, & Man, 2005) disease. It is positively associated with birth weight (Victora et al., 2008) and negatively affected by exposure to disease throughout life.

We focus especially on the causal determinants of selection on these morphometric traits. Specifically, we ask to what extent selection on morphometric traits can be accounted for by indirect selection via education and the participants' childhood environment. We compare the strength of overall selection on each measured trait, as captured by selection differentials, to the strength of 'direct selection', which we quantify using selection gradients that control for an individual's educational attainment, their origin in rural vs urban areas, their number of siblings, and their parents' socioeconomic position. Using structural equation models (Conner, 1996; Dai & Galloway, 2013; Henshaw, Jennions, & Kruuk, 2018; Kingsolver & Schemske, 1991; Latta & McCain, 2009; Morrissey, 2014), we also explicitly quantify the strength of indirect selection via educational attainment, which may

represent either 'spurious' or 'mediated' selection (see above). Methods for measuring phenotypic selection have diversified during recent years. We therefore combine traditional selection differentials and gradients, as developed by Lande and Arnold (1983), with complementary methods for quantifying the overall strength of directional and non-directional selection (Henshaw & Zemel, 2017) and numerical approximation of fitness surfaces using generalized additive models (Morrissey & Sakrejda, 2013; Schluter & Nychka, 1994; Walsh & Lynch, 2018; Wood, 2017).

We expected to find strong indirect selection on height and cranial volume, as both traits are known to associate positively with educational attainment (e.g., Ivanovic et al., 2019; Magnusson, Rasmussen, & Gyllensten, 2006). In the studied population, taller children and those with larger crania were more likely to proceed to secondary and/or tertiary education, independently of sex, socioeconomic position and rural vs urban origin (Valge, Meitern, & Hõrak, 2019). For traits linked to femininity of body and face shapes, we had no prior expectations regarding patterns of selection. Men are known to prefer women with more feminine bodies and faces (Little, Connely, Feinberg, Jones, & Roberts, 2011; Marcinkowska et al., 2014), so if the desirability of specific phenotypic traits constrains women's reproductive success (e.g., by affecting the timing of pair formation), one might predict that women with more feminine characteristics pair earlier, which typically results in higher lifetime reproductive success (LRS) (Sanjak et al., 2018). On the other hand, it has also been suggested that women may marry later if they are choosy with respect to partners (Stulp et al., 2012). If choosiness increases with desirability, this could lead to women with more feminine phenotypes engaging in a more time-consuming mate selection process, delaying their age of first birth and thereby negatively affecting LRS.

2. Material and methods

2.1. Morphometric and socioeconomic variables

Data on morphometric measurements and family background were obtained from the anthropometric study performed by Juhan Aul between 1956 and 1969 (for the historical background of this sample see Hõrak & Valge, 2015). Hip width (bicristal diameter) was measured as the distance between the external margins of the iliac crests. Shoulder width (biacromial diameter) was measured as the horizontal distance across the shoulders measured between the acromia. Measures of face size and shape are shown in Fig. 1. Cranial volume was estimated according to Rushton (1997): 7.884*(head length − 11) + (10.842*head width − 11) − 1593.96 (units in mm). Vital capacity of lungs was measured using a bellows-type spirometer. Maximum handgrip strength was registered with a handheld dynamometer. If data for handgrip strength were available for both hands, the highest measure was used. The development stage of breasts was assessed on the basis of the six-point Tanner scale (0–5). All measurements were recorded by a single person.

The full dataset for calculation of age-specific residuals of morphometric traits consisted of 9524 to 15,205 girls (depending on the trait) whose age ranged between 6.4 and 19.9 years. From this sample, we identified 10,096 individuals (average age = 12.9 ± 3.2 (SD) years) whose lifetime reproductive success (LRS) was recorded in the Estonian Population Registry (https://e-estonia.com/solutions/interoperability-services/population-registry/). A subset of these participants (6783 individuals) also provided data on their educational attainment (as self-report) during the Estonian population census in 2011 (https://www.stat.ee/phc2011). Among individuals with known LRS, rural vs urban origin was known for 10,054 persons, number of siblings for 10,044 persons and parental socioeconomic position (SEP) for 9656 persons. SEP (highest in the family) was assessed on the basis of parental professions recorded during data collection and assigned into three categories (unskilled manual workers, skilled manual workers or non-
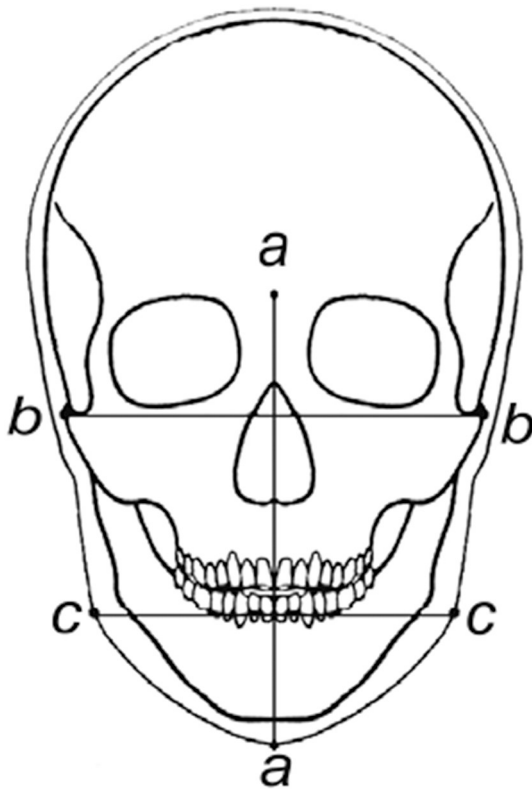
Fig. 1. Cranial measurements used in the study. b-b: face width, c-c: jaw width, b-b/a-a: face roundness (lfWHR, lower face width/height ratio).

manual workers). Educational attainment was grouped into three categories: primary (8 years of schooling or less), secondary (including secondary vocational) and tertiary (>11 years of schooling). Sample sizes vary between analyses because participants differed with respect to the number of anthropometric and biosocial traits recorded. Data processing was performed anonymously under the licence of the Research Ethics Committee of the University of Tartu (protocol # 275/T-1, issued on 20.11.1017) and approved by the Estonian Data Protection Directorate (Decision n2 2.2.-1/17/55, issued on 30.01.2018).

2.2. Age-specific residuals of morphometric traits

Since morphometric traits change with a girl's age, we used the raw data described above to calculate age-specific residuals for all measured anthropometric traits. Residuals were obtained from generalized additive models in which the focal trait was regressed against smooth non-parametric functions of age (in days) and birth date using the package 'mgcv' for R (Wood, 2017) with default smoothing parameters (R syntax: focal_trait ~ s(age) + s(birth_date); see supplementary materials for R code relating to all statistical analyses). We included birth date as a predictor to account for the steady increase in age-adjusted body dimensions over the study period (see Hõrak & Valge, 2015). Residuals were then standardized to z-scores. All results presented here are based on these standardized residuals, rather than raw trait values. In addition, LRS was standardized by dividing each individual's lifetime number of children by the average for her year's cohort (hereafter referred to as 'relative' LRS).

2.3. Selection differentials

The strength of selection acting on anthropometric traits via all possible causal pathways was quantified using selection differentials (Henshaw & Zemel, 2017; Lande & Arnold, 1983; Walsh & Lynch,

2018). Directional selection (i.e. selection for larger or smaller trait values) was estimated using the linear selection differential (s) (Lande & Arnold, 1983). Selection may also act on the shape of a trait distribution, rather than its mean (e.g. by favouring or disfavouring extreme trait values, known as 'disruptive' and 'stabilizing' selection respectively; Walsh & Lynch, 2018). We consequently used the distributional selection differential (d; Henshaw, Kahn, & Fritzsche, 2016; Henshaw & Zemel, 2017) to estimate total selection on anthropometric traits, including both directional and non-directional components. Lastly, we estimated non-directional selection as $d_N = d - s$ (Henshaw & Zemel, 2017). We note that all three differentials (s, d and d_N) are measured on the same scale as trait values.

Selection differentials should ideally measure the relationship between trait values and *expected* fitness, to which the realised fitness of individuals provides only a noisy approximation. When estimating directional selection, this noise does not introduce any systematic bias, because the linear selection differential is simply a covariance (Walsh & Lynch, 2018). On the other hand, the distributional selection differential and its non-directional component can be biased upwards by the presence of noise, especially when the relationship between traits and expected fitness is weak. This can lead to positive bias when estimating null distributions, and consequently to inflated *p*-values (see e.g. the results of Head, Kahn, Henshaw, Keogh, & Jennions, 2017). To prevent this issue, we estimated expected LRS conditional on trait values using generalized additive models, where relative LRS was regressed against a smooth non-parametric function of trait values (using the package 'mgcv' for R, Wood, 2017). When calculating d and d_N, we used the predicted values of LRS from this model in place of realised LRS.

P-values for selection differentials were calculated using exact permutation tests. First, we created 10,000 'null' datasets by permuting fitness values randomly among individuals, while leaving all other trait values intact. For each null dataset, we then calculated selection differentials on each trait using the procedures outlined above. This generated null distributions for each type of selection differential on each trait, from which *p*-values were calculated (significance level α = 0.05). Since the distributional selection differential and its non-directional component are always positive, we used one-tailed *p*-values for these statistics; all other *p*-values are two-tailed.

2.4. Selection gradients and fitness curves

Selection differentials quantify selection via all possible causal pathways. However, in many cases, selection operates via correlations between trait values and environmental variables. We consequently also estimated the portion of selection that remained after controlling for biosocial and environmental variables. For each anthropometric trait, we calculated linear selection gradients (β) and quadratic selection gradients ($β_Q$, γ) using standard linear and quadratic regressions (Lande & Arnold, 1983; Walsh & Lynch, 2018). Note that our estimates of γ are double the quadratic regression coefficients produced by most statistical software packages (Stinchcombe, Agrawal, Hohenlohe, Arnold, & Blows, 2008). In each case, we included an individual's educational attainment, rural/urban origin, number of siblings, and parental socioeconomic position (SEP) as covariates. Standard errors and *p*-values were estimated parametrically using ordinary least squares (note that the method of fitting had a negligible effect on results for this dataset).

Quadratic selection gradients give a rough indication of the shape of selection acting on a trait. To provide a more nuanced picture, however, we also modelled LRS as a smooth non-parametric function of each anthropometric trait using generalized additive models (R package 'mgcv'; Wood, 2017). These models yield 'fitness curves', showing the expected LRS of individuals as a function of their trait values (Fig. 3). We included an individual's educational attainment, rural/urban origin, number of siblings, and parental SEP as covariates in these models.

2.5. Indirect selection via educational attainment

Educational attainment is unique among the socioeconomic variables in our dataset, in that it occurs later in life and so might conceivably be causally influenced by an individual's anthropometric traits. We consequently used structural equation models to estimate indirect selection on anthropometric traits via education attainment, under the assumption that such a causal pathway exists (see path diagram in Fig. 2). To maximize statistical power, we constructed separate structural equation models for each anthropometric trait (but see below for a larger model). Our models allowed for each of the other covariates – rural/urban origin, number of siblings, and parental SEP – to influence both educational attainment and LRS directly. We fitted these models using the R package 'lavaan' (Rosseel, 2012; see R code in supplementary materials). Robust standard errors and *p*-values were calculated using weighted least squares with mean- and variance-adjusted test statistics (option 'WLSMV' in the 'lavaan' package; the method of fitting made only a negligible difference to our results). Although our structural models assume that indirect selection is mediated by educational attainment, it is equally possible that such selection arises due to common causal determinants of both anthropometric traits and education (i. e. 'spurious' rather than 'mediated' selection in the terminology of the introduction).

Most of our structural equation models involve only a single phenotypic trait. This is because samples for each trait in our dataset are partially non-overlapping and so the statistical power of a model falls rapidly with the number of modelled traits. In addition, some sets of traits are highly collinear (e.g. all size traits, or weight and BMI). Nonetheless, we also ran a structural equation model with a larger subset of traits (height, BMI, face roundness, shoulder-to-hip ratio, breast development rate, hand-grip strength, and lung capacity) and the same set of environmental covariates as above. The structure and fitting of this model were otherwise identical to above (see also Fig. 2). Note that replacing height with the first principal component of the linear size traits yielded nearly identical results (data not shown).

2.6. How much of selection is mediated by the age at first birth?

The age at which a woman first gives birth (AFB) is typically highly predictive of her lifetime reproductive success (reviewed by Sanjak et al., 2018). To understand the role that AFB plays in determining the strength of selection, we ran a structural equation model in which AFB can mediate the effects of both traits and education on fitness (Fig. S1 in
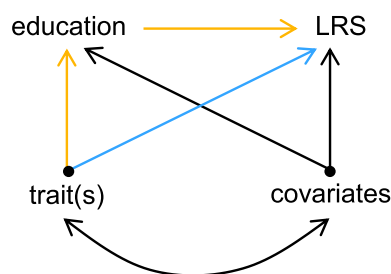

Fig. 2. Path diagram for structural equation models of the effects of traits on lifetime reproductive success, including both a direct effect (blue) and an indirect effect via education (yellow). Single-headed arrows represent potential causal effects, whereas double-headed arrows represent covariances that are not analysed causally. An individual's rural/urban origin, number of siblings, and parental socioeconomic position (SEP) are included as covariates. A separate model was fitted for each of the 13 anthropometric traits (results in Fig. 4). In addition, we ran a combined model including seven phenotypic traits (height, BMI, face roundness, should-to-hip ratio, breast development, hanggrip strength and lung capacity: results in Fig. 5). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

supplementary materials). We included the same larger subset of traits as in the previous section (height, BMI, face roundness, shoulder-to-hip ratio, breast development rate, hand-grip strength, and lung capacity). An individual's AFB was standardized as the absolute deviation (in years) from the mean age at first birth for each year cohort. Note that this model excludes women with zero LRS (299 women excluded for this reason).

2.7. Accounting for relatedness among participants

A small proportion of the girls in our dataset shared one or both parents or lived in the same household. This potentially leads to pseudo-replication in our main analyses due to genetic relatedness among the study participants. We consequently repeated all analyses after randomly excluding all but one girl from every group of relatives (612 girls excluded). The results of these analyses were extremely similar to our main findings and so are presented in the supplementary materials.

3. Results

Total selection, including both directional and non-directional components selection, was strongest on height ($d = 0.035$, $p < 10^{-4}$), followed by weight and jaw width ($d = 0.033$, $p < 10^{-4}$) (Table 1). Three of the measured traits – shoulder width, grip strength and lung capacity – did not reveal any significant overall associations with LRS. With the exception of face roundness and the shoulder/hip ratio, all linear selection differentials were negative, indicating selection for lighter girls with smaller linear dimensions of skeletal traits and slower rates of breast development (Table 1). Surprisingly, although the linear selection differential for shoulder width was negative ($s = -0.011$, marginally non-significant at $p = .074$), selection favoured girls with higher shoulder/hip ratio, i.e., with more triangular body build ($s = 0.020$, $p = .001$). In the case of face roundness (lFWHR), total selection was significant ($DSD = 0.013$, $p = .04$), but the directional and non-directional components of selection were individually non-significant ($p = .07$ and 0.14; Table 1). All non-directional components of distributional selection differentials were minute and non-significant (Table 1), indicating that most selection was directional.

After accounting for biosocial covariates (educational attainment, rural/urban origin, number of siblings, and parental SEP), only five morphometric traits retained significant directional selection (Table 2). Even after controlling for these potentially confounding effects, selection still favoured shorter and lighter girls with smaller BMI, narrower hips and narrower jaws. Given the high degree of correlation among linear size traits, it is difficult to separate out the effects of selection on each trait; in other words, significant selection on one size trait may be partly or fully driven by its correlation with another such trait. Examination of quadratic selection gradients (Table 2) suggested stabilizing selection on two traits: BMI and face roundness (again controlling for biosocial variables). Moreover, quadratic regressions revealed both directional and stabilizing components to selection on face roundness, which favoured girls with rounder-than-average faces (note that the directional component of selection on BMI became non-significant after accounting for the quadratic effect). Individual fitness curves as estimated by generalized additive models (Fig. 3) broadly, though not exactly, agree with the quadratic estimates in Table 2, indicating significant stabilizing selection on weight and BMI (with stabilizing selection on height being marginally non-significant). For face roundness, stabilizing selection is also significant, with an estimated peak near the mean trait value. However, fitness drops off more rapidly for very elongated faces than for very round faces, consistent with weak directional selection for rounded faces (cf. Tables 1, 2).

Estimates of direct selection from our structural equation models (Fig. 4) were broadly consistent with the linear selection gradients (cf. Table 2 and Fig. 3). These models also revealed that indirect selection via educational attainment generally favoured lighter girls with smaller

Table 1
Standardized selection differentials for 13 anthropometric traits. Shown are the distributional selection differential (d), the linear selection differential (s), and the non-directional component of the DSD (d_N), which quantify total, directional, and non-directional selection respectively. All differentials are based on standardized residuals of the trait against age and birth date using a generalized additive model (Gaussian family). Lifetime reproductive success (LRS) was calculated relative to the average LRS of that year's cohort. Estimates of directional selection are simply covariances between residual trait values and relative LRS, which are unbiased. For total and non-directional selection, we first estimated expected relative LRS as a smooth function of trait values. Estimates of total and non-directional selection were then calculated using these smoothed estimates to reduce bias due to noise. All p-values are based on exact permutation tests. Results shown in bold remain significant after Holm-Bonferroni correction for multiple comparisons.

	Total selection (d)	p-value	Directional selection (s)	p-value	Non-directional selection (d_N)	p-value	Sample size
Height	**0.035**	**< 10^{-4}**	−0.035	**< 10^{-4}**	0.000	0.31	10,096
Weight	**0.033**	**< 10^{-4}**	−0.033	**< 10^{-4}**	0.000	0.93	9666
BMI	**0.024**	**< 10^{-4}**	−0.023	**< 10^{-4}**	0.000	0.26	9665
Face width	**0.017**	**0.003**	−0.017	**0.006**	0.000	0.31	10,091
Jaw width	**0.033**	**< 10^{-4}**	−0.033	**< 10^{-4}**	0.000	0.47	6814
Face roundness (lFWHR)	0.013	0.04	0.011	0.07	0.002	0.14	10,072
Cranial volume	**0.018**	**0.003**	−0.018	**0.002**	0.000	0.32	10,093
Shoulder width	0.011	0.08	−0.011	0.08	0.002	0.26	10,088
Hip width	**0.028**	**< 10^{-4}**	−0.028	**< 10^{-4}**	0.000	0.31	10,069
Shoulder/hip ratio	**0.020**	**0.002**	0.020	**0.001**	0.000	0.29	10,060
Breast dev. rate	0.017	0.03	−0.017	0.03	0.000	0.50	6589
Hand grip strength	0.004	0.68	0.000	0.97	0.004	0.07	8276
Lung capacity	0.009	0.21	−0.009	0.18	0.000	0.67	7823

Table 2
Standardized linear and quadratic selection gradients for 13 anthropometric traits, based on separate regressions of relative LRS on each trait (Gaussian family). All regressions include an individual's educational attainment, rural/urban origin, number of siblings, and parental socioeconomic position (SEP) as covariates. Gradients are based on standardized residuals of the trait against age and birth date using a generalized additive model (Gaussian family). Lifetime reproductive success (LRS) was calculated relative to the average LRS of that year's cohort. Standard errors and p-values are maximum likelihood estimates.

	Linear selection gradient (β)	SE	p-value	Quadratic selection gradients (β_Q, γ)	SE	p-value	Sample size
Height	**−0.018**	**0.008**	**0.03**	−0.018	**0.008**	**0.03**	6451
				−0.020	0.011	0.06	
Weight	**−0.024**	**0.008**	**0.002**	−0.019	**0.009**	**0.03**	6182
				−0.014	0.008	0.08	
BMI	**−0.026**	**0.008**	**<10^{-3}**	−0.016	0.009	0.07	6181
				−0.023	**0.008**	**0.006**	
Face width	−0.013	0.008	0.11	−0.012	0.008	0.14	6449
				−0.013	0.011	0.24	
Jaw width	**−0.026**	**0.010**	**0.008**	−0.026	**0.010**	**0.008**	4547
				−0.001	0.013	0.94	
Face roundness (lFWHR)	0.015	0.008	0.06	**0.016**	**0.008**	**0.049**	6439
				−0.030	**0.011**	**0.008**	
Cranial volume	−0.010	0.008	0.21	−0.011	0.008	0.18	6449
				0.010	0.010	0.34	
Shoulder width	−0.010	0.008	0.20	−0.011	0.008	0.17	6449
				−0.017	0.009	0.06	
Hip width	**−0.022**	**0.008**	**0.006**	−0.021	**0.008**	**0.009**	6437
				−0.012	0.011	0.29	
Shoulder/hip ratio	0.015	0.008	0.06	0.015	0.008	0.06	6442
				0.001	0.009	0.91	
Breast dev. rate	−0.015	0.010	0.13	−0.014	0.010	0.14	4028
				0.011	0.012	0.36	
Hand grip strength	0.000	0.009	0.95	0.001	0.009	0.90	5155
				−0.004	0.011	0.70	
Lung capacity	−0.003	0.009	0.76	−0.003	0.009	0.75	4922
				0.001	0.011	0.94	

Results shown in bold remain significant after Holm-Bonferroni correction for multiple comparisons.

linear dimensions for skeletal traits (Fig. 4). In other words, larger girls were more highly educated on average, and, possibly as a result, produced fewer children over their lifetimes (note that all size traits are positively correlated with education in our dataset: permutation test, $p < .01$ for all size traits; see also Valge et al., 2019). Indirect selection also favoured girls with higher shoulder/hip ratios (i.e. a more triangular body build). Lastly, although selection on hand-grip strength and lung capacity was not significant overall, indirect selection favoured girls with weaker grip strength and lower lung capacity.

Direct and indirect selection almost always acted in the same direction for a given trait; however, indirect selection was generally weaker but more consistent (i.e. with smaller standard errors). These smaller errors arise because indirect selection is calculated as the product of two coefficients, representing the effect of a trait on education and of education on reproductive success respectively. Since estimates of these two coefficients are not expected to covary strongly, it is unlikely that both coefficient estimates will deviate drastically from their true values in the same direction, which leads to tighter estimates in the current dataset (note that the 'lavaan' package uses the delta method to estimate standard errors of derived variables).

The results of our combined structural equation model (Fig. 5), which included seven anthropometric traits, were generally congruent with those of the trait-specific SEM models (cf. Fig. 4), except that many relationships are no longer significant given the smaller sample size. The most notable difference was the lack of direct selection for delayed breast development.

expected lifetime reproductive success (LRS)
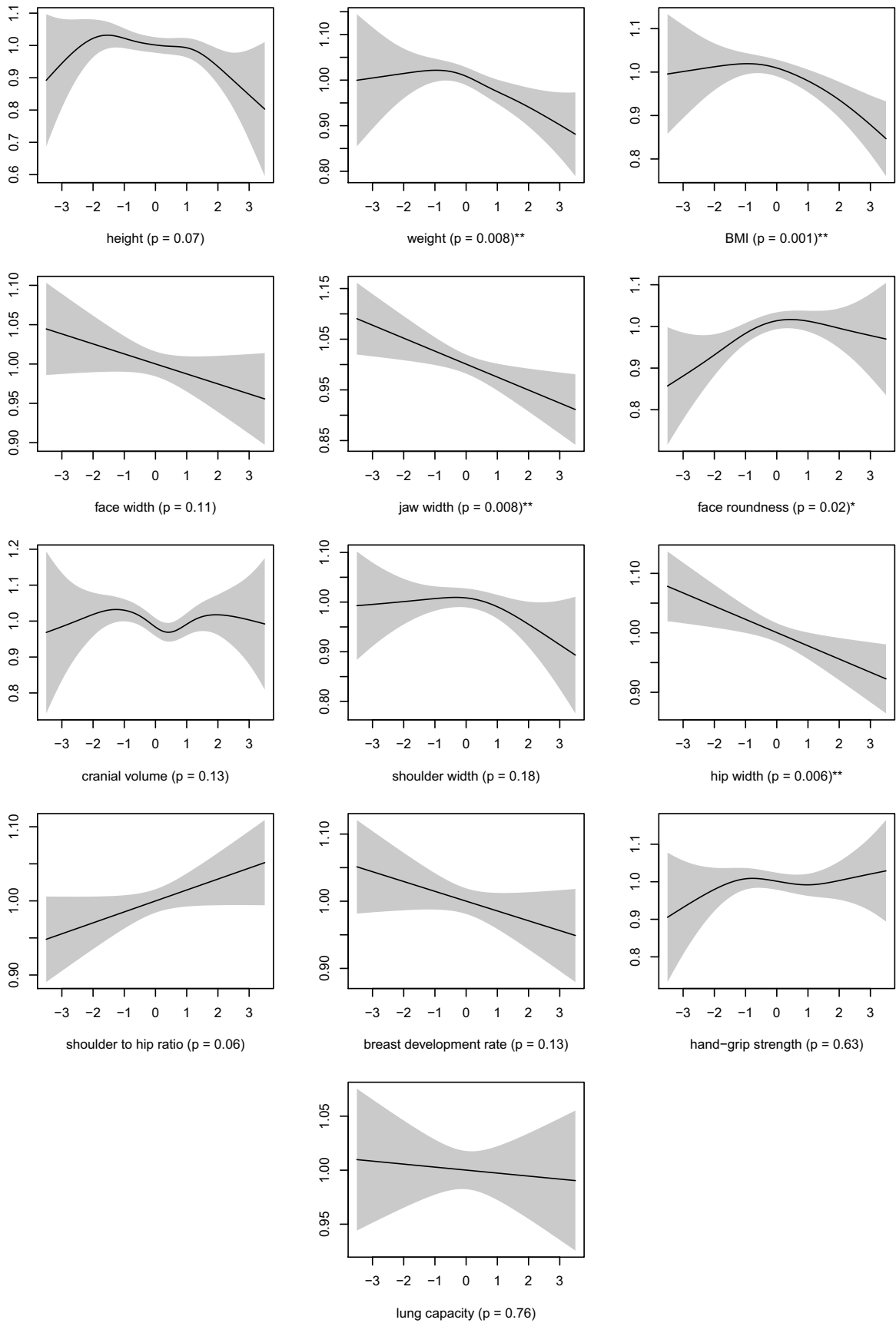
standardized residual of trait value

(caption on next page)

Fig. 3. Individual fitness curves for 13 anthropometric traits, showing the estimated relationships between standardized residuals of trait values and expected relative lifetime reproductive success (mean ± SEM). Curves were estimated using generalized additive models, in which relative LRS was regressed against a smooth non-parametric function of each anthropometric trait (R package 'mgcv'). An individual's rural/urban origin, number of siblings, and parental socioeconomic position (SEP) were included as covariates. *P*-values indicate the approximate significance of the smooth terms corresponding to the trait of interest. Note that minor local variation in the shapes of these curves (e.g. in the curve for cranial volume) sometimes arises from the fitting procedure and not all such variation is biologically meaningful.

Lastly, as expected, the age at first birth (AFB) has a strong negative effect on fitness, even after controlling for the other measured variables (the estimated path coefficient from AFB to LRS was $\beta = -0.039$, $p < 10^{-5}$). Selection via AFB accounts for a modest to substantial proportion of total selection, depending on the trait (Table S3 in supplementary materials). Most estimates of selection via specific pathways were non-significant in this model, likely because the number of modelled pathways is large relative to the sample size. However, selection via the pathway trait -> education -> AFB was significantly negative for height, hand grip strength and lung capacity.

4. Discussion

Different methods of characterising selection yielded broadly similar patterns. Directional selection generally favoured smaller and lighter girls, both overall (Table 1) and via each of the contributing causal pathways (direct or indirect via educational attainment) in our structural models (Figs. 2, 4). Our finding of negative indirect selection on height is consistent with our prior expectations, as this trait is known to be positively correlated with education (see Valge et al., 2019). Selection on two traits – hand-grip strength and lung capacity – was entirely indirect, i.e., due to correlations with educational attainment. In other words, stronger and healthier girls went on to obtain more education, and negative selection on these traits arose entirely from this

correlation. This pattern is consistent with both spurious selection (whereby common factors underly the anthropometric traits and educational attainment) or mediated selection (where the anthropometric traits directly influence educational attainment, which in turns influences reproductive success).

Non-directional selection was weaker and less consistent, with quadratic selection gradients and/or individual fitness curves suggesting stabilizing selection on weight, BMI and face roundness (Table 2, Fig. 3). In contrast, the non-directional component of the distributional selection differential (d_N) was always negligible and non-significant. This discrepancy between approaches might arise because d_N can sometimes be zero if weak stabilizing selection occurs in the presence of strong directional selection (in the framework of Henshaw & Zemel, 2017, the optimal 'flow' may still be entirely unidirectional). Overall, linear selection differentials ranged in magnitude from approximately zero to 0.035, whereas linear and quadratic selection gradients lay between zero and 0.025. These values are similar to those found for 37 life-history, physiological, behavioural and morphometric traits (23 of which showed significant nonzero directional selection gradients) among 217,728 female participants of UK Biobank (UKB) (Sanjak et al., 2018).

In contrast to the UKB study, we found negative linear selection differentials on weight (−0.033 vs 0.044) and BMI (−0.023 vs 0.060). One possible reason for this discrepancy is that in the current study,
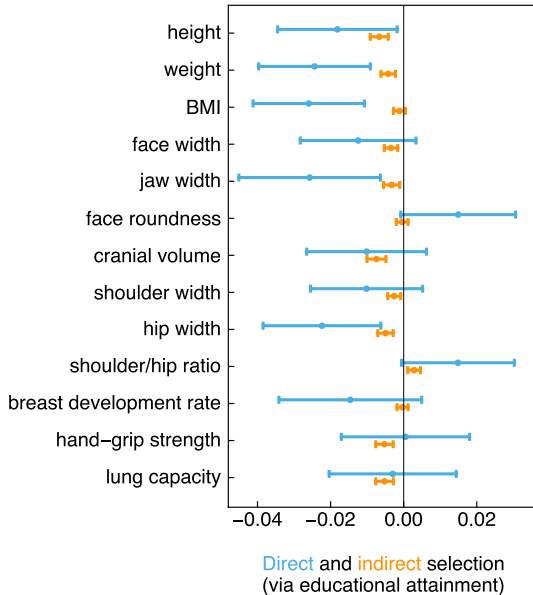

Direct and indirect selection
(via educational attainment)

Fig. 4. Estimates of direct selection (blue) and indirect selection via educational attainment (yellow) based on separate structural equation models for each of 13 anthropometric traits (mean ± 2SEM). An individual's rural/urban origin, number of siblings, and parental socioeconomic position (SEP) are included as exogenous covariates (Fig. 2). It is assumed that each trait and covariate can influence lifetime reproductive success either directly or indirectly, as mediated by educational attainment. Robust standard errors were calculated using weighted least squares with mean- and variance-adjusted test statistics (option 'WLSMV' in the 'lavaan' package). The data used to produce this figure are available as Table S1 in supplementary materials. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
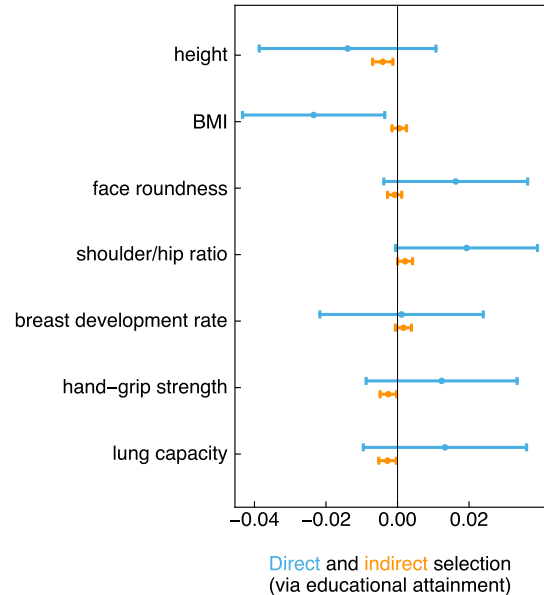

Direct and indirect selection
(via educational attainment)

Fig. 5. Estimates of direct selection (blue) and indirect selection via educational attainment (yellow) based on a single structural equation model involving 7 anthropometric traits (mean ± 2SEM). An individual's rural/urban origin, number of siblings, and parental socioeconomic position (SEP) are included as exogenous covariates (Fig. 2). It is assumed that each trait and covariate can influence lifetime reproductive success either directly or indirectly, as mediated by educational attainment. Robust standard errors were calculated using weighted least squares with mean- and variance-adjusted test statistics (option 'WLSMV' in the 'lavaan' package). The data used to produce this figure are available as Table S2 in supplementary materials. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

measures of body mass and BMI are not affected by parity. In contrast, the UKB relies on measurements of adult women, for whom weight is known to increase with the number of previous births (Harris, Ellison, & Holliday, 1997). Other studies (in the US) that relied on adult measurements have similarly found directional selection for increased weight (Byars, Ewbank, Govindaraju, & Stearns, 2010) and BMI (Beauchamp, 2016). A study of contemporary Finnish women found that only adolescent but not adulthood BMI was quadratically associated with LRS (Jokela et al., 2007). Similarly, both the current and the UKB studies found stabilizing selection on BMI in addition to directional selection (Sanjak et al., 2018). Such stabilizing selection might arise via a decreased likelihood of attaining a partner by both under- and overweight individuals, as well as dysfunctions of reproductive physiology characteristic to such individuals (Jokela et al., 2007).

The linear selection differential for height (−0.035) in this study was slightly larger than the one recorded in UKB (−0.028; Sanjak et al., 2018) and nearly 6 times as large as the differential detected in the US Health and Retirement Study (−0.006; Beauchamp, 2016; see also Conley et al., 2016). In contrast to these studies, Dutch women (born between 1935 and 1967) who were of average height experienced higher fertility than shorter or taller women, with no significant directional selection (Stulp, Barrett, Tropf, & Mills, 2015). With the exception of this Dutch study, our finding of selection for shorter stature in women aligns with those reported in other industrialised societies (e.g. in a recent review, selection on women's height was negative in all six studies that found a significant directional relationship; Stulp & Barrett, 2016). Notably, higher reproductive success of shorter girls in Estonia could not be entirely ascribed to indirect selection via educational attainment, nor via other measured socioeconomic variables such as rural/urban origin, although indirect selection via education did account for a large portion of total selection (Fig. 4). The finding that selection against height remains after controlling for education or income (that favours less-educated individuals who are generally shorter than highly-educated ones) is consistent with findings of studies reviewed by Stulp and Barrett (2016).

In contrast to height, the majority of selection for smaller cranial volume acted indirectly via educational attainment, whereas the direct path of selection in the SEM model was non-significant (Figs. 2 and 4). In other words, consistent with our prior expectations, girls with larger heads were selected against because they were more likely to obtain higher education than girls with smaller heads. Lower education (Tiit, 2013) and rural origin (Kulu, 2005) have been independently and additively associated with higher fertility in Estonia throughout the past century. The reason for the link between education and fertility is that early reproduction, a major determinant of LRS, is not compatible with schooling for both cultural and genetic reasons (Kong et al., 2017; Sanjak et al., 2018). To the best of our knowledge, selection on head size has not been previously studied, so it is unknown how widespread indirect selection on cranial parameters might be. However, since phenotypic and genetic correlations between cranial dimensions, cognitive abilities and educational attainment have been established in multiple studies (Haworth et al., 2019; Nave, Jung, Karlsson Linnér, Kable, & Koellinger, 2019; Savage et al., 2018), we predict that indirect selection for smaller head size is common everywhere where selection via educational attainment is strong (i.e. in the majority of the developed world).

Breast development rate is a marker of sexual development and the age-specific shoulder/hip ratio likely also carries such information (Ellison, 2001). The rate of sexual development is often highly sensitive to environmental influences. For instance, in this study population, girls from well-off families (who go on to obtain more education) also mature faster (Hõrak et al., 2019). It is thus tempting to speculate that social selection acting via growth conditions generated an apparent selection pressure favouring slowly maturing girls (Table 1), which arises mainly via the negative environmental correlation between the rates of maturation and reproduction. In other words, girls growing up under harsh

conditions both mature slowly and have higher LRS because they are released from constraints set on early reproduction by an academic career. However, seemingly inconsistent with this interpretation is the finding that selection on absolute hip width (a trait which develops under the influence of ovarian steroids and which strongly correlates with menarcheal age; Ellison, 2001) was still negative after accounting for the effects of socioeconomic variables on LRS. At present we have no explanation for this discrepancy, except that relative hip width (in relation to shoulders) might appear more sensitive to environmental constraints during growth than absolute (age-specific) hip width. On the other hand, negative direct selection on absolute hip width is consistent with direct selection for smaller size more generally.

For other traits linked to perceived femininity, we had no straightforward prior expectations as the relationship between attractiveness and the age of first reproduction is unknown. Selection on these traits revealed highly diverse patterns. For instance, despite any overall selection for shoulder width per se, we found significant linear selection for girls with narrow hips relative to their shoulders (Table 2, Fig. 3). Further, selection for narrower jaws persisted even after accounting for selection favouring rural and less-educated woman, while selection for narrower faces was no longer significant after controlling for these factors. Selection favouring rounder faces was, in turn, only significant in models allowing for non-linear effects (i.e. quadratic or generalized additive models: Table 2, Fig. 3) and controlling for biosocial variables. Altogether, these findings indicate that patterns of selection on sexually dimorphic traits are hardly uniform and that even strongly correlated dimensions of body size and shape (that share partly overlapping hormonally mediated developmental pathways) may differentially associate with reproductive success. Among other things, this information has practical implications for the studies of sexual selection. For instance, establishing how individual facial measures and their ratios relate to hormone levels (see, e.g., Hodges-Simeon et al., 2016) or their genetic underpinnings (Roosenboom et al., 2018) and attractiveness might be more informative than relying on composite traits or images.

Finally, a noteworthy finding of this study is the absence of any direct selection on two markers of overall health and nutritional status – handgrip strength and lung capacity. Both markers are well-known predictors of morbidity and mortality in the elderly (see Introduction), yet direct selection on these traits was negligible. Interestingly, the linear selection differential for grip strength (0.005) was identical to that found by Sanjak et al. (2018) in a huge sample of UKB, which indicates that (nearly) absent fecundity selection on physical strength is not a phenomenon specific to the current study conditions. The question of why well-established markers of health and vigour are not directly related to reproductive success (e.g., contrary to facial dimensions) remains puzzling and calls for future research on sexual and natural selection on human health. One possibility is that these traits are only predictive of health later in life, but not in children.

4.1. Strengths, limitations and implications

To our knowledge, this study is the first to measure natural selection on cranial volume, a well-established anatomical correlate of cognitive ability. Also for the first time, we measured selection on breast development rate (a marker of the speed of sexual maturation) and altogether six sexually dimorphic facial and bodily dimensions which are potential targets of sexual selection. Selection was recorded in a post-industrial society under the Soviet regime, where demographic patterns partly differed from those in Western societies, in which natural selection on humans is most frequently studied. For historical reasons, the study was free of volunteer bias and all the participants were younger than 20, which almost entirely eliminates mortality bias. Such biases are, for instance, unavoidable in studies based on biobanks (see Sanjak et al., 2018).

Measurements of children have the limitation that they mature at individually variable rates. For instance, a child might be small for age at

13 but still mature at above average size if her pubertal growth spurt starts later than average. This is an unavoidable problem of all cross-sectional morphometric studies of children. Our study treats absolute deviations from age-specific mean trait values equally, regardless of an individual's age. Trait variance in older children is likely more predictive of later reproductive success, and such variance may be more highly weighted in our model because absolute trait variation increases modestly with age within our dataset. We cannot, however, exclude the possibility that bias arises from this methodology. If such bias exists, it would probably affect linear dimensions for skeletal traits less strongly than other (e.g., weight-related) traits. For instance, in a study of the 1958 British birth cohort, correlations among girls between height at ages 7, 11, and 16 years, respectively, and age 23 years were pretty strong ($r = 0.70$, $r = 0.65$, and $r = 0.93$). Corresponding correlations for weight were 0.54, 0.59 and 0.73 (Power, Lake, & Cole, 1997). On the other hand, measuring pre-reproductive women has the advantage that their body mass and BMI are not affected by parity (Harris et al., 1997), which would heavily interfere with measurement of selection on the markers of obesity (Jokela et al., 2007).

The observed patterns of selection on cranial volume, face width, and shoulder/hip ratio are an example of gene-culture coevolution where selection on morphometric traits occurs largely or even entirely through correlated cultural and behavioural traits. However, whether such selection would result in a net decrease in these morphometric traits in the near future is doubtful, given the current secular increase in human body dimensions resulting from general improvements in nutrition and health (e.g., Hõrak & Valge, 2015). On the other hand, evolutionary changes can sometimes be rapid, as confirmed by an Icelandic study, showing that selection against genetic variants associated with educational attainment can lead to measurable change in the genetic composition of a population in as little as a few generations (Kong et al., 2017). Given that the heritabilities of morphometric and behavioural traits (Polderman et al., 2015) and the rate of sexual maturation (Hõrak et al., 2019) in humans are high and increasing with ongoing equalisation of growth conditions (Rutter, Moffitt, & Caspi, 2006), one thus cannot exclude the possibility that indirect selection on morphometric traits could be a major source of phenotypic change in the future. The potential for genetic change in such traits in high. For instance, heritabilities range from 0.70 to 0.90 for height (Jelenkovic et al., 2011) and from 0.75 to 0.87 for cranial measures (Haworth et al., 2019). However, since we currently lack information about selection on morphometric traits in boys of our population, this study does not enable us to predict the direction of evolutionary change. Selection often (but not always) favours men with higher education (reviewed in Nisén, Martikainen, Myrskylä, & Silventoinen, 2018). In our study population, height and cranial volume predicted educational attainment among both boys and girls (Valge et al., 2019). We thus cannot exclude the possibility that sexually antagonistic selection on morphometric traits via education would dampen or even cancel net selection and any resulting evolutionary change.

Data accessibility statement

Original data will be available as electronic supplementary material.

Funding

Declaration of Competing Interest

We declare we have no competing interests.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.evolhumbehav.2020.07.013.

References

Batty, G. D., Gunnell, D., Langenberg, C., Smith, G. D., Marmot, M. G., & Shipley, M. J. (2006). Adult height and lung function as markers of life course exposures: Associations with risk factors and cause-specific mortality. *European Journal of Epidemiology, 21,* 795–801.

Beauchamp, J. P. (2016). Genetic evidence for natural selection in humans in the contemporary United States. *Proceedings of the National Academy of Sciences, 113,* 7774–7779.

Byars, S. G., Ewbank, D., Govindaraju, D. R., & Stearns, S. C. (2010). Natural selection in a contemporary human population. *Proceedings of the National Academy of Sciences, 107,* 1787–1792.

Conley, D., Laidley, T., Belsky, D. W., Fletcher, J. M., Boardman, J. D., & Domingue, B. W. (2016). Assortative mating and differential fertility by phenotype and genotype across the 20th century. *Proceedings of the National Academy of Sciences, 113,* 6647–6652.

Conner, J. K. (1996). Understanding natural selection: An approach integrating selection gradients, multiplicative fitness components, and path analysis. *Ethology Ecology & Evolution, 8,* 387–397.

Dai, C., & Galloway, L. F. (2013). Sexual selection in a hermaphroditic plant through female reproductive success. *Journal of Evolutionary Biology, 26,* 2622–2632.

Ellison, P. T. (2001). *On fertile ground: A natural history of human reproduction.* Cambridge, Massachusetts: Harvard University Press.

Frejka, T., & Sardon, J.-P. (2004). *Childbearing trends and prospects in low-fertility countries: A cohort analysis.* Dordrecht: Springer Science & Business Media.

Gallup, A. C., White, D. D., & Gallup, G. G., Jr. (2007). Handgrip strength predicts sexual behavior, body morphology, and aggression in male college students. *Evolution and Human Behavior, 28,* 423–429.

Gignac, G. E., & Bates, T. C. (2017). Brain volume and intelligence: The moderating role of intelligence measurement quality. *Intelligence, 64,* 18–29.

Guerra, S., Sherrill, D. L., Venker, C., Ceccato, C. M., Halonen, M., & Martinez, F. D. (2010). Morbidity and mortality associated with the restrictive spirometric pattern: A longitudinal study. *Thorax, 65,* 499–504.

Hagenaars, S. P., Harris, S. E., Davies, G., Hill, W. D., Liewald, D. C. M., Ritchie, S. J., … Deary, I. J. (2016). Shared genetic aetiology between cognitive functions and physical and mental health in UK biobank (N=112151) and 24 GWAS consortia. *Molecular Psychiatry, 21,* 1624–1632. https://doi.org/10.1038/mp.2015.225.

Harris, H., Ellison, G., & Holliday, M. (1997). Is there an independent association between parity and maternal weight gain? *Annals of Human Biology, 24,* 507–519.

Haworth, S., Shapland, C. Y., Hayward, C., Prins, B. P., Felix, J. F., Medina-Gomez, C., et al. (2019). Low-frequency variation in TP53 has large effects on head circumference and intracranial volume. *Nature Communications, 10,* 357.

Head, M. L., Kahn, A. T., Henshaw, J. M., Keogh, J. S., & Jennions, M. D. (2017). Sexual selection on male body size, genital length and heterozygosity: Consistency across habitats and social settings. *Journal of Animal Ecology, 86,* 1458–1468.

Henshaw, J. M., Jennions, M. D., & Kruuk, L. E. B. (2018). How to quantify (the response to) sexual selection on traits. *Evolution, 72,* 1904–1917.

Henshaw, J. M., Kahn, A. T., & Fritzsche, K. (2016). A rigorous comparison of sexual selection indexes via simulations of diverse mating systems. *Proceedings of the National Academy of Sciences, 113,* E300–E308.

Henshaw, J. M., & Zemel, Y. (2017). A unified measure of linear and nonlinear selection on quantitative traits. *Methods in Ecology and Evolution, 8,* 604–614.

Hodges-Simeon, C. R., Hanson Sobraske, K. N., Samore, T., Gurven, M., & Gaulin, S. J. C. (2016). Facial width-to-height ratio (fWHR) is not associated with adolescent testosterone levels. *PLoS One, 11,* Article e0153083.

Hõrak, P., & Valge, M. (2015). Why did children grow so well at hard times? The ultimate importance of pathogen control during puberty. *Evolution, Medicine, and Public Health,* 167–178.

Hõrak, P., & Valge, M. (2016). Old-for-grade girls reproduce but do not mature early: Simply a mechanistic link between educational progress and pace of life? *Intelligence, 57,* 41–47.

Hõrak, P., Valge, M., Fischer, K., Mägi, R., & Kaart, T. (2019). Parents of early maturing girls die younger. *Evolutionary Applications, 12,* 1050–1061.

Ivanovic, D. M., Almagià, A. F., Arancibia, V. C., Ibaceta, C. V., Arias, V. F., Rojas, T. R., … Orellana, Y. Z. (2019). A multifactorial approach of nutritional, intellectual, brain development, cardiovascular risk, socio-economic, demographic and educational variables affecting the scholastic achievement in Chilean students: An eight- year follow-up study. *PLoS One, 14,* Article e0212279.

Jelenkovic, A., Ortega-Alonso, A., Rose, R. J., Kaprio, J., Rebato, E., & Silventoinen, K. (2011). Genetic and environmental influences on growth from late childhood to

adulthood: A longitudinal study of two Finnish twin cohorts. *American Journal of Human Biology, 23*, 764–773.

Jokela, M., Kivimäki, M., Elovainio, M., Viikari, J., Raitakari, O. T., & Keltikangas-Järvinen, L. (2007). Body mass index in adolescence and number of children in adulthood. *Epidemiology (Cambridge, Mass.), 18*, 599–606.

Kingsolver, J. G., & Schemske, D. W. (1991). Path analyses of selection. *Trends in Ecology & Evolution, 6*, 276–280.

Klesment, M. (2013). *Diminishing returns to education in the soviet period. Results from the estonian household income data.* Tallinn: Estonian Institute for Population Studies Tallinn University.

Klesment, M., Puur, A., & Valge, J. (2010). *Childbearing and macro-economic trends in Estonia in the XX century. Estonian Institute for Population Studies.* Tallinn: Tallinn University.

Kong, A., Frigge, M. L., Thorleifsson, G., Stefansson, H., Young, A. I., Zink, F., … Stefansson, K. (2017). Selection against variants in the genome associated with educational attainment. *Proceedings of the National Academy of Sciences., 114*, E727–E732. https://doi.org/10.1016/j.tree.2008.11.008).

Kulu, H. (2005). Migration and fertility: Competing hypotheses re-examined. *European Journal of Population/Revue européenne de Démographie, 21*, 51–87.

Lande, R., & Arnold, S. J. (1983). The measurement of selection on correlated characters. *Evolution, 37*, 1210–1226.

Latta, R. G., & McCain, C. (2009). Path analysis of natural selection via survival and fecundity across contrasting environments in Avena barbata. *Journal of Evolutionary Biology, 22*, 2458–2469.

Little, A. C., Connely, J., Feinberg, D. R., Jones, B. C., & Roberts, S. C. (2011). Human preference for masculinity differs according to context in faces, bodies, voices, and smell. *Behavioral Ecology, 22*, 862–868.

Magnusson, P. K. E., Rasmussen, F., & Gyllensten, U. B. (2006). Height at age 18 years is a strong predictor of attained education later in life: Cohort study of over 950 000 Swedish men. *International Journal of Epidemiology, 35*, 658–663.

Marcinkowska, U. M., Kozlov, M. V., Cai, H., Contreras-Garduño, J., Dixson, B. J., Oana, G. A., … Rantala, M. J. (2014). Cross-cultural variation in men's preference for sexual dimorphism in women's faces. *Biology Letters, 10*.

Meisenberg, G. (2019). Social and reproductive success in the United States: The roles of income, education and cognition. *The Mankind Quarterley, 59*, 357–393.

Morrissey, M. B. (2014). Selection and evolution of causally covarying traits. *Evolution, 68*, 1748–1761.

Morrissey, M. B., & Sakrejda, K. (2013). Unification of regression-based methods for the analysis of natural selection. *Evolution, 67*, 2094–2100.

Nave, G., Jung, W. H., Karlsson Linnér, R., Kable, J. W., & Koellinger, P. D. (2019). Are bigger brains smarter? Evidence from a large-scale preregistered study. *Psychological Science, 30*, 43–54.

Nisén, J., Martikainen, P., Myrskylä, M., & Silventoinen, K. (2018). Education, other socioeconomic characteristics across the life course, and fertility among Finnish men. *European Journal of Population, 34*, 337–366.

Norman, K., Stobäus, N., Gonzalez, M. C., Schulzke, J.-D., & Pirlich, M. (2011). Hand grip strength: Outcome predictor and marker of nutritional status. *Clinical Nutrition, 30*, 135–142.

Polderman, T. J. C., Benyamin, B., de Leeuw, C. A., Sullivan, P. F., van Bochoven, A., Visscher, P. M., & Posthuma, D. (2015). Meta-analysis of the heritability of human traits based on fifty years of twin studies. *Nature Genetics, 47*, 702–709.

Power, C., Lake, J. K., & Cole, T. J. (1997). Body mass index and height from childhood to adulthood in the 1958 British born cohort. *The American Journal of Clinical Nutrition, 66*, 1094–1101.

Puur, A., Rahnu, L., Maslauskaitė, A., & Stankūnienė, V. (2016). The transforming educational gradient in marital disruption in northern Europe: A comparative study based on GGS data. *Journal of Comparative Family Studies, 47*, 87–109.

Roosenboom, J., Indencleef, K., Lee, M. K., Hoskens, H., White, J. D., Liu, D., … Hodges-Simeon, C. (2018). SNPs associated with testosterone levels influence human facial morphology. *Frontiers in Genetics, 9*, 497.

Rosseel, Y. (2012). Lavaan: An R package for structural equation modeling and more. Version 0.5–12 (BETA). *Journal of Statistical Software, 48*, 1–36.

Rushton, J. P. (1997). *Race, evolution, and behavior: A life history perspective.* New Brunswick and London: Transaction Publ.

Rutter, M., Moffitt, T. E., & Caspi, A. (2006). Gene–environment interplay and psychopathology: Multiple varieties but real effects. *Journal of Child Psychology and Psychiatry, 47*, 226–261.

Saar, E., & Aimre, K.-A. (2012). *Unequal educational transitions in Estonia: Tracking and family background.* Tallinn: Tallinna Ülikool.

Sakkeus, L., Klesment, M., & Puur, A. (2016). Parental home characteristics of the 1924–1983 birth cohorts in Estonia. *Generations in Estonia: Contemporary Perspectives on Turbulent Times, 5*, 70–102.

Sanjak, J. S., Sidorenko, J., Robinson, M. R., Thornton, K. R., & Visscher, P. M. (2018). Evidence of directional and stabilizing selection in contemporary humans. *Proceedings of the National Academy of Sciences, 115*, 151–156.

Savage, J. E., Jansen, P. R., Stringer, S., Watanabe, K., Bryois, J., de Leeuw, C. A., Nagel, M., et al. (2018). Genome-wide association meta-analysis in 269,867 individuals identifies new genetic and functional links to intelligence. *Nature Genetics, 50*, 912–919.

Schluter, D., & Nychka, D. (1994). Exploring fitness surfaces. *The American Naturalist, 143*, 597–616.

Silventoinen, K., Posthuma, D., van Beijsterveldt, T., Bartels, M., & Boomsma, D. I. (2006). Genetic contributions to the association between height and intelligence: Evidence from Dutch twin data from childhood to middle age. *Genes Brain and Behavior, 5*, 585–595.

Sim, K. (2013). The relationship between sex-typical body shape and quality indicators. *Journal of Social, Evolutionary, and Cultural Psychology, 7*, 97–120.

Sin, D. D., Wu, L., & Man, S. P. (2005). The relationship between reduced lung function and cardiovascular mortality: A population-based study and a systematic review of the literature. *Chest Journal, 127*, 1952–1959.

Skirbekk, V. (2008). Fertility trends by social status. *Demographic Research, 18*, 145–180.

Stearns, S. C., Byars, S. G., Govindaraju, D. R., & Ewbank, D. (2010). Measuring selection in contemporary human populations. *Nature Reviews Genetics, 11*, 611–622.

Stinchcombe, J. R., Agrawal, A. F., Hohenlohe, P. A., Arnold, S. J., & Blows, M. W. (2008). Estimating nonlinear selection gradients from quadratic regression coefficients: Double or nothing? *Evolution, 62*, 2435–2440.

Stulp, G., & Barrett, L. (2016). Evolutionary perspectives on human height variation. *Biological Reviews, 91*, 206–234.

Stulp, G., Barrett, L., Tropf, F. C., & Mills, M. (2015). Does natural selection favour taller stature among the tallest people on earth? *Proceedings of the Royal Society of London B: Biological Sciences, 282*.

Stulp, G., Verhulst, S., Pollet, T. V., & Buunk, A. P. (2012). The effect of female height on reproductive success is negative in western populations, but more variable in non-western populations. *American Journal of Human Biology, 24*, 486–494.

Tiit, E.-M. (2013). *Marriage and childbirth trends* (pp. 32–38). Tallinn: Census snapshots. Statistics Estonia.

Tyrrell, J., Jones, S. E., Beaumont, R., Astley, C. M., Lovell, R., Yaghootkar, H., … Frayling, T. M. (2016). Height, body mass index, and socioeconomic status: Mendelian randomisation study in UK biobank. *BMJ, 352*, i582.

Valge, M., Meitern, R., & Hõrak, P. (2019). Morphometric traits predict educational attainment independently of socioeconomic background. *BMC Public Health, 19*, 1696.

Victora, C. G., Adair, L., Fall, C., Hallal, P. C., Martorell, R., Richter, L., & Sachdev, H. S. (2008). Maternal and child undernutrition: Consequences for adult health and human capital. *The Lancet, 371*, 340–357.

Walsh, B., & Lynch, M. (2018). *Evolution and selection of quantitative traits.* Oxford University Press.

Wood, S. N. (2017). *Generalized additive models: An introduction with R.* Chapman and Hall/CRC.

Żelaźniewicz, A., & Pawłowski, B. (2018). Maternal hand grip strength in pregnancy, newborn sex and birth weight. *Early Human Development, 119*, 51–55.