

MARKUS VALGE

Testing the predictions of life history  
theory on anthropometric data





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on anthropometric data



UNIVERSITY OF TARTU

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Department of Zoology, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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## LIST OF ORIGINAL PAPERS

- I. Hõrak, P., Valge, M., Fischer, K., Mägi, R., Kaart, T. (2019). Parents of early maturing girls die younger. *Evolutionary Applications*, 12 (5), 1050–1061. <https://doi.org/10.1111/eva.12780>
- II. Valge, M., Meitern, R., Hõrak, P. (2019). Morphometric traits predict educational attainment independently of socioeconomic background. *BMC Public Health*, 19 (1), ARTN 1696. <https://doi.org/10.1186/s12889-019-8072-7>
- III. Valge, M., Hõrak, P., Henshaw, J. M. (2021). Natural selection on anthropometric traits of Estonian girls. *Evolution and Human Behaviour*, 42 (2), 81–90. <https://doi.org/10.1016/j.evolhumbehav.2020.07.013>
- IV. Valge, M., Meitern, R., Hõrak, P. (2021). Anthropometrics of Estonian children in relation to family disruption: Thrifty phenotype and Trivers–Willard effects. *Evolution Medicine and Public Health*, 9 (1), 276–286. <https://doi.org/10.1093/emph/eoab022>
- V. Valge, M., Meitern, R., Hõrak, P. (2022). Pubertal maturation is independent of family structure but daughters of divorced (but not dead) fathers start reproduction earlier. *Evolution and Human Behaviour*, 43 (2), 107–114. <https://doi.org/10.1016/j.evolhumbehav.2021.11.004>
- VI. Valge, M., Meitern, R., Hõrak, P. (2022). Sexually antagonistic selection on educational attainment and body size in Estonian children. *Annals of the New York Academy of Sciences*, in press

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	I	II	III	IV	V	VI
<b>Original idea</b>	*	**	**	**	**	**
<b>Study design</b>	**	***	***	***	***	***
<b>Data collection</b>	***	***	***	***	***	***
<b>Data analysis</b>	*	**	*	**	**	**
<b>Manuscript preparation</b>	*	**	**	**	**	**

# 1. INTRODUCTION

## 1.1 Life history theory

The *life history* (LH) of an organism describes its pattern of survival and reproduction across different stages of ontogenesis. Organisms must harvest and allocate limited resources between LH traits (i.e., traits that affect fitness). Each investment has its cost in time and energy and the same resource cannot be invested into different traits at the same time. This leads to trade-offs between competing traits and functions. It does not mean that organisms can only excel in one or the other, but that evolution is not constrained to linearity - optimal allocation between different fitness components is dynamic and varies within time and space. (Stearns & Hoekstra, 2005)

In the classical sense LH traits are traits directly related to reproduction and survival: size at birth, growth and maturation rate, adult size, number of offspring, lifespan, etc (Stearns & Hoekstra, 2005). In many organisms, these phenotypic outcomes are partly mediated by behavioural decisions and preferences (Del Giudice, 2020). According to LH theory, such variation is not distributed randomly, but selection should favour behavioural and physiological traits in intercorrelated adaptive sets (Reale et al., 2010). Covaried sets of classical LH traits and broad behavioural predispositions that mediate fitness outcomes form *life history strategies* (LHS) which can be thought of on a fast-slow continuum (Del Giudice, 2020).

The fast-slow continuum (or r/K) is based on population dynamics. r stands for an organisms' reproduction rate and K stands for the environment's carrying capacity. According to the original concept of r/K theory, selection is expected to maximise r in environments where fitness does not depend on population density, for example expanding populations that are well below the environment's carrying capacity. This occurs often in unpredictable settings, where the (cyclical) extrinsic mortality prevents the population from reaching resource depletion. When the size of a population grows and approaches the environment's carrying capacity, the density-dependent competition for available resources increases. If surviving such competition is determined by individual variation, the optimal allocation is predicted to shift from maximising reproductive ability towards the ability to compete over limited resources. In short, the fast-slow continuum describes LH trade-offs between quantity and quality. (MacArthur & Wilson, 1967; Pianka, 1970)

The original r/K framework found little empirical support as it assumed that r-selection should always favour the opposite traits of K-selection (Del Giudice, 2020). A direct link between population density or fluctuation and specific LH characteristics has not been established (Jeschke et al., 2008). For example, investing into a larger body under resource limitation is not necessarily optimal as larger individuals need more energy to sustain themselves (Jeschke et al., 2008). Or, even near an environments' carrying capacity, a trade-off towards rapid reproduction may give an edge in competitiveness (Reznick et al., 2002). Optimal

resource allocation between individual traits depends on local adaptive peaks which vary according to species' ecology and ontogenetic constraints (Del Giudice, 2020), and selection pressures on intercorrelated fitness components are hardly uniform. However, even if oversimplified, the key aspects of r/K selection theory are still accepted: LH traits vary in patterns and different traits are selected for in expanding populations than in populations nearing the environments' carrying capacity (Jeschke et al., 2008).

Among mammals, the fast-slow axis accounts for 70–80% of variance in the classical LH traits at the interspecies level (Del Giudice, 2020). The amount of variance described by a single axis drops to 30–50% after controlling for body size (Jeschke & Kokko, 2009). However, body size itself implicates LH trade-offs, making the theoretical basis for controlling it questionable (Del Giudice, 2020). The adaptive view of r/K selection is further disputed as much of the trait covariation is explained by phylogeny (Jeschke & Kokko, 2009; Stearns & Rodrigues, 2020). The closer the taxonomic units are zoomed in, from order to the families, from species towards the individual level, the less variance is reliably accounted for by the single axis. Even when the general patterns of LH variation are real, phylogenetic constraints and adaptive causes are not clearly distinguishable.

All else being equal, it costs more time and energy to produce larger, more durable offspring. In the adaptive paradigm, K-selection is expected to optimise for the ability to compete, i.e., somatic quality, larger size and survivability but also results in lower reproductive output, longer gestation, later maturity, etc. Fast LHS is characterised by traits that optimise for reproduction rate, this means quantity is preferred over quality: rapid growth and sexual maturation, higher fecundity, lower level of parental care, shorter life, higher impulsivity and risk-taking. (Pianka, 1970; Reale et al., 2010)

## **1.2 Life history strategies in humans**

Theoretical basis and empirical support for the adaptive clustering of LH traits at intra-specific level among individuals and groups is controversial (Royaute et al., 2018). Rushton (1985) proposed that individual, socioeconomic and racial variation, such as differences in brain size and intelligence, sexual maturation and behavior, parental care and lifespan, can be explained by differences in LHS. Since then, the idea that individual differences in behaviour and physiology can be understood by linking them to the fast-slow continuum has become popular in evolutionary psychology and behavioural genetics.

The opposition claims that extending interspecies trait covariation to individual differences is unjustified, based on flawed theoretical premises and incoherent methodology (Sear, 2020; Stearns & Rodrigues, 2020; Zietsch & Sidari, 2020). In self-reported behavioural traits for humans, trait placement on the fast-slow continuum is often inferred from correlation with other supposed traits, not by consistent theoretical background (Zietsch & Sidari, 2020). Others have questioned



the validity of mechanisms to retain LH variance inside populations (Stearns & Rodrigues 2020; Zietsch & Sidari, 2020).

In support of LHS differences between humans, genes associated with the variation in age at menarche, body size, intelligence, but also those influencing sexual behavior and time preference are intercorrelated in a predicted manner (Day et al., 2016; Mills et al., 2021). This suggests past interplay of similar selection pressures, directed by synergy of covaried behavioural and physiological traits (Figueredo et al., 2004). There is considerable heritable variation for human behaviour and LH (Figueredo et al., 2004; Turkheimer, 2000), including in traits directly correlating with fitness such as lifespan (van den Berg, et al., 2017) and speed of maturation (Ge et al., 2007; Kirk et al., 2001). When there is strong and consistent directional selection on a trait, natural selection tends to use up most of the genetic variation, reducing the heritable variance in that trait (Brisson, 2018). Hence, existence of such genetic variation suggests between trait trade-offs (Stearns, 1989). More is not always better when each investment has its cost. Genetic differences within population could be preserved by frequency-dependent selection and/or societal niches with varying LHS optima (Woodley of Menie et al., 2020).

Evidence for LHS differences at the level of phenotype are ambivalent and leave room for interpretation. Due to gene-environment interaction, different outcomes in phenotypes do not necessarily reflect different investments of the same magnitude (Black et al., 2017; Figueredo et al., 2014). While genetic correlation among traits is generally expressed in a similar correlation in phenotype (Sodini et al., 2018), differences in individual condition and resources may diminish or even reverse genetic correlation between expressed traits (Del Giudice, 2020; Lauringson et al., 2020; Stearns, 1989). In favourable settings, individuals may be able to harvest and invest more resources into multiple fitness components at the same time or reach fitness outcomes more easily, relaxing constraints in decisions of resource allocation (Del Giudice, 2020). For example, organisms could mature faster without sacrificing developmental quality (Hayward & Lummaa, 2013) or attractive individuals may achieve the same mating success with less effort (Del Giudice, 2020). To the contrary, lack of resources may restrict development and reduce heritable variance in trait expression (Stearns, 1989; Wells, 2013). Predicted covariation between the LH traits may become apparent only after confounding variance is controlled for.

Another debate contrasts genetic coadaptation with adaptive developmental plasticity (Zietsch & Sidari, 2020). Adaptive developmental plasticity centres on evolved developmental rules to early environmental conditions, aligning behaviour and developmental trajectories with perceived harshness of the environment (Draper & Harpending, 1982; Nettle & Bateson, 2015). Hence, trait covariation could reflect their plastic response to the same environmental stimuli, not heritable LHS on which natural selection can act upon. With recent discoveries in genetics, theories advancing fully environmental explanations have fallen out of favour (Zietsch & Sidari, 2020), but debate over proportions of adaptive plasticity and genetic predispositions as explanations for individual differences remains.

### 1.3 Gene-culture coevolution

Culture mediates the effect behaviour has on fitness outcomes (Figueredo et al., 2014). For example, with access to contraception, stronger urge to mate does not have to translate into more offspring. In addition, welfare states, universal health-care and technology drastically change dynamics of resource acquisition and mortality (Black et al., 2017; Del Giudice, 2020). Meanwhile, cultural adaptations and resource acquisition itself has a genetic component (Dawkins, 1982; Wells & Stock, 2020) and current choices determine organisms' future condition and opportunities. This forms a gene-culture feedback loop: culture which is influenced by biological predispositions modifies an ecological background. The ecological background is the stage for evolutionary selection; dampening or amplifying traits effect on fitness (Briley et al., 2015; Rutter et al., 2006).

As industrial production has increased the environment's carrying capacity exponentially, it is generally assumed that there should be a shift towards faster reproduction or r-strategy. This is not supported by broad trends in demography, as during the last century, the birth rates have drastically fallen for richer nations and social classes (reviewed by Lawson & Mace, 2010). LH theory does not predict individually optimised responses to novel cultural change, but that optimal response is determined by the population dynamics (MacArthur & Wilson, 1967). In industrial economies, the trade-off towards earlier maturation and *age at first birth* (AFB) seems to increase *lifetime reproductive success* (LRS) (Day et al., 2016; Sanjak et al., 2018; Tropf et al., 2015). The number of children is a strong positive predictor for the number of grandchildren, validating the use of LRS as a proxy for fitness (Kaplan et al., 1995; Zietsch et al., 2014). Culture can shift at a faster rate than biological selection is able to respond, creating a veil that masks underlying selection.

Reproductive interests are genetic interests: a distinction can be made between the ultimate interest, which serves genetic fitness and proximate, behaviorally expressed interests such as good health, partner and material wealth (Salter, 2006). The latter are subordinate goals that are valued because they mediate or have once mediated fitness outcomes. Perceived proximate interests and behavioural predispositions can be misplaced in a fast-changing cultural environment. Such mismatch does not imply that variation in phenotypes can not be studied, but that there are additional layers of variables to consider (Black et al., 2017). As long as there is genetic variance in fitness response to changing environments (Briley et al., 2015; Kirk et al., 2001), there is selection to align behavioural preferences and reproductive physiology with genetic interests (Collins & Page, 2019).

## 1.4 Aim of the thesis

Measuring LH differences in phenotypes is noisy. Nevertheless, natural selection can operate only on expressed traits (Sanjak et al., 2018; Stearns, 1989). This work aims to explore LH constraints and trade-offs in human growth and reproduction and to gain insight into cultural effects mediating these outcomes. I tried to describe the manifestation of LH differences and their complex feedback loops with everchanging environments. I wanted to add into the debate over adaptive plasticity and genetic coadaptation between LH traits by exploring contrasting scenarios as explanations for observed variation.

In the **first paper** I tested whether two markers of the rate of sexual maturation of girls, measured under different settings, predict parental lifespan and whether this relation depends on the quality of home environment, assessed on the basis of parental education and *socioeconomic position* (SEP). I predicted that the association between daughters' pubertal maturation and parental lifespan would be manifested contingent upon interaction with the quality of home environment, so that the measures of puberty predict parental lifespan most strongly in well-off families. This prediction is based on the assumption that among girls growing up in families of well-educated parents or those in non-manual professions, variation in the rate of sexual development is more likely to reflect genetic differences between individuals than among girls growing up in less affluent environments (Bolund et al., 2015).

In the **second paper** I described the relation between anthropometric traits and educational attainment. Links between morphometric traits and educational attainment are relevant because higher education is nearly universally associated with low fertility in women and often with high fertility in men (Stearns et al., 2012). Hence, morphometric traits associated with educational attainment could be targets of natural selection. I explored the generality of associations between individual morphometric traits and educational attainment for both sexes in different environmental settings while controlling for allometrically intercorrelated body dimensions.

In the **third paper** I described fecundity selection on 13 anthropometric traits in girls. I described direct and indirect selection via behavioural pathways and explored the idea of gene-culture coevolution. Individual variation can causally influence cultural outcomes, which in turn have influences over LRS (Stulp et al., 2012). Meanwhile, common biological predispositions have influence over both. Such cultural layers can dampen or amplify traits' effect on fitness outcomes, mediate biological selection and create external thresholds for optimal LHS.

In the **fourth paper** I tested the predictions of the thrifty phenotype and Trivers-Willard hypothesis (TWH) in relation to family disruption. According to the thrifty phenotype hypothesis, under resource limitation, organs essential for survival are protected at the cost of less important body parts (Pomeroy et al., 2012; Wells, 2013). Since LRS is more sensitive to condition in males than for females, the TWH (Trivers & Willard, 1973) posits that selection should favour production of daughters in poor conditions. By extension, Wells (2000) suggests

that natural selection should favour greater male sensitivity to early life environmental stress. I compared growth patterns of children from different types of disrupted families, ranked according to the level of psychosocial stress and material affluence. I expected to detect distinctive plasticity in different body parts and manifestation of sex-specific constraints in growth.

In the **fifth paper** I examined the rate of maturation and patterns of reproduction of girls from disrupted families. Family disruption provides cues about the conditions and stability of the future environment. In an unpredictable environment the optimal trade-off is thought to be biased towards earlier reproduction with adaptive plasticity theories predicting a shift towards faster LHS and short-term mating strategy in response to poor parental care (Belsky et al., 1991). Sexual development may be especially sensitive, as some studies cite deceleration and some acceleration of maturation in response to psychosocial stress (reviewed by Ellis, 2004). I described the rate of maturation, AFB and LRS of girls from different types of disrupted families and explored alternative scenarios as explanations for the findings.

In the **sixth paper** I described fecundity selection for both males and females in relation to educational attainment and anthropometric traits. Morphometric traits predict the odds of obtaining higher education in a similar fashion for both men and women (Valge et al., 2019). However, studies suggest that education has a sexually antagonistic effect on fitness. I described the magnitude of selection for body shape and size, the role of educational attainment in mediating this selection and sex differences in the patterns of parity transitions.

## 2. MATERIALS AND METHODS

### 2.1 Historical background

The social setting of the current study is different from that of the typically studied *western, educated, industrialised, rich and democratic* (WEIRD) populations. While culturally and genetically European (Nelis et al., 2009), Estonia was neither rich nor democratic.

The main dataset used in the study includes children born between 1936 and 1962 (average = 1949 ± 4.8 (SD)). During the study period, Estonian economy was under the Soviet state socialist regime characterised by low returns from education in the labour market, state-guaranteed full employment, highly structured career paths and broad coverage of public childcare.

The demographic history of Estonia during the study period differs from WEIRD countries. The post-war baby boom was absent in Estonia, which from the late 1940s to the middle of 1960s had one of the lowest fertility rates in the world (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 et al., 2010). Despite these demographic differences, the social factors known to influence reproductive behaviour developed at similar or faster rates in Estonia than in many WEIRD populations. For instance, divorce rates started to rise already during the interwar period (Sakkeus et al., 2016), equalling or exceeding those of Scandinavian countries from the 1970s onwards. Over the same period, unmarried cohabitation began to prevail over marriage (Puur et al., 2016).

Beginning with the birth cohorts of the 1930s, women outnumbered men in secondary and tertiary education (Klesment, 2013). 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). Comparable statistics for male LRS and educational level in Estonia remain absent, but studies suggest a directionally opposite effect of education on male LRS (Jalovaara et al., 2018; Stearns et al., 2012).

Prof. Juhan Aul's anthropometric dataset was studied in **papers I–VI**. In addition to anthropometric data, the Estonian Biobank sample was analysed in **paper I**.

## 2.2 Materials

### 2.2.1 Prof. Juhan Aul's anthropometric dataset

The anthropometric data was collected by the founder of physiological anthropology in Estonia, prof. Juhan Aul (1897–1994). The aim of the original project was typical to the first half of the 20th century: to map the diversity of body size and shape, as well as rates of growth and pubertal maturation of children concerning their birth years, geographic location, social, urban/rural origin (Aul, 1982). During his career, prof. Juhan Aul measured and described over 50 000 people (Kaevats, 2000).

**Papers I–VI** are based on data collected on schoolchildren's morphometry and family background (Fig.1) between 1956 and 1969 (Aul, 1982). Anthropometric variables were recorded according to Martin (1928). Handgrip strength was registered with a dynamometer. Rate of sexual maturation was described on the basis of visual inspection in five stages according to the Tanner scale (Marshall & Tanner, 1969; Marshall & Tanner, 1970).

The dataset covers Estonian schools in major cities (Tallinn, Tartu, Pärnu, Kohtla-Järve) and extensive rural areas in mainland Estonia (Fig. 2). Since Russian language schools are missing from the sample, the study is nationally representative for the Estonian speaking population only.

Prof. Aul's dataset is free of volunteer bias and covers all social strata in both urban and rural populations. The sample is almost free of survivorship bias, as all participants were younger than 20 years. Measurements were collected before the participants finalised their education or started to reproduce, excluding potential bi-directional effects.

### 2.2.2 Estonian Biobank dataset

For **paper I**, the Estonian Biobank data was obtained from the Estonian Genome Centre. Estonian Genome Centre at the University of Tartu is a population-based biobank that recruited a cohort of 51 756 participants, including adults from all counties in Estonia, accounting for approximately 5% of the Estonian adult population during the recruitment period between 2002 and 2012 (Leitsalu et al., 2014). An extensive phenotype questionnaire, including questions about parental age at death and participant's age at menarche, with a precision of 1 year, was conducted together with a measurement panel.

Nr. 35 Antropoloogiline vaatlusleht. Vorm nr. 3

Name Valteri t.

Date of Birth [redacted] Age: 16 y. 2 m.

Studies at [redacted] school X grade

Address/ukoht [redacted]

Parental origin [redacted]

Parental workplace [redacted]

Parental occupation [redacted]

Parental ethnicity estlane Sisters - Brothers avg.

Hair colour must, pruun, ruuge; hele, tume, kollakas, tuhkas Nr. 7

Eye colour kirju, hele, tume; sinine, hall, rohekas, kollakas, pruun, 46

Nose shape otse, nõgus, kumer, lainjas; vähe, palju

Body type on: lepto-, meso-, eürüsoomne; muskulaarne, respiratoorne, digestiivne, tserebraalne. Toitumus: 1 2 3 4 5

Mam 0 1 2 3 4 Pub 0 1 2 3 4 Axilla 0 1 2 3, Men

Skinfold Illiospinale 110 Thigh 520

Academic perf. weak below avg. average good very good circum.

Märkusi Epheides 1 2 3 10. 74.50 54.2

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750 rotaplaat 1967. 3500. 2. 396.

1) i. 300 wh 3) 2pk.  
e. 120  
2) i. 3 i. 4 0.7

Height 162.3 42.6

Shoulderph. 132.3, 632, 691

Sitting h. 900 55.4

Shoulder w. 357 21.9

Chest meas. 140, 174, 72, 10

Hip width 266 16.3

Chest circum. 810 28

Head length 181

Head width 148

Face width 111, 135, 103

Face height 123 11.5

Weight 53.6 156

Lung capacity 3.6

Hand grip str. 30/27

Rohrerri ind. 1.26

Queletel ind. 2.04

Pea p. l. ind. 81.8

M. näoindeks 85.2

Grade Point Average 27

Figure 1. The anthropometric data sheet used by prof. Juhan Aul.

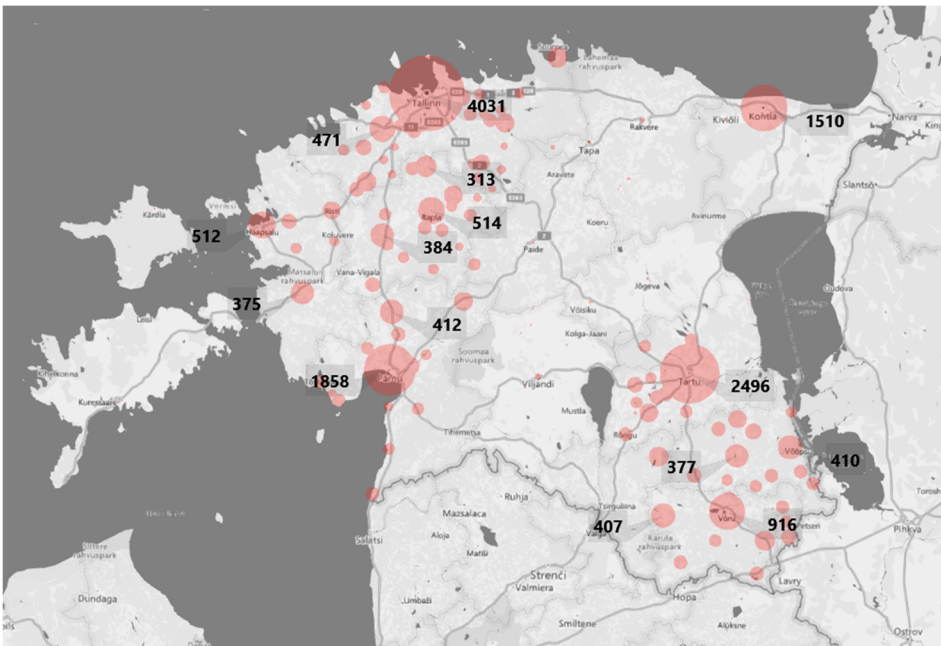


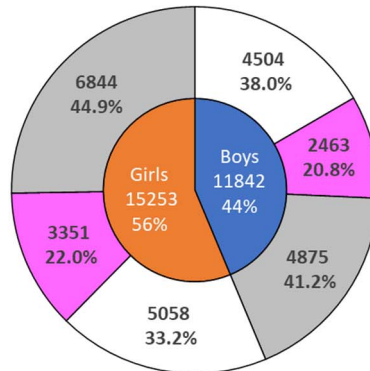
Figure 2. The anthropometric dataset covers Estonian schools in major cities (Tallinn, Tartu, Pärnu, Kohtla-Järve) and extensive rural areas in mainland Estonia. Numbers indicate sample sizes for major regions.

## 2.3 Methods

### 2.3.1 Study design

The data for LRS, AFB, educational attainment and parental lifespan for the anthropometric sample and the data for parental education for the biobank sample was obtained from the Estonian Population Registry. Records on lifespan and LRS were available as of 2018. Data on educational attainment was based on the Estonian population census of 2011. Data processing was carried out anonymously under the licence of the Research Ethics Committee of the University of Tartu.

The full anthropometric dataset involved 15 253 girls and 11 842 boys (for both, average age =  $12.7 \pm 6.4$  (SD) years, range = 6.4–20.0 years). About 60% could later be identified to assess their LRS. For a subset of those identified, 11 719 had their educational attainment recorded (Fig. 3). 11 502 individuals had their fathers' and/or 11 244 had their mothers' age of death (or age, if alive) available.



**Figure 3.** Sample sizes from the anthropometric dataset. Unshaded areas – children with anthropometric data only, grey – data for both educational attainment and LRS, purple – data for LRS but not for educational attainment.

In the Estonian Biobank sample, 17 280 girls born between 1925 and 1996 (average =  $1970 \pm 13.9$  (SD)) had data for menarcheal age and parental education available. Of these, 15 210 girls had their fathers' and/or 15 381 had their mothers' age of death (or age, if alive) recorded.

The study design collating data of individual ontogenetic variation and socioeconomic background along with biosocial outcomes (Table 1) enabled to test for a number of LH theory predictions. Differences in LRS determine strength and direction of selection. Educational attainment gives insight into the gene-environment interaction and the potential behavioural pathways mediating selection. Variation in growth and maturation under different socioeconomic settings provides cues about trade-offs and constraints in construction of the individual body.



**Table 1.** An example of traits and biosocial variables used in the studies.

<b>Trait</b>	<b>Predicts</b>	<b>Cite</b>
Cranial volume	(+) brain size; (+) intelligence; (+) socioeconomic success	Rushton & Ankney, 2009
Face width	(+) adolescent testosterone; (+) perceived dominance	Hahn et al., 2017; Lefevre et al., 2013; Tyrrell et al, 2016
Jaw width	(+) adolescent testosterone; (+) male attractiveness; (+) perceived dominance	Fink et al., 2005; Whitehouse et al., 2015
Shoulder width	(+) male attractiveness; (+) male maturation; (+) testosterone	Kasperk et al., 1997; Sim, 2013
Shoulder/hip ratio	(-) female attractiveness; (+) male attractiveness; (+) male maturation; (+) testosterone	Gallup & Fink, 2018; Sim, 2013
Handgrip strength	(+) health outcomes; (+) male attractiveness; (+) male maturation; (+) testosterone	Gallup et al., 2007; Gallup & Fink, 2018
Height	(+) intelligence; (-) female LRS; (+) male attractiveness; (+) socioeconomic success; (+) somatic quality	Keller et al., 2013; Stulp & Barrett, 2014
Sitting height	least plastic indicator of height	Bogin & Varela-Silva, 2010; Rios et al., 2020
Leg length	(+) childhood environmental quality; most plastic indicator of height	Bogin & Varela-Silva, 2010; Rios et al., 2020
Leg/torso ratio	(+) attractiveness; (+) childhood environmental quality; (+) health outcomes	Bogin & Varela-Silva, 2010; Rios et al., 2020
Thorax circumference	(+) health outcomes; (+) respiratory function	Zeng et al., 2017
Lung (vital) capacity	(+) health outcomes; (+) respiratory function	Batty et al., 2006; Victora et al., 2008
Hip width	(+) estrogen; (+) female attractiveness; (+) female maturation	Ellison, 2001
Breast dev.rate	(+) estrogen; (+) female maturation	Ellison, 2001; Euling et al., 2007
(earlier) age at menarche	(-) adult height; (+) BMI; (+) earlier AFB; (+) earlier first intercourse; (+) LRS; (-) longevity	Day et al., 2016; Mills et al., 2021; Mostafavi et al., 2017
BMI	(-) female attractiveness; (+) female maturation; (+) nutritional state	Courtiol et al., 2010; Day et al., 2016
<b>Covariate</b>	<b>Predicts</b>	<b>Cite</b>
(childhood) SEP/Parent. ed.	(+) childhood environmental quality; (+) height; (+) intelligence	Ivanovic et al., 2019; Silventoinen, 2003; Strenze, 2015
Parental absence	(-) childhood environmental quality; (+) earlier maturation; (+) earlier AFB; (+) earlier first intercourse	Day et al., 2016; Sear et al., 2019; Webster et al., 2014
Ed. attainment	(+) intelligence; (-) female LRS; (+) male LRS; (+) socioeconomic success	Stearns et al., 2012; Strenze, 2015
(earlier) AFB	(+) earlier maturation; (+) LRS; (-) longevity	Day et al., 2016; Mills et al., 2021; Mostafavi et al., 2017; Sanjak et al., 2018

### **2.3.2 Data analysis**

In **all papers** educational attainment was divided into three categories: primary (8 years of schooling or less), secondary (including secondary vocational) and tertiary (> 11 years of schooling). On the basis of parental professions recorded during data collection, participants were assigned to parental SEP values (highest in the family) as unskilled manual workers, skilled manual workers or non-manual workers.

Cranial volume was estimated from measures of head height and width using formulas by Rushton (2000). Age- and sex-specific residuals of anthropometric traits were calculated from generalised additive models in which the focal trait was regressed against smooth nonparametric functions of age (in days) and birth date. Birth date was included as a predictor to account for the steady increase in age-adjusted body dimensions over the study period. Residuals were then standardised to z-scores within sexes. All results presented in the studies are based on these standardised residuals rather than raw trait values.

In females, LRS and AFB were standardised relative to the average of her year's cohort. As the data on cohort-specific fertility of Estonian men is less precise, LRS in males was standardised relative to the average of the studied sample.

For **papers IV, V and VI** the method of exact covariate matching was used. In covariate matching, each child from “treatment” group was matched with children from “control group” based on sex, age, year of birth, urban/rural origin and family SEP.

To assess the heritability of menarcheal age in **paper I**, its variance components were calculated from the pedigree data which provides estimates of heritability, additive genetic, phenotypic and residual variance (Groeneveld et al., 2010). This was based on an animal model, in which an individual's phenotype is broken down into its components of additive genetic value and other random and fixed effects. The pedigree was based on information about mother–daughter pairs and sisters with known menarcheal age.

Sample sizes vary between studies and analyses because participants differed with respect to the number of anthropometric and biosocial traits recorded.

## 3. RESULTS AND DISCUSSION

### 3.1 Adaptive plasticity and heritable predispositions (I; IV; V)

#### 3.1.1 *Daughters' rate of sexual maturation and parental lifespan (I)*

A phenotype is genes expressed in an environment. In an identical environment all variance in expressed traits must be genetic. The environmental contribution to the variance in phenotypes increases along the differences in between-individual availability of resources (Del Giudice, 2020; Lauringson et al., 2020). Growth in vital organs may be prioritised under resource limitation (Wells, 2013). Given that there are common requirements for survival, such organ-specific plasticity might reduce between-individual variability in poor conditions. Meanwhile, growth response to environmental improvements is subject to diminishing returns as phenotypes near their genetic optimum (Lynn, 1996). As variance in developmental plasticity diminishes in environmental extremes, genetic differences are likely most exposed under affluent material settings where attenuated energetic constraints enable phenotypes to realise their potential more easily (Conley et al., 2016; Silventoinen, 2003).

Faster sexual development has its costs on somatic growth and quality (Mendle et al., 2007; Charalampopoulos et al., 2014). When mortality is less dependent on individual condition, the optimal trade-off is tilted towards earlier reproduction (Stearns & Hoekstra, 2005). Thus, according to the LH theory, speed of maturation should evolve to track the variation in mortality rates. In **paper I** I tested whether markers of the rate of sexual maturation of women predict the age at death of their parents.

Children inherit 50% of each of their parents' genomes, so that the phenotype of offspring can be used as a proxy measure of parental genotype (Conley & Sotoudeh, 2016). Children with a genetic predisposition for faster sexual maturation are predicted to have parents with propensity to die early. Measuring the rate of maturation in the offspring and age at death of their parents excludes some of the potentially confounding effects of external factors that could affect individual maturation and lifespan simultaneously (Conley & Sotoudeh, 2016). I expected to detect a pattern in which predicted genetic differences are best revealed in the phenotype under conditions of environmental affluence.

The biobank dataset was used to calculate the heritability of menarcheal age in relation to parental education. As predicted, heritability was highest in well-educated families. In accordance with the secular trend, age at menarche decreased with the year of birth. The rate of this decline was faster among women from families with primary education than among those from highly educated families, suggesting diminishing returns from the improvement of living standards and/or social stratification by the lines of genetic predispositions for speed of maturation. Such stratification was further indicated by the finding that

differences in menarcheal age between the women from highly and poorly educated families increased in the model adjusting for BMI and height.

Age at menarche among the participants of the Estonian Biobank did not predict the age of death of their mothers, but in the interaction with education it did predict survival of their fathers. In families where at least one of the parents had tertiary education, one year delay in menarche corresponded to a 9% lower hazard of fathers' death. In anthropometric dataset, irrespective of parental SEP, the rate of breast development predicted lifespan of both mothers and fathers, so that parents of rapidly maturing girls died at a younger age. Mothers of the girls within the highest quantile of breast development rate had 11% higher chances of death than mothers of those in the first quarter. In the case of fathers, the difference was 14%.

The biobank sample was different from the anthropometric sample in that the parents of the biobank participants were born on average two decades later. Therefore, most of the parents in the biobank sample were still alive at the time of study and those who died died at a relatively young age. As the heritability of lifespan is highest among the elderly (Giuliani et al., 2018), genetic differences in longevity distinguishing parents of slowly and rapidly maturing girls may manifest only after a certain age. This was illustrated in the interaction between daughters' breast development and parental lifespan – the trend emerged after the age 80 in mothers and 75 in fathers (97% of parents from the anthropometric sample were dead as of 2018). As to why there was interaction between age of death and daughters age at menarche for fathers, but not for mothers, may be because life expectancy in Estonia has been 9–10 years lower for males than for females during most of the study period (Rahu et al., 2019).

The detected pattern in interaction between daughters' maturation and parental lifespan is best explained by genetic covariation of LH traits. Accelerated development was not induced by parental death, but parents of early-maturing girls died younger. Heritability of menarcheal age was highest in well-educated families and the interaction between daughters' age at menarche and fathers' lifespan depended on the quality of home environment.

### **3.1.2 The thrifty phenotype (IV)**

Trade-offs manifest in the construction of the individual body, between competing traits and functions (reviewed in Shirley et al., 2017). According to the thrifty phenotype hypothesis, environmental stress affects different tissues of developing organisms to different degrees (Wells, 2013). Under predicament, limited resources are predicted to be channelled into functions that are essential for survival. Vital organs such as the brain and lungs, i.e., growth of head and trunk are expected to be prioritised over extremities (Pomeroy et al., 2012).

Human growth is not linear and development has critical timespans during which different traits are sensitive to environmental stress (Hörak & Valge, 2015; Said-Mohamed et al., 2018). Trade-offs during these periods are not fully reversible once the developmental windows have passed (Wells, 2013). While it is generally

agreed that poor energetic conditions stunt growth and delay development for everyone, the effect of psychosocial stress is more ambivalent (Ellis, 2004). Predictive-adaptive hypothesis emphasises the role of perceived parental care as a cue for stability of the future environment, predicting a shift towards faster LHS in response to neglect (Draper & Harpending, 1982). Contrary, studies find developmental delays not fully explained by nutrition in institutionalised children (reviewed by van Ijzendoorn et al., 2020). In **paper IV** I compared growth patterns of children from different types of disrupted families, ranked according to the level of psychosocial stress and material affluence.

I compared children growing up in orphanages, those with dead mothers or fathers, and those with divorced fathers with children from bi-parental families. I expected to find the most extreme patterns of stunted growth in institutionalised children, followed by children whose mothers were dead as mothers invest more time and effort towards parenting (Lawson & Mace, 2009). Assuming that separated fathers were obliged to pay alimony, their children were likely better off than children with a dead parent in terms of material affluence. Further, men prone to divorce may have higher testosterone (Schmitt, 2015); so, I predicted that their children possess more masculine bodies. I considered heritable LH differences as alternative explanations for observed growth patterns (Figueredo et al., 2005).

In most traits, growth of boys and girls were similarly suppressed in orphanages. Orphans displayed the most extreme differences compared to controls from bi-parental families, with 9 traits out of 14 affected. The largest difference was in leg length, followed by height and cranial volume. Orphans had narrower hips, shoulders and faces, and boys were 0.5 SD weaker than controls. Legs of institutionalised children were on average 0.5 SD shorter, whereas the difference in sitting height was only 0.2 SD, thorax circumference and BMI were not different from that of controls. As the cranial volume of orphans was 0.4 SD smaller than controls, protection of brain growth was not observed.

I did not have data about the parents of the orphans so I could not distinguish between environmental constraints and hereditary effects as causes for their small size. Parents of institutionalised children do not comprise of a random population sample concerning alcohol abuse, psychiatric disabilities and poverty (Landgren et al., 2006). As brain size is causally related to intelligence and socioeconomic success (Rushton & Ankney, 2009), a sizable proportion of children in orphanages may possess parents with small brains, so that the average cranial volume of institutionalised children may be small for hereditary reasons. I did not have an explanation as to why parents of institutionalised children should possess relatively larger trunks than the general population. Thus, the findings from orphanages offer partial support for the hypothesis that at resource limitation, vital organs are protected at a cost of extremities.

### **3.1.3 Sex differences and Trivers-Willard hypothesis (IV; V)**

The TWH (Trivers & Willard, 1973) posits that under poor conditions, selection should favour production of and investment in daughters. Most daughters are likely to be mated, whereas poorly developed sons are likely to be outcompeted by other males. By the same logic, Wells (2000) suggests that selection should favour greater male vulnerability to early life conditions. Growth in boys is more likely to be stunted and their sexual development is delayed further than in girls under poor conditions (Euling et al., 2007; Thurstans et al., 2020). The dynamics underlying TWH predictions are further reflected in the general trend of females entering puberty earlier and undergoing faster pubertal transition (Wells, 2007). The optimal balance for energy allocation between somatic and reproductive investment is likely sex dependent (Ellison, 2001).

Males and females invest energy differently between competing body parts during the course of their lives (Ellison, 2001; Shirley et al., 2017). During puberty, endocrine systems play a major role in regulating trade-offs between growth and reproduction, allowing sexes to prioritise different traits (Ellison, 2001). Resulting sexual dimorphism is largely attributable to sex steroid hormones, testosterone being especially important for men (Shirley et al., 2017). The coordinating role of endocrine systems in many LH trade-offs but also the effect hormones have on behaviour makes variance in traits influenced by hormonal levels especially interesting (reviewed by Del Giudice, 2020). In **paper IV** I tested for the occurrence of sex-specific growth responses to family disruption and in **paper V** I examined patterns of female maturation under the same conditions.

Compared to girls, boys were relatively most affected by the loss of their mothers. Boys with dead mothers were about 0.2 SD weaker and lighter, had smaller thorax circumference, and narrower shoulders and faces than boys from the bi-parental families. Maternal orphanhood had sex-specific associations with height, weight, thorax circumference, shoulder width, cranial volume and face width. The direction of sex-specific divergence was similar but less pronounced in the conditions with a missing father. Sons of divorced fathers had wider shoulders and a (statistically insignificant) tendency to be of a larger growth than boys whose fathers were dead. Breast development rate did not differ between girls from disrupted and bi-parental families.

The findings cast doubt on the generality of male vulnerability, as for most of the traits, growth in orphanages was similarly suppressed in both sexes. The sex-specific divergence of growth in disrupted families was more pronounced in children living with a biological parent. These children were likely less deprived than those who were institutionalised and confounding variance was reduced when comparing them with the controls, as their parental SEP and origin could be matched for. Survival may be prioritised over growth in poor conditions (Wells, 2013). Hence, sex-divergent growth could be more outlined in favorable settings after the gender-neutral goal of subsistence is ensured (Falk & Hermle, 2018; German & Hochberg, 2020). However, even in orphanages boys (but not girls) were weaker than controls.

The sex-specific growth suppression, most pronounced in the children with dead mothers, revealed a common (yet in several cases statistically insignificant) pattern. In all types of family disruptions, girls were relatively larger than boys and in some traits girls were even larger than bi-parental controls. Comparatively, boys were most affected by the loss of the mother and least affected under the condition of paternal divorce. Clearest sex-specific associations were detected in testosterone dependent traits, such as face width, handgrip strength and shoulder width (Gallup & Fink, 2018). The suppression of these traits in boys could reflect their slower pubertal development. For girls growing up with one parent, measures of weight and trunk were not negatively affected but showed a tendency to be larger than those of controls, potentially indicating earlier female maturation in disrupted families (Bogin & Varela-Silva, 2010; Day et al., 2016).

Evidence for earlier maturation in disrupted families from non-WEIRD countries are mixed, but the general trend suggests that the boys are more likely to delay and girls to accelerate puberty (Sear et al., 2019). If the growth of girls was less inhibited than the growth of boys in disrupted families due to these girls maturing faster sexually, it was not reflected in the rate of their breast development. The utilisation of breast development rate when comparing the pubertal development of girls was a major difference with most studies, as rate of maturation is typically assessed by menarcheal age. A meta-analysis of 33 studies found that in 32 of those, absence of the father was associated with earlier menarche (Webster et al., 2014). Although age at menarche and the rate of breast development depend on the same hormones (Ellison, 2001), the few studies that have examined phenotypic correlations between these traits at the individual level have found only moderate associations (Euling et al., 2007; Rapkin et al., 2006). Developmental pathways linking these two markers of the rate of sexual maturation may not be identical, but relate in non-linear fashion (Euling et al., 2007).

Accelerated maturation under psychosocial stress was not detected. Growth was most suppressed in both sexes in orphanages, there was clear sex-dependent interaction in which male (but not female) growth was suppressed in children with dead mothers and conditions with missing fathers revealed significant interaction only for a few traits. Hence, the death of a mother, a condition assumed to have higher psychosocial stress, but less material disadvantage than the death of a father, had no specific effect on female maturation but inhibited growth in boys. These results fit best with a model in which maturation in both sexes responds to high psychosocial stress and poor material conditions negatively, boys being more sensitive to both.

Children from disturbed households likely inherit propensity for faster LHS from their parents (Figueredo et al., 2005). Hence, the association between pubertal maturation and family disruption might reflect effects of transmitted genes that contribute to both (Barbaro et al., 2017; Mendle et al., 2006; Mills et al., 2021). Genetic factors account for 13–53% of variation in divorce (Salvatore et al., 2018). In men, this variation is partly mediated by levels of testosterone (Schmitt, 2015), which in turn correlates with morphological differences (Gallup & Fink, 2018; Shirley et al., 2017). This is consistent with the finding that sons of divorced fathers had more masculine-shaped bodies than those whose fathers were dead.

Assuming that divorced fathers were obligated to pay alimony, their children were least likely deprived materially and relatively low on psychosocial stress. Consequently, the growth in boys, which is more sensitive to environmental stress (Thurstans et al., 2020; Wells, 2000), was comparatively least affected.

The results suggest that poor material conditions and psychosocial stress inhibit development in both sexes. Speed of sexual maturation depends on the environment, but there is also heritable variation in trade-offs and in thresholds of time and condition mediating developmental plasticity (Said-Mohamed et al., 2017). Under this scenario, earlier sexual maturation associates with parental neglect, because children from disrupted families inherit genetic predisposition for faster LHS from their parents. As male growth is more sensitive to environmental stress, there is likely a sex-dependent environmental threshold to expose such predispositions (Euling et al., 2007; Thurstans et al., 2020). This notion is supported in a review by Sear et al. (2019): studies of parental absence and pubertal development undertaken in rich environments tend to find accelerated maturation in both sexes, in poor environments in neither, and mixed results tilted towards faster maturation in girls in settings in between.

### **3.2 Morphometric traits and educational attainment (II)**

While phenotype is an expression of genes in an environment, the environment itself is manipulated by the genes (Briley et al., 2015; Dawkins, 1982; Wells & Stock, 2020). Early life conditions are shaped by genetically similar kin (Kendler & Baker, 2007) and individual predispositions affect preferences and ability when choosing their own societal niche (Woodley of Menie et al., 2020).

According to LH theory, traits characteristic for slow life have coevolved with high intelligence and conscientious personality (Figueredo et al., 2013), i.e., traits commonly associated with the ability to acquire resources in the modern environment (Strenze, 2015). Patterns of growth covary with intelligence and socioeconomic success (Ivanovic et al., 2019; Silventoinen, 2003), but causal chains are hard to determine. Common environmental factors could underpin variation in both with morphological differences having no effect on their own (Brito et al., 2017; Kobayashi et al., 2019). In addition, growth is allometrically intercorrelated, which makes accounting for general size factor important when trying to identify individual morphometric traits as predictors for socioeconomic outcomes. In **paper II** I examined cranial volume, height and face width (a testosterone-dependent trait) as independent predictors for educational attainment and tested for the generalisability of such associations between sexes and different social settings.

Parental SEP was the best predictor for children's educational attainment. Children whose parents were in non-manual professions had 3.6 times higher and children whose parents were in skilled manual professions had 1.5 times higher cumulative odds of obtaining an educational level beyond primary than the children of unskilled manual workers. Being of rural (vs urban) origin reduced the odds of obtaining education beyond primary level by 44% and being a boy



(vs girl) by 47%. After adjusting for biosocial variables, all morphometric traits independently predicted educational attainment. Within each category of parental SEP, rural and urban origin and sex, taller children and those with larger heads and narrower faces were more likely to proceed to higher education.

The simplest explanation why cranial volume is a predictor for educational attainment is its correlation with brain size, which in turn is correlated with intelligence (Rushton & Ankney, 2009). The results are very similar to the largest study conducted on the relation between education and brain size which, after controlling for SEP and height, found a positive correlation between brain volume and educational attainment in the UK Biobank sample (Nave et al., 2017). Brain size seems to be a robust predictor of educational attainment, irrespective of the method of measurement or whether the educational system exists under market or soviet economy.

The study adds to the findings that height is positively associated with educational attainment. One of the likely reasons for this association is genetic correlation between height and IQ (Silventoinen et al., 2006). This may occur either because the sets of genes affecting these traits pleiotropically overlap and/or because cross-trait assortative mating for height and education as components for individual quality (Keller et al., 2013). Importantly, the effect of height on education was independent of cranial volume. Taller children did not obtain more education because their brains were larger than those of shorter children; height alone was also important.

Unlike for height and cranial volume, I had no firm predictions about the direction of association between face width and educational attainment. The result that both boys and girls with narrower, less masculine faces were more likely to obtain higher education is notable as it contrasts with previous finding that both male and female university students with relatively wider faces gained better grades in orally examined courses (Kausel et al., 2018) and that facial masculinity predicts success in various competitive settings (Hahn et al., 2017). On the other hand, the results compare favourably with those of a study of US military veterans whose serum testosterone levels correlated negatively with the years of education (Dabbs, 1992). Dabbs suggests that characteristic interests could lead high-testosterone individuals away from school and towards a world of action. High levels of testosterone are linked to impulsivity and weaker behavioural control (Doi et al., 2015), i.e., traits associated with the fast LHS and low educational attainment (Del Giudice, 2014). The relation between testosterone and accomplishment is likely context specific.

The findings provide important cues about the study environment. The more freedom people have from cultural and material restraints, the more individual genetic variation is expressed in their chosen environment (Barban et al., 2021; Schmitt et al., 2009). Irrespective of exact causality pathways, it is shown that within and between socioeconomic strata, a detectable meritocracy and free choice existed in the Estonian educational system under the Soviet regime. Hence, individual covariates such as parental SEP and urban/rural origin are at least in part endogenous (Dawkins, 1982; Saar & Helemäe, 2021; Trzaskowski et al., 2014). Independent links between morphological characteristics and educational

attainment demonstrate how cultural niches pull together people with similar biological variation (Abdellaoui et al., 2019; Woodley of Menie et al., 2020). Resulting social assortment may lead to genetically stratified indirect selection (Hugh-Jones & Abdellaoui, 2021).

### **3.3 Reproduction (III; V; VI)**

#### ***3.3.1 Selection for body shape and size (III; V; VI)***

Variation in growth and maturation is important, but in a broad view development is simply a phase preceding ultimate genetic interests of reproduction. Predictions of LH theory and TWH derive from the variation in fitness from which other covariations are deduced. Ancestral mismatch and gene-environment interaction complicates the usage of evolutionary framework in the study of fitness outcomes, but these outcomes determine strength and direction of ongoing selection.

The general prediction is that a shift towards faster reproduction is adaptive in a population well below environment's carrying capacity (MacArthur & Wilson, 1967). But in a sexually reproducing species, the increased investment into reproduction is not as straightforward as a simple quality or quantity factor. Even in an environment with diminished mortality, male LRS is directly related to his ability to acquire mates (Trivers & Willard, 1973; Weatherhead & Robertson, 1979). While stronger and larger males are generally considered most attractive (Gallup & Fink, 2018), females may weigh physical attractiveness and long term provisioning in their partners differently depending on their own LH predispositions (Buss & Schmitt, 2019). When parental investment gets decoupled from offspring fitness, the selection in males is predicted to shift from long-term parental care towards a short-term mating effort (Trivers, 1972; Weatherhead & Robertson, 1979). In such conditions, women tend to put more value in traits that emphasise genetic quality and competitiveness, e.g., physical attractiveness, masculinity and dominance when choosing a mate (Buss & Schmitt, 2019).

While most studies find a negative effect of height on female LRS in WEIRD societies, the findings in the developing countries are more varied, likely mediated by a higher rate of (infant) mortality and pregnancy complications of smaller women (Stearns et al., 2012; Stulp & Barrett, 2014). When mortality is reduced, female fertility is mainly limited by their ability to convert time and energy into costly offspring (Ellison, 2001; Trivers, 1972). Diminished culturally enforced monogamy reduces the need for females to compete over mates. In such environments, the selection in females is predicted to shift from somatic growth and quality towards earlier maturation and reproduction (Sanjak et al., 2018; Stearns et al., 2012). In sum, r-selection is expected to optimise for male ability to acquire mates and female ability to convert energy into the offspring.

In **paper V** I compared reproductive outcomes of girls from different types of disrupted families with those of girls from bi-parental households. I expected that the absence of a parent would associate with faster LHS and earlier AFB. In **paper III** and **VI** I explored fecundity selection and parity-transition patterns in

relation to morphometric traits. As the results in **paper III** for girls using relative LRS as a fitness proxy were very similar to those found in **paper VI** where exact covariate matching was used for both sexes, **paper III** is discussed only where the measured traits do not overlap.

Parity transition showed a sex-specific pattern: selection occurred almost exclusively through childlessness in boys, while among the girls most of the traits that were associated with becoming a mother were additionally associated with a transition from one child to higher parities (Table 2). The variance in the number of children and prevalence of childlessness was higher in males ( $SD=1.34$  and 17%) than in females ( $SD=1.18$  and 10%).

With positive selection for 10 traits out of 14, heavier and stronger boys with larger linear dimensions had generally higher odds of transitioning to parenthood. The shape of selection was curvilinear for most traits, i.e., selection against weaker and smaller boys was stronger than the selection favoring the boys who were larger than average. Directional selection was strongest for height, sitting height and handgrip strength, followed by shoulder width, leg length and weight. Transition from single to higher parities was more ambivalent. Selection on two traits – cranial volume and face width – was entirely stabilising, acting against individuals with extreme values of these traits.

The pattern of selection was different for girls. 11 traits from 15 were associated with odds of becoming a mother and most of these traits were additionally associated with a transition from one child to higher parities. In the case of two traits – height and leg length – the selection for smaller size was consistent over all measured parity transitions. Odds of becoming a mother and transition from one child to higher parities were associated with smaller cranial volume, shorter legs and stature and narrower hips and faces. Girls with average thorax circumference, BMI and weight had higher odds of becoming a mother so that selection acted more strongly against girls that were heavier than average than against the slimmest girls. Girls with a masculine body shape (i.e., with higher shoulder/hip ratio), narrow faces and average face roundness (face width/lower face height ratio) had higher odds of becoming a mother and transitioning from one child to higher parities. Girls with fast and slow rates of breast development had higher odds of having more than two children than average girls. Girls with divorced fathers started reproducing 9.2 months earlier and those with dead fathers had a tendency for 3.5 months earlier AFB than bi-parental controls. In **paper III** delayed AFB had a strong negative effect on female LRS and selection via AFB accounted for a modest to substantial proportion of total selection, depending on the morphometric trait. There was strong directional selection against girls with wider jaws. Selection was absent for lung capacity.

**Table 2.** Direction of selection on anthropometric traits of boys and girls in different parities.  $\Omega$  means stabilising selection, U means disruptive selection. Shaded cells denote traits where selection acted on opposite directions for boys and girls. Reproduced from **paper VI**.

Trait	Sex	Comparisons of parities			LRS
		0 vs 1+	1 vs 2+	2 vs 3+	
Cranial volume	Boys	$\Omega$			
	Girls	-	-		-
Face width	Boys	$\Omega$			$\Omega$
	Girls	$-\Omega$	-		$-\Omega$
Face roundness (fWHR-lower)	Boys				
	Girls	$\Omega$	$\Omega$		$\Omega$
Shoulder width	Boys	+			+
	Girls				$-\Omega$
Shoulder/hip ratio	Boys				
	Girls	+	+		+
Handgrip strength	Boys	$+\Omega$	+		+
	Girls				
Height	Boys	$+\Omega$			$+\Omega$
	Girls	-	-	-	-
Sitting height	Boys	$+\Omega$			+
	Girls		-		-
Leg length	Boys	$+\Omega$			$+\Omega$
	Girls	-	-	-	$-\Omega$
Leg/torso ratio	Boys				
	Girls	-			
Thorax circumference	Boys	+			
	Girls	$\Omega$	-		$-\Omega$
Hip width	Boys	$+\Omega$			+
	Girls	-	-		$-\Omega$
Breast dev.rate	Girls			U	
Weight	Boys	+			+
	Girls	$-\Omega$	-		-
BMI	Boys				
	Girls	$\Omega$	-		$-\Omega$

The magnitude of selection varied between OR of 0.89 (95% CI = 0.84 – 0.95) for hip width and 1.07 (95% CI = 1.01 – 1.13) for shoulder/hip ratio in girls. In boys, the selection was generally stronger, with the most pronounced effect for increase in height (OR = 1.18, 95% CI = 1.09 – 1.26). In aggregate, selection favoured stronger and larger boys, and smaller girls.

The selection pattern in women favoring smaller but also a more masculine body has a common factor. Both smaller size and sex-atypical body require less somatic investment than larger growth and elaborate sexual ornamentation (Sim, 2013). Selection towards a more masculine body type in girls was driven by narrower hips, not wider shoulders. Assuming that earlier AFB and higher LRS in smaller girls reflects a faster LHS, this trend could indicate a trade-off from somatic quality towards the speed of reproduction (Sanjak et al., 2018; Stearns et al., 2012). The shape of selection for female BMI, thorax circumference and hip width may indicate constraints of reproductive physiology in extreme values of these traits (Ellison, 2001; Jokela et al., 2007).

Girls with missing fathers started reproducing earlier, but their breast development did not differ from controls. While variation in both is highly heritable (Polderman et al., 2015; Turkheimer, 2000), the gene-environment interaction on the expression of behavioural and morphological traits may differ systematically. Behaviour is plastic and varies in time, energetic constraints on growth are rigid and directional (Dochtermann, 2011). Hence, LHS predispositions may be more consistently associated with differences in (reproductive) behaviour than with growth (Black et al., 2017; Sear et al., 2019). Covariation between behavioural traits and energetically demanding physical maturation may emerge only when environmental variance is controlled for (Hörak et al., 2019).

As the average number of children in developed countries is well below the biological reproductive capacity of females, preferences and not ability may be their main limiting factor for family size. Women predisposed for slower LHS may be more selective in respect to their partners, with studies showing taller women being more likely to marry later and to delay their reproductive onset resulting in lower LRS; meanwhile, shorter women may possess higher fertility motivations manifesting at an earlier age (Stulp & Barrett, 2014). In such conditions, selection for female body size is driven by behavioural correlations with morphology and not by the variation in body size itself. Importance of female preferences (and not ability) is illustrated by a UK Biobank study, which found that the burden of rare mutations in genes associated with lower educational attainment and general intelligence, as well as an increased risk of intellectual disability and some psychiatric disorders, reduce LRS substantially in males but much less so in females (Gardner et al., 2020).

Differently from girls, the selection on bodily traits in boys was mostly related to transitioning to fatherhood. Thus, male fitness was primarily determined by traits related to mating success. Once a willing mate is acquired, the decision for a larger family might be influenced by different characteristics, likely dependent on cultural factors associated with resource acquisition. Different traits may be valued in short and long-term mates (Buss & Schmitt, 2019).

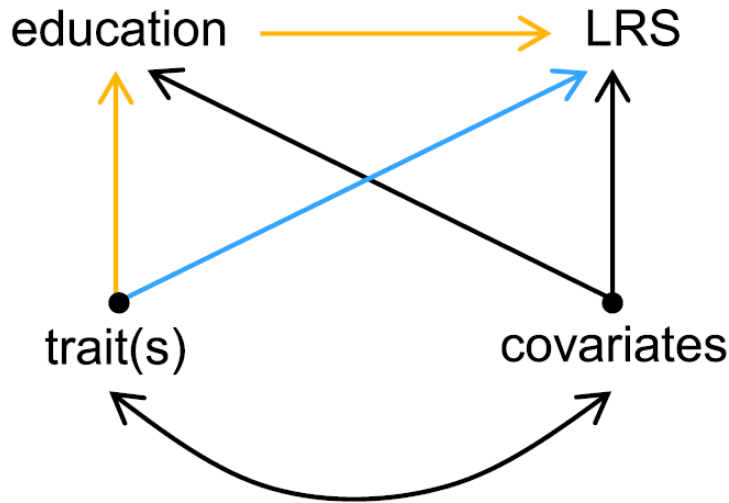
### 3.3.2 Indirect selection (III; VI)

Phenotype's fitness is determined by its interactions with the environment. If the interaction with any external variable – material, cultural or biological – that affects LRS has heritable variation, another layer of selection is created. Such layers of selection are described by indirect selection. Selection may not act on traits directly affecting fitness outcome but on traits correlated with external outcome, which in turn affects fitness (Stulp et al., 2012). As there exists a causal link between the genes and their environment (Valge et al., 2019), such selection pressures are not distributed randomly in the population (Hugh-Jones & Abdellaoui, 2021; Woodley of Menie et al., 2020).

Common genetic factors may underlie the variation in anthropometric traits and socioeconomic outcomes (Tyrrell et al., 2016). For example, height is pleiotropically correlated with intelligence (Silventoinen et al., 2006). Hence, phenotypical height is in part an indicator for underlying genetic variation influencing behaviour. Such genetic variation is correlated with the odds of obtaining higher education and variation in height, without height having to have any causal impact on educational attainment. In such terms, if only educational attainment affects fitness, covaried morphometric traits are pulled along for correlational reasons. In addition, morphometric traits (e.g., brain size) may directly influence the odds of attaining higher education, which in turn correlates with fitness. In such terms, education mediates a two-step causal chain for the selection of a trait. Selection may act on multiple, partially overlapping, traits affecting morphology, biosocial covariates and behavioural outcomes at the same time.

Describing how cultural layers mediate selection is not straightforward as lines between direct and types of indirect selection can be blurred and causal chains between individual variation and biosocial covariates are bi-directional (Fig.4). Though causal chains can be ambivalent, identifying such mediators is important, because selection inside a mediating layer can be opposite to the selection between layers or optimise for different traits. If the mediator acts as an amplifier for genetic predispositions, direct and indirect selection are expected to act in the same direction. In **paper III** and **VI** I explored LRS in relation to educational attainment and the role of education in mediating selection on morphometric traits.

Among boys, the odds of transitioning to fatherhood had a strong positive association with education. Compared to boys with primary education, obtaining tertiary education was associated with 3.5 times and secondary education with two times higher odds of becoming a father. Tertiary (but not secondary) education was also associated with progression from one to more children, while progression from two children to higher parities was independent of education. The girls displayed an opposite pattern: transition to motherhood was not related to educational attainment, while education above primary was associated with lower odds to progression to parities above one and two. For both sexes, educational attainment magnified the strength of selection on most traits, i.e., direct and indirect selection almost always acted in the same direction.



**Figure 4.** Path diagram outlining the effects of traits on LRS, including both direct (blue) and indirect (yellow) effects via education. Reproduced from **paper III**.

Head size increases with stature and is the best independent anthropometric trait for predicting educational attainment (Valge et al., 2019), and tall and educated men enjoyed a clear fitness advantage. Consequently, stabilising selection on the cranial volume in males was an unexpected result. Education may not correlate with male LRS as a proxy for intelligence, but as a social marker of status and competitiveness, traits considered attractive in males (Buss & Schmit, 2019). Negative genetic correlations between educational attainment and LRS (in both men and women) have been reported in several large European samples (Barban et al., 2016; Warrington et al., 2021). In Icelanders born between 1910 and 1990, obtaining higher education had a negative effect on LRS for females but not for males; meanwhile there was selection in both sexes against the genes associated with educational attainment (Kong et al., 2017).

The findings emphasise the same general direction of direct and indirect selection. Education pulls together males and females with similar predispositions (Valge et al., 2019), but is associated with LRS in sex-divergent manner. Hence, common cultural factors can have a contrasting impact on fitness due to differences in reproductive strategies. A divergent selection in different subgroups of society was also detected in a UK Biobank study, which found that selection against genes associated with intelligence and height, and the selection for genes associated with a higher number of sexual partners and substance abuse (traits related to faster LHS) are mainly concentrated to the lower socioeconomic strata, while among high education/income groups, selection effects are reversed (Hugh-Jones & Abdellaoui, 2021). The cultural environment of socioeconomic outcomes amplified the selection for traits associated with the same outcome.

### 3.3.3 Evolutionary implications (VI)

It is difficult to estimate evolutionary response to selection because socioeconomic covariates such as education, urban/rural origin, income – all which correlate with LRS and trait expression are in part endogenous (Trzaskowski et al., 2014; Valge et al., 2019). Controlling for them may smooth out causal genetic variation (Abdellaoui et al., 2019). Although it is likely that the model used in **paper VI** ignored some of the endogenous causality, I retained controlling for urban/rural origin because fertility in the rural areas was considerably higher in studied birth cohorts and ignoring it would have resulted in a systematic bias. Genetic influences on the expression of morphometric and behavioural traits in humans are high (Polderman et al., 2015). Therefore, selection on these traits likely leads to the change in the genetic composition in the population.

Selection for educational attainment and dimensional bodily traits was sexually antagonistic, i.e., selection acted on males and females in the opposite direction. Genetic expression of most traits is similar in both sexes (Stinger et al., 2017). As a result, contrasting selection pressure in one sex constrains the other from achieving its sex-specific fitness optimum (Stearns et al., 2012). However, it should be noted that the strength of selection was stronger in males than in females. Thus, the possibility that the studied population has a potential to evolve towards an increased genetic propensity for growing larger cannot be excluded, primarily through the selection which acts via male childlessness. Stabilising selection on cranial volume in males makes educational attainment harder to put into the evolutionary context, but indirect selection seems to strongly favour males obtaining higher education.

Response to selection may be stronger on dimorphic traits where genetic basis allows for (partial) sex-specific trait expression (Stearns et al., 2012; Stångberg, 2017). For example, the genetic component of variation in testosterone differs between sexes with limited overlap of polygenic risk scores and some genes associated with higher testosterone in men have inverse effects for women (Ruth et al., 2020). Thus, potential targets for increased dimorphism may be traits strongly influenced by sex hormones (Gilks et al., 2014; Rawlik et al., 2016), such as handgrip strength and shoulder width in men (Gallup & Fink, 2018). Albeit genomic variants for male and female pubertal timing are highly correlated, there is also evidence for specific genes having sex-divergent or even directionally opposite effects (Stringer et al., 2017; Mustanski et al., 2004). Hence, selection for faster LHS in women might lead to increased dimorphism in the speed of maturation.

Patterns of natural selection are not universal but operate differently in different niches of society through complex interaction of genes, culture and material affluence (Hugh-Jones & Abdellaou, 2021). Such interactions are in dynamic change which makes evolutionary predictions difficult (Stearns et al., 2010; Stearns et al., 2012). Nevertheless, the selection pressures resulting from the changes in the patterns of resource acquisition and mortality can be predicted using the framework of LH theory.



## 4. SUMMARY AND CONCLUSIONS

The results are most parsimoniously explained by the models of genetic coadaptation between LH traits rather than those emphasising adaptive (developmental) plasticity (**I**; **IV**; **V**). However, under environmental stress, the growth of some organs may be prioritised (**IV**). Early maturation was not induced by parental death, but parents of early-maturing girls died younger (**I**). Psychosocial stress did not accelerate sexual maturation, but inhibited growth in boys (**IV**; **V**). Children inherit LH differences from their parents, but propensity for earlier maturation may be expressed only under favorable conditions (**I**; **IV**; **V**). LHS predispositions may be more consistently associated with (reproductive) behaviour (**V**). This does not falsify covariance of behavioural and LH traits but highlights the need to control for background variables (**I**; **IV**; **V**).

Male fitness was primarily determined by traits related to mating success with positive selection for body size and educational attainment (**VI**). Females were selected for increased ability to convert energy into the offspring, while trading growth for earlier reproduction (**III**; **VI**). Higher relative investment into reproduction did not equal higher investment into sexual ornamentation in females (**III**; **V**; **VI**). While the shape of selection in males indicated a body size threshold to attract mates, a similar selection acted against women smallest in hip width, BMI and thorax, indicating constraints in reproductive physiology (**III**; **VI**). Albeit selection was sexually antagonistic for body size and education, strength of selection was stronger in males (**VI**).

Cultural factors that correlate with LRS add extra layers of selection, but such mediated selection may not be linear (**II**; **III**; **VI**). Under different social settings, the same intrinsic traits can be related to cultural adaptations, but these adaptations may have an opposite impact on fitness due to differences in reproductive strategies (**II**; **III**; **VI**). The sex-specific fitness patterns orchestrating selection on different morphometric traits in different parities in interaction with educational attainment demonstrate how partially overlapping but distinguished selection pressures shape and recombine heritable variation (**III**; **VI**).

In models where genes choose their own environment, controlling for background variables smooths out genetic variation responsible for these covariates (**II**; **III**; **VI**). Meanwhile, genetic influences on trait expression depend on the environment (**I**; **IV**; **V**). Though the future environment itself is unpredictable, the selection pressures subject to the patterns of resource acquisition and (extrinsic) mortality and the resulting trade-offs can be predicted in the framework of LH theory (**I–VI**).

## SUMMARY IN ESTONIAN

### Elukäikude evolutsiooni teooria ennustuste kontrollimine antropomeetriliste andmete alusel

Elukäikude evolutsiooni teooria kirjeldab, kuidas organismid jaotavad erinevatel arenguetappidel piiratud ressursse ellujäämist ja sigimisedukust mõjutavate funktsioonide ehk elukäiguomaduste vahel. Evolutsiooniliselt täiuslik organism maksimeeriks korraga kõiki elukäiguomadusi ehk hakkaks paljunema kohe pärast sündi ning teeks seda lõpmatult kiiresti ja palju, sealjuures elades ise igavesti. Tegelikuses selliseid organisme ei esine, sest jaotatavad ressursid on piiratud. Igal funktsioonil on hind ajas ja energias. Kui aga igal funktsioonil on hind, siis rohkem ei ole alati parem. Peamisteks tingimusteks, mis optimaalset ressurside jaotust mõjutavad, on ressurside kättesaadavus ja keskkonnast tingitud suremus ning nende mõlema variatsiooni sõltuvus individuaalsest kvaliteedist.

Elukäiguteooria järgi ei evolutsioneeru elukäiguomadused ja käitumuslikud eelsoodumused teineteisest sõltumatult, vaid moodustavad erinevates oludes toimimiseks kokkusobivaid komplekte ehk elukäigustrateegiaid. Aeglast elutempot seostatakse suurema kasvu, hilisema suguküpsuse ja paljunemise alustamise ning vähemaarvuliste, kuid kvaliteetsemate ehk konkurentsivõimelisemate järglastega. Kiire elutempo viitab suhteliselt suuremale investeringule sigimiskiirusesse, kuid selline investering tuleb reeglina järglaste kvaliteedi ja ellujäämise arvelt. Nii moodustub põhiline elukäiguomaduste lõivsuhe sigimise ja ellujäämise ehk kvantiteedi ja kvaliteedi vahel.

Elukäiguteooria raamistiku sobivus inimestevaheliste erinevuste kirjeldamiseks tekitab poleemikat. Sellegipoolest on ülegenoomsetes assotsiatsiooniuuringutes tuvastatud elukäiguteooria poolt ennustatud geneetilisi korrelatsioone, mh suguküpsuse saavutamise kiiruse, seksuaalkäitumise, keha suuruse ning eluea, aga ka nt intelligentsuse ja riskivalmiduse vahel. Tõendid indiviidi tunnuste tasemel jäävad mitmeti mõistetavateks. Elukäiguomaduste koosvarieerumine võib viidata ka fenotüübi plastilisusele mõne keskkonnastiimuli suhtes – nt on puudulik toitumine seotud korraga nii väikese kasvu kui ka madalama intelligentsusega. Selline uurimissuund on veelgi raskendatud geeni-kultuuri vastasmõju tõttu. Geneetilised eelsoodumused mõjutavad kultuuri loomist ja omaksvõttu, kultuur mõjutab omakorda geneetiliste eelsoodumuste väljendumist ning nende mõju kohasusele.

Väitekirjas testisin elukäiguteooria ennustusi antropomeetrilises andmekogumis, uurisin lõivsuhteid ning piiranguid keha arengus ja paljunemises ning mõtestasin kultuuri ja keskkonna rolli nende seoste avaldumisel. Artiklites (I–VI) kasutasin prof Juhan Auli juhtimisel 1956–69 kogutud koolilaste andmestikku. Prof Auli mõõdetud koolilaste hariduse, laste arvu ning nende vanemate eluea kohta saadi anonümiseeritud andmed rahvastikuregistrist. Lisaks antropomeetrilistele andmetele testisin artiklis (I) elukäiguteooria ennustusi Eesti Geenivaramu valimil.

**Esimeses** artiklis uurisin antropomeetrilisel ja geenivaramu andmestikul, kas tüdrukute seksuaalse küpsenise kiirus on seotud nende vanemate elueaga. Antropomeetrilises andmestikus ennustas tüdrukute varasem rindade areng nende

vanematele lühemat eluiga. Geenivaramu andmestikul ei ennustanud tüdrukute vanus *menarche* algamisel nende emade eluiga, küll aga ennustas nende isade ellujäämist, kuid seda ainult perekondades, kus ühel vanemal oli kõrgharidus. See toetab arusaama, et geneetiline variatsioon avaldub fenotüübis selgemini soodsa keskkonnaoludes. Antud eeldust toetas ka *menarche* algamise vanuse suurem pärilikuse määr kõrgemalt haritud peredes. Mõlemas valimis ilmnes seos tütarde sugulise küpsemise ning vanemate eluea vahel ainult vanematel, kes surid kõrges vanuses. Leiud toetavad seisukohta, et inimestel on varasem suguküpsus evolutsioneerunud koos lühema elueaga.

**Teises** artiklis uurisin poiste ja tüdrukute antropomeetriliste tunnuste – pikkuse, koljumahu ja näo laiuse (testosteroonist sõltuv tunnus) seoseid hariduse omandamise ning nende seoste kehtivust erinevates sotsiaalmajanduslikes oludes. Seosed morfomeetriliste tunnuste ja hariduse vahel ning nende esinemine erinevates keskkonnatingimustes on huvipakkuvad, sest kõrgemat haridust seostatakse naistel madalama ja meestel kõrgema kohasusega. Seega võib hariduse omandamine mõjutada looduslikku valikut kehale. Taustmuutujatest oli perekonna sotsiaalmajanduslik positsioon olulisim omandatava haridustaseme ennustaja. Hariduse omandamist ennustas ka sugu, maa- või linnapäritolu ja õdede-vendade arv. Taustmuutjaid ja morfomeetriliste tunnuste allomeetrilisi seoseid statistiliselt kontrollides leidsin, et igas sotsiaalmajanduslikus kategoorias saavutasid nii poiste kui tüdrukute seas pikemad, suurema koljumahu ning suhteliselt kitsama näoga lapsed tõenäolisemalt kõrgema haridustaseme. Seega ei ennustanud morfomeetrilised tunnused hariduse omandamist ainult seetõttu, et nende mõlema varieerumist oleks mõjutanud samad keskkonnaolud. Selline interaktsioon bioloogiliste eelsoodumuste ja kultuuriliste väljundite vahel viib geneetilistel erinevustel põhineva sotsiaalse kihistumiseni. Kihistumine, kus geneetiliselt erinevad inimesed puutuvad kokku erinevate keskkonnaoludega, võib omakorda viia lahkneva valikusurve sotsiaalsete kihtide vahel.

**Kolmandas** artiklis käsitlesin Eesti tüdrukuid mõjutavat looduslikku valikut. Kirjeldasin viljakusvalikut 13-le antropomeetrilisele tunnusele. Kohasemad olid lühemad ja kõhnemad, väiksema koljumahu ja maskuliinsema kehakujuga tüdrukud. Valik koljumahule ja näo laiusele seostus oluliselt haridusega – tunnused mõjutasid hariduse omandamise tõenäosust, mis omakorda mõjutas tüdrukute sigimisedukust. Seega on valik neile tunnustele mõjutatud geeni-kultuuri koevolutsioonist.

Kokkuhoidliku keha hüpotees ennustab, et ressursside piiratuse korral säästetakse elundite kasvu valikuliselt, et säilitada ellujäämiseks kriitiliste funktsioonide, nt aju ja kopsude, toimimine. Trivers-Willardi hüpotees (TWH) ennustab, et poisid on ressursside piiratuse korral haavatavamad kui tüdrukud. Mõlemat hüpoteesi kontrollisin **neljandas** artiklis järjestades peretüübid materiaalse kitsikuse ja psühhosotsiaalse stressitaseme järgi. Võrdlesin keha arengut lastel, kelle ema või isa oli surnud, lastel, kelle isa oli lahutatud, ning lastekodulastel kahe bioloogilise vanemaga kasvavate laste arenguga kontrollgrupis. Lastekodulaste kasv oli tugevalt pärsitud. Nende jalad olid keskmiselt 0,5 standardhälvet (SD) lühemad kui kontrollgrupil, nende pikkus ja koljumaht erinesid kontrollgrupist 0,4 SD võrra. Kehapikkus, kaal ja rinnaümbermõõt erinesid lastekodulastel

kontrollgrupist 0,2 SD võrra. Lastekodudes oli poiste ja tüdrukute kasv pärsitud sarnasel tasemel. Poisid, kelle emad olid surnud, olid kontrollgrupiga võrreldes väiksemad ja nende keha proportsioonid viitasid aeglasemale sugulisele küpsemisele, kui samasugustest peredest pärit tüdrukute arengumustrid. Lahutatud isade poegadel olid laiemad õlad kui poistel, kelle isad olid surnud. Seega võib TWH ennustus poiste arengu haavatavuse kohta kehtida vaid teatud tingimustel. Kokkuvõtteks keha hüpotees oli osaliselt toetatud: ülakeha kasvu säästeti jalgade kasvu arvelt. Aju arengu säästmise kohta tõendeid ei ilmnenu.

**Viendas** artiklis uurisin erinevates peretingimustes kasvavate tüdrukute sugulist küpsemist ja sigimisedukust. Mitmed evolutsioonilised hüpoteesid ennustavad, et tüdrukud, kes kasvavad isata, küpsevad ja alustavad sigimist varem, kuna isa puudumine on vihje keskkonna ebakindlusele, mis omakorda soodustab nihet kiiremale elukäigustrateegiale. Erinevusi erinevatest peretüüpidest pärit tüdrukute rindade arengu kiiruses ei tuvastatud. Küll aga alustasid isata kasvanud tüdrukud sigimist varem. See leid on kooskõlas eeldusega, et lahutama kalduvad isad (ja/või nende abikaasad) erinevad oma elukäigustrateegia poolest ja et sellised eelsoodumused antakse geneetiliselt edasi ka lastele.

**Kuuendas** artiklis kirjeldasin valikut antropomeetritele tunnustele Eesti poistel ja tüdrukutel ning selle varieeruvust esma- ja järgnevate sündide võrdlusele. Hariduse omandamisele ja keha suurusele rakenduv valik oli sooliselt antagonistlik ning toimus poistel ja tüdrukutel erineva sündide järjestuse kaudu. Põhiharidusega poisid jäid 3,5 korda suurema tõenäosusega lastetuks, kui kõrghariduse omandanud. Emaks saamise tõenäosus ei olnud seotud haridustasemega, samas kui põhiharidusest kõrgem haridustase vähendas tüdrukute tõenäosust saada kaks või enam last. Valik antropomeetritele tunnustele osas toimus peaaegu eranditult läbi poiste lastetuse, samas kui tüdrukute seas oli enamik emaks saamisega seotud tunnuseid seotud lisaks ka teiste ja kolmandate laste sünniga. Meeste (kuid mitte naiste) kohasuse määrasid seega peamiselt paarumuseduga seotud tunnused. Kohasemad olid tugevamad ja suuremad poisid ning väiksemad tüdrukud.

Kokkuvõtvalt on leitud kooskõlas elukäigustrateegiate geneetilistele erisustele keskenduvate mudelitega (**I**; **IV**; **V**). Tüdrukute kiirem suguküpsemine ei olnud põhjustatud nende vanema surmast, aga vanemad, kelle tütred küpsesid varakult, surid nooremana (**I**). Psühhosotsiaalne stress ei kiirendanud sugulist küpsemist (**V**), küll aga pärssis poiste kasvu (**IV**). Lapsed pärivad elukäigu erisused oma vanematelt, kuid eelsoodumused varasemaks suguliseks arenguks saavad avalduda ainult soodsas keskkonnas (**IV**; **V**). Käitumuslikud eelsoodumused võivad fenotüübis avalduda järjepidevamalt (**V**). Erinevates keskkonningimustes võivad bioloogilised eelsoodumused mõjutada sotsiaalmajanduslikke saavutusi sarnaselt (**II**), kuid nende saavutuste mõju kohasusele sõltub elukäigustrateegiate erinevustest ning soospetsiifilistest sigimisstrateegiatest (**III**; **VI**). Tulemused näitavad, et lõivsuhted erinevate kohasuse komponentide vahel esinevad ka kaas-aegsetes populatsioonides elukäiguteooria poolt ennustatud viisil (**I–VI**).

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## REFERENCES

- Abdellaoui, A., Hugh-Jones, D., Yengo, L., Kemper, K.E., Nivard, M.G., Veul, L., ... Visscher, P.M. (2019). Genetic correlates of social stratification in Great Britain. *Nat. Hum Behav.* doi: 10.1038/s41562-019-0757-5
- Aul, J. (1982). *Eesti Kooliõpilaste antropoloogia*. Tallinn: Valgus
- Barban, N., R. Jansen, R. de Vlaming, *et al.* (2016). Genome-wide analysis identifies 12 loci influencing human reproductive behaviour. *Nat. Genet.* 48: 1462–1472
- Barbaro, N., Boutwell, B.B., Barnes, J.C., Shackelford, T.K. (2017). Genetic confounding of the relationship between father absence and age at menarche. *Evol. Hum. Behav.* 38, 357–365. doi:10.1016/j.evolhumbehav.2016.11.007
- Barban, N., De Cao, E., Francesconi, M., (2021). *Gene-Environment Effects on Female Fertility*. Centre for Economic Studies and ifo Institute (CESifo). Munich
- 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
- Belsky, J., Steinberg, L., Draper, P. (1991). Childhood experience, interpersonal development, and reproductive strategy: An evolutionary theory of socialisation. *Child Development*, 62, 647–670
- Black, C. J., Figueredo, A. J., Jacobs, W. J. (2017). Substance, History, and Politics: An Examination of the Conceptual underpinnings of Alternative Approaches to the Life History Narrative, *Evolutionary Psychology*, 1–16. DOI: 10.1177/1474704916670402
- Bogin, B., Varela-Silva, M. I. (2010). Leg length, body proportion, and health: a review with a note on beauty. *International journal of environmental research and public health*. 7: 1047–1075
- Bolund, E., Hayward, A., Pettay, J. E., Lummaa, V. (2015). Effects of the demographic transition on the genetic variances and covariances of human life-history traits. *Evolution*, 69(3), 747–755. doi.org/10.1111/evo.12598
- Briley, D. A., Harden, K. P., Tucker-Drob, E. M. (2015). Genotype × cohort interaction on completed fertility and age at first birth. *Behaviour Genetics*, 45(1), 71–83
- Brisson, D. (2018). Negative frequency-dependent selection is frequently confounding. *Frontiers in Ecology & Evolution*, 6, 10
- Brito, N.H., Piccolo, L.R., Noble, K.G. (2017) Associations between cortical thickness and neurocognitive skills during childhood vary by family socioeconomic factors. *Brain Cogn.* 116:54–62
- Buss, D.M., Schmitt, D.P. (2019). Mate Preferences and Their Behavioural Manifestations. *Annual Review of Psychology* 70(1), 77–110. DOI: 10.1146/annurev-psych-010418-103408
- Charalampopoulos, D., McLoughlin, A., Elks, C. E., Ong, K. K. (2014). Age at menarche and risks of all-cause and cardiovascular death: A systematic review and meta-analysis. *American Journal of Epidemiology*, 180(1), 29–40. doi.org/10.1093/aje/kwu113
- Collins, J., Page, L. (2019). The heritability of fertility makes world population stabilisation unlikely in the foreseeable future. *Evolution and Human Behaviour*. 40, 105–111.
- Conley, D., Laidley, T. M., Boardman, J. D., Domingue, B. W. (2016). Changing polygenic penetrance on phenotypes in the 20th century among adults in the US Population. *Scientific Reports*, 6, 30348

- Conley, D., Sotoudeh, R. (2016). Genotyping the dead: Using offspring as a proxy to estimate the genetic correlation of education and longevity. *Proceedings of the National Academy of Sciences*, 113(47), 13269–13271. doi.org/10.1073/pnas.1616274113
- Courtiol, A., Picq, S., Godelle, B., Raymond, M., Ferdy, J-E. (2010). From Preferred to Actual Mate Characteristics: The Case of Human Body Shape. *PLoS ONE*. doi.org/10.1371/journal.pone.0013010
- Dabbs, J.M. (1992). Testosterone and occupational achievement. *Soc Forces*. 70(3): 813–24
- Dawkins, R. (1982). *The extended phenotype: The gene as the unit of selection*. Oxford Oxfordshire: Freeman
- Day, F.R., Helgason, H., Chasman, D.I., Rose, L.M., Loh, P.R., ... Perry, J.R.B. (2016). Physical and neurobehavioral determinants of reproductive onset and success. *Nature Genetics*.; 48(6): 617–623. doi: 10.1038/ng.3551
- Del Giudice, M. (2014). An evolutionary life history framework for psychopathology. *Psychol Inquiry*. 25 (3–4):261–300.
- Del Giudice, M. (2020). Rethinking the fast-slow continuum of individual differences. *Evolution and Human Behaviour*. Vol 41, 6
- Dochtermann, N. A. (2011). Testing Cheverud’s conjecture for behavioural correlations and behavioural syndromes. *Evolution*, 65, 1814–1820
- Doi, H., Nishitani, S., Shinohara, K. (2015). Sex differences in the relationship between salivary testosterone and inter-temporal choice. *Horm. Behav.* 69:50-8
- Draper, P., Harpending, H. (1982). Father absence and reproductive strategy: an evolutionary perspective. *J. Anthropol. Res.* 38, 255–273. doi:10.1086/jar.38.3.3629848
- Ellis, B.J. (2004). Timing of pubertal maturation in girls: an integrated life history approach. *Psychol. Bull.* 130, 920–958. doi:10.1037/0033-2909.130.6.920
- Ellison, P.T. (2001). *On fertile ground: A natural history of human reproduction*. Cambridge: Harvard University Press.
- Euling, S.Y., Herman-Giddens, M.E, Lee, P.A., Selevan, S.G., Juul, A., Sorensen, T.I, ... Swan, S.H. (2008). Examination of US puberty-timing data from 1940 to 1994 for secular trends: panel findings. *Paediatrics*; 121
- Falk, A., Hermle, J. (2018). Relationship of gender differences in preferences to economic development and gender equality. *Science*, 362, 307
- Figueredo, A.J., Vásquez, G., Brumbach, B.H., Schneider, S.M.R. (2004). The heritability of life history strategy: The k-factor, covitality, and personality. *Social Biology*, 51, 121–143
- Figueredo, A. J., Vásquez., G., Brumbach, B. H., Sefcek, J. A., Kirsner, B. R., Jacobs, J. W. (2005). The K-factor: individual differences in life history strategy. *Personality and individual differences*, vol 39, 8, 1349–1360, doi.org/10.1016/j.paid.2005.06.009
- Figueredo, A.J., Cabeza de Baca, T., Woodley, M.A. (2013). The measurement of human life history strategy. *Personality and Individual Differences*. 55:251–5
- Figueredo, A. J., Wolf, P. S. A., Olderbak, S. G., Gladde, P. R., Fernandes, H. B. F., Wenner, C., ... Rushton, J. P. (2014). The Psychometric Assessment of Human Life History Strategy: A Meta-Analytic Construct Validation. *Evolutionary Behavioral Sciences*. Vol 8, 3
- Fink, B., Grammer, K., Mittroecker, P., Gunz, P., Schaefer, K., Bookstein, F. L., Manning, J. T. (2005). Second to fourth digit ratio and face shape. *Proceedings of the Royal Society B*, 272, 1995–2001

- 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. *Evol Hum Behav*; 28: 423–9
- Gallup, A. C., Fink, B. (2018). Handgrip Strength as a Darwinian Fitness Indicator in Men. *Frontiers in psychology*, 9, 439. doi.org/10.3389/fpsyg.2018.00439
- Gardner, E. J., Neville, M. D. C., Samocha, K. E., Barclay, K., Kolk, M., Niemi, M. E., ... Hurles, M. E. (2020). Sex-biased reduction in reproductive success drives selective constraint on human genes. *bioRxiv*. doi.org/10.1101/2020.05.26.116111
- Ge, X., Natsuaki, M. N., Neiderhiser, J. M., Reiss, D. (2007). Genetic and environmental influences on pubertal timing: Results from two national sibling studies. *Journal of Research on Adolescence*, 17(4), 767–788. doi.org/10.1111/j.1532-7795.2007.00546.x
- German, A., Hockberg, Z. (2020). Sexual Dimorphism of size ontogeny and life History. *Frontiers in Pediatrics*. 10.3389/fped.2020.00387
- Gilks, W. P., Abbott, J. K., Morrow, E. H. (2014) Sex differences in disease genetics: evidence, evolution, and detection. *Trends Genet.* 30, 453–463 (2014)
- Giuliani, C., Garagnani, P., Franceschi, C. (2018). Genetics of human longevity within an eco-evolutionary nature-nurture framework. *Circulation Research*, 123(7), 745–772. doi.org/10.1161/CIRCRESAHA.118.312562
- Groeneveld, E., Kovac, M., Mielenz, N., (2010). *VCE User's Guide and Reference Manual Version 6.0*, Neustadt, Germany
- Hahn, T., Winter, N.R., Anderl, C., Notebaert, K., Wuttke, A.M., Clément, C.C., Windmann, S. (2017). Facial width-to-height ratio differs by social rank across organisations, countries, and value systems. *PLoS One*. 2017; 12(11):e0187957
- Hayward, A. D., Lummaa, V. (2013). Testing the evolutionary basis of the predictive adaptive response hypothesis in a preindustrial human population. *Evolution, Medicine, and Public Health*, Volume 2013, Issue 1, 2013, Pages 106–117, doi.org/10.1093/emph/eot007
- Hugh-Jones D., Abdellaoui A. (2021) Human capital mediates natural selection in contemporary humans. *In School of Economics Working Paper* Norwich, University of East Anglia
- Hörak, 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. doi:10.1093/emph/eov017
- Hörak, P; Valge, M, Fischer, K; Mägi, R; Kaart, T (2019). Parents of early maturing girls die younger. *Evolutionary Applications*, 12 (5), 1050–1061. doi.org/10.1111/eva.12780
- Ivanovic, D.M., Valenzuela, R.B., Almagià, A.F., Barrera, C.R., Arancibia, V.C., Larraín, C.G.,... Villagrán, F.S. (2019). Impact of anthropometric nutritional parameters on the university selection test in Chile: a multifactorial approach. *Nutrition*. 2019; 57: 74–83
- Jalovaara, M., Neyer, G., Andersson, G., Dahlberg, J., Dommermuth, L., Fallesen, P., Lappeård. (2019). Education, Gender, and Cohort Fertility in the Nordic Countries. *European Journal of Population*. 35: 563–586
- Jeschke, J. M., Gabriel, W., Kokko, H. (2008). r-Strategist/K-Strategists. In S. E. Jørgensen., B. D. Fath (Eds.), *Encyclopedia of ecology* (pp. 3113–3122). Oxford: Elsevier
- Jeschke, J. M., Kokko, H. (2009). The roles of body size and phylogeny in fast and slow life histories. *Evolutionary Ecology*, 23, 867–878



- Jokela, M., Kivimäki, M., Elovaino, M., Viikari, J., Raitakari, O. T., Keltikangas-Järvinen, L. (2007). Body Mass Index in Adolescence and Number of Children in Adulthood. *Epidemiology*. 18: 599–606
- Kaevats, Ü. (Ed.). (2020). *Eesti Entsüklopeedia 14. köide*. Eesti Entsüklopeediakirjastus: Tallinn
- Kaplan, H. S., Lanchester, J. B., Johnson S. E., Endler, J. A. (1995). Does observed fertility maximise fitness among New Mexican men? *Human Nature* 6, 325–360. doi:10.1007/BF02734205
- Kasperk, C., Helmboldt, A., Börcsök, I., Heuthe, S., Cloos, O., Niethard, F., Ziegler, R. (1997). Skeletal site-dependent expression of the androgen receptor in human osteoblastic cell populations. *Calcif. Tissue Int.* 61, 464–473
- Kausel, E.E., Ventura, S., Datawheel, L., Díaz, D., Vicencio, F. (2018). Does facial structure predict academic performance? *Personal Individ Differ.* 2018; 129: 1–5
- Keller, M.C., Garver-Apgar, C.E., Wright, M.J., Martin, N.G., Corley, R.P., Stallings, M.C., ... Zietsch, B.P. (2013) The genetic correlation between height and IQ: shared genes or Assortative mating? *PLoS Genet.* 2013; 9(4): e1003451
- Kendler, K. S., Baker, J. H. (2007). Genetic influences on measures of the environment: A systematic review. *Psychological Medicine*, 37, 615–626. doi.org/10.1017/S0033291706009524
- Kirk, K.M., Blomberg, S. P., Duffy, D. L., Health, A. C., Owens, I. P., Martin, N. G. (2001). Natural selection and quantitative genetics of life-history traits in Western women: A twin study. *Evolution* 55(2): 423–435
- 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
- Klesment, M. (2013). Diminishing returns to education in the soviet period. Results from the Estonian household income data. *Estonian Institute for Population Studies*. Tallinn: Tallinn University
- Kobayashi, L.C., Berkman, L.F., Wagner, R.G., Kahn, K., Tollman, S., Subramanian, S. (2019). Education modifies the relationship between height and cognitive function in a cross-sectional population-based study of older adults in rural South Africa. *Eur J Epidemiol.* 2019; 34(2): 131–9
- Landgren, M., Andersson Grönlund, M., Elfstrand, P-O., Simonsson, J-E., Svensson, L., Strömmland, K. (2006). Health before and after adoption from Eastern Europe. *Acta Paediatr.* 95 (6)
- Lauringson, V., Veldre, G., Hörak, P. (2020). Adolescent Cranial Volume as a Sensitive Marker of Parental Investment: The Role of Non-material Resources? *Frontiers in Psychology*. doi: 10.3389/fpsyg.2020.602401
- Lawson, D.W, Mace, R. (2009). Trade-offs in modern parenting: a longitudinal study of sibling competition for parental care. *Evol Hum Behav* 2009; 30:170–83
- Lawson, D. W., Mace, R. (2010). Optimising modern family size: trade-offs between fertility and the economic costs of reproduction. *Hum Nat.* 21:39–61
- Lefevre, C. E., Lewis, G. J., Perrett, D. I., Penke, L. (2013). Telling facial metrics: facial width is associated with testosterone levels in men. *Evolution and Human Behaviour.* 34, 4, Pages 273–279
- Leitsalu, L., Haller, T., Esko, T., Tammesoo, M.-L., Alavere, H., Snieder, H., ... Metspalu, A. (2014). Cohort profile: Estonian biobank of the Estonian Genome Centre, University of Tartu. *International Journal of Epidemiology*, 44(4), 1137–1147. doi.org/10.1093/ije/dyt268

- Lynn, R. (1996). *Dysgenics: Genetic deterioration in modern populations*. Great Britain: Ulster institute for Social Research
- MacArthur, R.; Wilson, E.O. (1967). *The Theory of Island Biogeography* (2001 reprint ed.). Princeton University Press
- Marshall, W.A., Tanner, J.M. (1969). Variations in the pattern of pubertal changes in girls. *Arch. Dis. Child.* 44 (235): 291–303. doi:10.1136/adc.44.235.291. PMC 2020314. PMID 5785179
- Marshall, W.A., Tanner, J.M. (1970). Variations in the pattern of pubertal changes in boys. *Arch. Dis. Child.* 45 (239): 13–23. doi:10.1136/adc.45.239.13. PMC 2020414. PMID 5440182
- Martin, R., (1928). *Lehrbuch der Anthropologie (2nd ed.)*. Jena: Fischer
- Mills, M. C., Tropf, F. C., Brazel, D. M., van Zuydam, N., Vaez, A., Pers, T. H., ... Day, F. R. (2021). Identification of 371 loci for age at onset of sexual and reproductive behaviour, highlighting common aetiology with reproductive biology, externalizing behaviour. *Nature Human Behaviour*. doi.org/10.1038/s41562-021-01135-3
- Mendle, J., Turkheimer, E., D’Onofrio, B. M., Lynch, S. K., Emery, R. E., Slutske, W. S., Martin, N. G. (2006). Family structure and age at menarche: a children-of-twins approach. *Developmental psychology*, 42(3), 533–542. doi.org/10.1037/0012-1649.42.3.533
- Mendle, J., Turkheimer, E., Emery, R. E. (2007). Detrimental psychological outcomes associated with early pubertal timing in adolescent girls. *Developmental Review*, 27(2), 151–171. doi.org/10.1016/j.dr.2006.11.001
- Mostafavi, H., Berisa, T., Day, F. R., Perry, J. R. B., Przeworski, M., Pickrell, J. K. (2017). Identifying genetic variants that affect viability in large cohorts. *PLOS Biology*, 15(9), e2002458. doi.org/10.1371/journal.pbio.2002458
- Mustanski, B.S., Viken, R.J., Kaprio, J., Pulkkinen, L., Rose, R.J. (2004) Genetic and environmental influences on pubertal development: longitudinal data from Finnish twins at ages 11 and 14. *Dev Psychol.* Nov;40(6):1188–98. doi:10.1037/0012-1649.40.6.1188. PMID: 15535766
- 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. *Psychol Sci.*; 30(1):43–54
- Nelis, M., Esko, T., Mägi, R., Zimprich, F., Zimprich, A., Toncheva, D., ... Metspalu, A. (2009). Genetic Structure of Europeans: A View from the North-East. *Plos One*, 5 (3): doi.org/10.1371/journal.pone.0005472
- Nettle, D., Bateson, M. (2015). Adaptive developmental plasticity: what is it, how can we recognize it and when can it evolve? *Proceedings of the Royal Society B: Biological Sciences*, 282(1812), 20151005. doi:10.1098/rspb.2015.1005
- Pianka, E. R. (1970). On r- and K-selection. *The American Naturalist*, 104, 592–597
- 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. *Nat Genet.* 47: 702–709
- Pomeroy, E., Stock, J.T., Stanojevic, S. Miranda, J. J., Cole, T. J., Wells, J. C. K. (2012). Trade-offs in relative limb length among Peruvian children: extending the thrifty phenotype hypothesis to limb proportions. *PLoS One*;7: e51795
- Puur, A., Rahnu, L., Maslauskait, A., Stankuniene, 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

- Rahu, K., Rahu, M., Zeeb, H. (2019). Sex disparities in premature adult mortality in Estonia 1995–2016: a national register-based study. *BMJ Open* 9, e026210. doi:10.1136/bmjopen-2018-026210
- Rawlik, K., Canela-Xandri, O., Tenasa, A. (2016). Evidence for sex-specific genetic architectures across a spectrum of human complex traits. *Genome Biology*, 17: 166
- Rapkin, A.J., Tsao, J.C., Turk, N., Anderson, M., Zeltzer, L.K. (2006). Relationships among self-rated tanner staging, hormones, and psychosocial factors in healthy female adolescents. *J Pediatr Adolesc Gynecol*. Jun;19(3):181–7. doi: 10.1016/j.jpag.2006.02.004. PMID:16731411
- Reale, D., Garant, G., Humphries, M.M., Bergeron, P., Careau, V., Montiglio, P-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Phil. Trans. R. Soc B*. 365: 4051–4063. doi.org/10.1098/rstb.2010.0208
- Reznick, D., Bryant, M. J., Bashey, F. (2002). r- and K-selection revisited: The role of population regulation in life-history evolution. *Ecology*, 83, 1509–1520
- Rios, L., Teran, J. M., Varea, C., Bogin B. (2020). Plasticity in the growth of body segments in relation to height-for-age and maternal education in Guatemala. *Am J Hum Biol* ;32:e23376
- Royauté, R., Berdal, M. A., Garrison, C. R., Dochtermann, N. A. (2018). Ppaceless life? A meta-analysis of the pace-of-life syndrome hypothesis. *Behavioural Ecology and Sociobiology*, 72, 64
- Rushton, J. P. (1985). Differential K theory: The sociobiology of individual and group differences. *Personality and Individual Differences*. vol 6,4
- Rushton, J. P. (2000). *Race, Evolution, and Behaviour: A Life History Perspective, 3rd ed.* Charles Darwin Research Institute: Port Huron
- Rushton, J. P., Ankney, C.D. (2009). Whole brain size and general mental ability: a review. *Int J Neurosci*;119(5):692–732
- Ruth, K. S., Day, F. R., Tyrrell, J., Thompson, D.J., Wood, A.R., Mahajan, A., ... Perry, J.R.B. (2020). Using human genetics to understand the disease impacts of testosterone in men and women. *Nat Med*. doi: 10.1038/s41591-020-0751-5
- Rutter, M., Moffitt, T.E., Caspi, A. (2006). Gene–environment interplay and psychopathology: multiple varieties but real effects. *J Child Psychol Psychiatry*. 47(3–4): 226–61
- Saar, E., Helemäe, J. (2021). Inequality across Three Generations under Pressure from Sovietization Policies: Forcing Discontinuity between Two Generations to Strengthen the Impact of Grandparents. *Comparative Sociology*. DOI:10.1163/15691330-bja10032
- Said-Mohamed, R., Pettifor, J. M., Norris, S. A. (2018). Life History theory hypotheses on child growth: potential implications for short and long-term child growth, development and health. *Am. J. Phys. Anthropol*. 165, 4–19. doi: 10.1002/ajpa.23340
- 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
- Salvatore, J. E., Larsson Lönn, S., Sundquist, J., Sundquist, K., Kendler, K. S. (2018). Genetics, the rearing environment, and the intergenerational transmission of divorce: A Swedish National Adoption Study. *Psychological Science*, 29(3), 370–378
- Salter, F. (2006). *On Genetic Interests: Family, Ethnicity and Humanity in an Age of Mass Migration*. Transaction Publishers: New Brunswick
- Sanjak, J. S., Sidorenko, J., Robinson, M. R., Thornton, K. R., Visscher, P. M. (2018). Evidence of directional and stabilising selection in contemporary humans. *Proceedings of the National Academy of Sciences*, 115, 151–156

- Schmitt, D. P., Realo, A., Voracek, M., Allik, J. (2009). Why can't a man be more like a woman? Sex differences in big five personality traits across 55 cultures: Correction to Schmitt et al. (2008). *Journal of Personality and Social Psychology*, 96(1), 118. doi.org/10.1037/a0014651
- Schmitt, D.P. (2015). *Fundamentals of human mating strategies*. In: DM Buss (ed.). *The Handbook of Evolutionary Psychology*. NJ: John Wiley & Sons
- Shirley, M.K., Cole, T.J., Charoensiriwath, S., Treleaven, P., Wells, J. C. K. (2017). Differential investment in body girths by sex: evidence from 3D photonic scanning in a Thai cohort. *Am J Phys Anthropol*; 163: 696–706
- Sear, R., Sheppard, P., Coall, D. A. (2019). Cross-cultural evidence does not support universal acceleration of puberty in father-absent households. *Philosophical Transactions of the Royal Society B*, 374(1770), 20180124
- Sear, R. (2020). Do human 'life history strategies' exist? *Evolution and Human Behavior*, 41(6), 513–526
- Silventoinen, K. (2003). Determinants of variation in adult body height. *Journal of Biosocial Science*. 35: 263–285
- 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 Behaviour*; 5(8): 585–95
- Sim, K. (2013). The relationship between sex-typical body shape and quality indicators. *Journal of Social, Evolutionary and Cultural psychology*. 7, 97–120
- Sodini, S. M., Kemper, K. E., Wray, N. R., Trzaskowski, M. (2018). Comparison of genotypic and phenotypic correlations: Cheverud's conjecture in humans. *Genetics*, 209, 941–948
- Stearns, S. (1989). Trade-offs in life-history evolution. *Functional Ecology*, 3, 259–268. doi.org/10.2307/2389364
- Stearns, S. C. Hoekstra, R. F. (2005). *Evolution: and introduction, second edition*. New York: Oxford University Press
- Stearns, S. C., Byars, S. G., Govindaraju, D. R., Ewbank. (2010). Measuring selection in contemporary human populations. *Nat. Rev. Genet.* 11:611–622
- Stearns, S.C., Govindaraju, D.R., Ewbank, D., Byars, S.G. (2012). Constraints on the coevolution of contemporary human males and females. *Proc Biol Sci*. doi.org/10.1098/rspb.2012.2024
- Stearns, S. C., Rodrigues, A. M. M. (2020). On the use of "life history theory" in evolutionary psychology, *Evolution and Human Behavior*, Volume 41, Issue 6, 2020, Pages 474–485, ISSN 1090–5138
- Strenze, T. (2015). *Intelligence and socioeconomic success: A study of correlations, causes and consequences*. Tartu Ülikool
- Stringer, S., Polderman, T. J. C., Posthuma, D. (2017). Majority of human traits do not show evidence for sex-specific genetic and environmental effects. *Scientific reports*. 7: 8688
- 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
- Stulp, G., Barrett, L. (2016). Evolutionary perspectives on human height variation. *Biological Reviews*. 91: 206–234
- Stångberg, J. (2017). The evolution of sexual dimorphism in life history traits. *Introductory Research Essay*. 108. Uppsala University

- Thurstans, S., Opondo, C., Seal, A., Wells, J., Khara, T., Dolan, C.,.... Kerac, M. (2020) Boys are more likely to be undernourished than girls: a systematic review and meta-analysis of sex differences in undernutrition. *BMJ Global Health*
- Tropf, F.C., Stulp, G., Barban, N., Visscher, P.M., Yang, J., Snieder, H, Mills, M.C. (2015). Human Fertility, Molecular Genetics, and Natural Selection in Modern Societies. *PLoS One* 10, 1–14. doi:10.1371/journal.pone.0126821
- Trzaskowski, M., Harlaar, N., Arden, R., Krapoh, E., Rimfeld, K., McMillan, A.,... Plomin, R. (2014). Genetic influence on family socioeconomic status and children’s intelligence. *Intelligence*. 42: 83–88
- Tiit, E-M. (2013). Marriage and childbirth trends. In: *Census snapshots*. Tallinn: Statistics Estonia
- Trivers, R. L. (1972). Parental investment and sexual selection. In Campell, B. (Ed). *Sexual Selection and the Descent of Man 1871–1971*, ed. Bernard Campbell, 136–179. Chicago: Aldine Publishing Company
- Trivers, R. L., Willard, D.E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science*. No 4068, 90–92
- Turkheimer, E. (2000). Three laws of behavior genetics and what they mean. *Current Directions in Psychological Science*, 9(5), 160–164. doi.org/10.1111/1467-8721.00084
- 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*, doi.org/10.1186/s12889-019-8072-7
- van den Berg, N., Beekman, M., Smith, K. R., Janssens, A., Slagboom, P. E. (2017). Historical demography and longevity genetics: Back to the future. *Ageing Research Reviews*, 38, 28–39. doi.org/10.1016/j.arr.2017.06.005
- van Ijzendoorn, M. H., Bakermans-Kranenburg, M. J., Duschinsky, R., Fox, N. A., Goldman, P. S., Gunnar, M. R.,... Sonuga-Barke, E. J. (2020). Institutionalisation and deinstitutionalisation of children I: a systematic and integrative review of evidence regarding effects on development. *Lancet Psychiatry*, 7. 703–20
- 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
- Warrington, N.M., Hwang, L-D., Nivard, M. Evans, D. M. (2021). Estimating direct and indirect genetic effects on offspring phenotypes using genome-wide summary results data. *Nature Communications*. 12: 5420
- Weatherhead, P. J., Robertson, R. J. (1979). Offspring quality and the polygyny threshold: the sexy son hypothesis. *The American Naturalist*. 113 (2): 201–208. doi:10.1086/283379. JSTOR 2460199.S2CID 85283084
- Webster, G. D., Graber, J. A., Gesselman, A. N., Crosier, B. S., & Schember, T. O. (2014). A life history theory of father absence and menarche: A meta-analysis. *Evolutionary Psychology*, 12(2), 273–294
- Wells, J. C. K. (2000). Natural selection and sex differences in morbidity and mortality in early life. *J Theor Biol*, 202:65–76
- Wells, J. C. K. (2007). Sexual dimorphism of body composition. Best Practice & Research. *Clinical Endocrinology & Metabolism*, 21, 415–430
- Wells, J. C. (2013). Commentary: the thrifty phenotype and the hierarchical preservation of tissues under stress. *Int J Epidemiol*; 42:1223–7

- Wells, J. C. K., Stock, J.T. (2020). Life history transitions at the origins of agriculture: a model for understanding how niche construction impacts human growth, demography and health. *Front Endocrinol*; 11:325
- Whitehouse, A. J. O., Gilani, S. Z., Shafait, F., Mian, A., Tan, D. W., Maybery, M. T., ... Eastwood, P. (2015). Prenatal testosterone exposure is related to sexual dimorphic facial morphology in adulthood. *Proceedings of the Royal Society, B*. doi.org/10.1098/rspb.2015.1351
- Woodley of Menie, M. A., Luoto, S., Peñaherrera-Aguierre, M., Sarraf, M. A. (2020). Life History is a Major Source of Adaptive Individual and Species Differences: A Critical Commentary of Zietsch and Sidari (2020). *Evolutionary Psychological Science*. doi.org/10.1007/s40806-021-00280-2
- Zeng, X., Xu, X., Zhang, Y., Li, W., Huo, X. (2017). Chest circumference and birth weight are good predictors of lung function in preschool children from an e-waste recycling area. *Environ Sci Pollut Res*, 24:22613–21
- Zietsch, B. P., Kuja-Halkola, R., Walum, H., Verweij, K. J. (2014). Perfect genetic correlation between number of offspring and grandoffspring in an industrialised human population. *Proceedings of the National Academy of Sciences*, 111, 1032–1036
- Zietsch, B. P., Sidari, M. J. (2020). A critique of life history approaches to human trait covariation. *Evolution and Human Behaviour*, 41, 527–535

## **PUBLICATIONS**

## CURRICULUM VITAE

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### Education:

2017– ... Animal ecology PhD, University of Tartu  
2015–2017 Psychology M.A, University of Tartu  
2012–2015 Psychology B.A, University of Tartu

**Language skills:** Estonian (native); English (fluent)

### Employment history:

2021– ... Analyst, Health Board of Estonia

### Honors and awards:

2016, 1st prize in the Estonian national scientific research competition for university students on the master's level in biological and environmental sciences for the research: "Father's death does not affect growth and maturation but hinders reproduction: evidence from adolescent girls in post-war Estonia."

### Publications and presentations

- Valge, M.**, Meitern, R., Hõrak, P. (2022). Sexually antagonistic selection on educational attainment and body size in Estonian children. *Annals of the New York Academy of Sciences*, in press
- Valge, M.**; Meitern, R; Horak, P. (2022). Pubertal maturation is independent of family structure but daughters of divorced (but not dead) fathers start reproduction earlier. *Evolution and Human Behaviour*, 43 (2), 107–114. <https://doi.org/10.1016/j.evolhumbehav.2021.11.004>
- Valge, M.**; Meitern, R; Hõrak, P. (2021). Anthropometrics of Estonian children in relation to family disruption: Thrifty phenotype and Trivers–Willard effects. *Evolution Medicine and Public Health*, 9 (1), 276–286. DOI: 10.1093/emph/eoab022.
- Valge, M.**, Hõrak, P., Henshaw, J. M. (2021). Natural selection on anthropometric traits of Estonian girls. *Evolution and Human Behaviour*, 42 (2), 81–90. DOI: 10.1016/j.evolhumbehav.2020.07.013.



- Valge, M.**, Meitern, R., Hõrak, P. (2019). Morphometric traits predict educational attainment independently of socioeconomic background. *BMC Public Health*, 19 (1), ARTN 1696. DOI: 10.1186/s12889-019-8072-7.
- Hõrak, P.; **Valge, M.**, Fischer, K; Mägi, R; Kaart, T. (2019). Parents of early maturing girls die younger. *Evolutionary Applications*, 12 (5), 1050–1061. DOI: 10.1111/eva.12780.
- 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*. vol 57, 41–47, <https://doi.org/10.1016/j.intell.2016.04.004>
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2021– ... Analüütik, Terviseamet

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### Publikatsioonid ja ettekanded

- Valge, M.**, Meitern, R., Hõrak, P. (2022). Sexually antagonistic selection on educational attainment and body size in Estonian children. *Annals of the New York Academy of Sciences*, in press
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- Valge, M.**, Hõrak, P., Henshaw, J. M. (2021). Natural selection on anthropometric traits of Estonian girls. *Evolution and Human Behaviour*, 42 (2), 81–90. DOI: 10.1016/j.evolhumbehav.2020.07.013

- Valge, M.**, Meitern, R., Hõrak, P. (2019). Morphometric traits predict educational attainment independently of socioeconomic background. *BMC Public Health*, 19 (1), ARTN 1696. DOI: 10.1186/s12889-019-8072-7
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- 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*. vol 57, 41–47, <https://doi.org/10.1016/j.intell.2016.04.004>
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