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The role of nutrition and genetics as key determinants of the positive height trend

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ABSTRACT

The aim of this study was to identify the most important variables determining current differences in physical stature in Europe and some of its overseas offshoots such as Australia, New Zealand and USA. We collected data on the height of young men from 45 countries and compared them with long-term averages of food consumption from the FAOSTAT database, various development indicators compiled by the World Bank and the CIA World Factbook, and frequencies of several genetic markers. Our analysis demonstrates that the most important factor explaining current differences in stature among nations of European origin is the level of nutrition, especially the ratio between the intake of high-quality proteins from milk products, pork meat and fish, and low-quality proteins from wheat. Possible genetic factors such as the distribution of Y haplogroup I-M170, combined frequencies of Y haplogroups I-M170 and R1b-U106, or the phenotypic distribution of lactose tolerance emerge as comparably important, but the available data are more limited. Moderately significant positive correlations were also found with GDP per capita, health expenditure and partly with the level of urbanization that influences male stature in Western Europe. In contrast, male height correlated inversely with children's mortality and social inequality (Gini index). These results could inspire social and nutritional guidelines that would lead to the optimization of physical growth in children and maximization of the genetic potential, both at the individual and national level.

1. Introduction

The increase of height in the industrialized world started only ~150 years ago. In the past, adult stature reflected fluctuations in environmental factors influencing physical growth (mainly climate, diseases, availability of food and population density) and considering that these conditions have almost never been optimal, it is not surprising that height could not approach maximal genetic limits. Paradoxically, the tallest people in Europe before the start of the industrial revolution may have been Early Upper Paleolithic hunters from the Gravettian culture that emerged at least ~36,000 calibrated years ago (Prat, 2011) and is connected with the migration from the Near East that brought Y haplogroup (male genetic lineage) I-M170 to Europe (Semino et al., 2000). The estimated stature of Gravettian men is thought to be tall in the whole of Europe: 176.3 cm in Moravian localities ($n = 18$) and 182.7 cm in the Mediterranean ($n = 11$) (Dočkalová and Vančata, 2005). These exceptional physical parameters can be explained by

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a very low population density and a diet rich in high quality animal proteins. However, Late Upper Paleolithic and especially Mesolithic Europeans were noticeably smaller; Formicola and Giannecchini (1999) estimated that the average height of Mesolithic males was 173.2 cm ($n = 75$) in the Carpathian Basin and Eastern Europe, and only 163.1 cm ($n = 96$) in Western Europe. Perhaps the lowest values in European history were recorded in males from the Late Neolithic Lengyel culture (in the Carpathian Basin during the 5th millenium BC), who were only 162.0 cm tall ($n = 33$) (Éry, 1998).

A new increase (up to ~169 cm) came during the 3rd millenium BC with the advance of Eneolithic cultures (Corded Ware culture, Bell-Beaker culture) (Vančata and Charvátová, 2001; Dobisíková et al., 2007) and it is tempting to speculate that it was just in this period, when beneficial genes of lactose tolerance spread in Central and Northern Europe, because their origin is placed in the Neolithic era (Itan et al., 2009). During the next millenia, stature of Europeans changed mostly due to climatic conditions and usually remained within the range of ~165–175 cm (Hermanussen, 2003; Steckel, 2004; Koepke and Baten, 2005; Mummert et al., 2011 etc.).

The modern increase of stature in the developed world is closely tied with the positive effect of the industrial revolution. Ironically, these socioeconomic changes were accompanied by a new temporary decline of body size in the late 18th century and then again in the 1830s, which probably resulted from bad living conditions in overcrowded cities, a worsening of the income distribution and the decline of food available per capita[1] (Komlos, 1998; Steckel, 2001; Zehetmeyer, 2011). These negative circumstances were overcome at the end of the 19th century and since that time the trend of height increase in Europe has been practically linear (Baten, 2006; Danubio and Sanna, 2008; Baten and Blum, 2012). Before WWII, its pace was faster in the northern and middle zone of industrialized Europe, while after WWII, it was mainly countries in Southern Europe that experienced the biggest increments (Hatton and Bray, 2010). Approximately since the 1980s, a beginning deceleration or even stagnation started to be apparent in some nations. After being the tallest in the world for 200 years, the US was overtaken by many Northern and Western European countries such as Norway, Sweden and the Netherlands (Komlos and Lauderdale, 2007).

Various authors tried to identify the most important environmental variables that contributed to this dramatic increase of height in the industrialized world. Besides GDP per capita (as the main indicator of national wealth), the most frequently mentioned factors are children's mortality, the general quality of health care, education, social equality, urbanization and nutrition (Komlos and Baur, 2004; Baten, 2006; Bozzoli et al., 2007; Baten and Blum, 2012; Hatton, 2013 etc.). However, the number of investigated European countries is usually limited to the western half of the continent and to former European colonies, because information from the rest of Europe is less accessible. In the present work, we fill this gap. The aim of this study can be summarized in four basic points:

1. Mapping the current average height of young males in nations of European descent and describing the actual dynamics of the height trend.
2. Identifying main exogenous (environmental) factors that determine the final male stature.
3. Creating recommendations that could lead to the maximization of the genetic potential in this regard.
4. Investigating the role of genetics in the existing regional differences in male height.

2. Methods

2.1. Collection of anthropometric data

In order to have the most representative basis for our comparisons, we collected a large number of anthropometric studies of young European males from the whole continent (including Turkey and the Caucasian republics), and also data on young white males from Australia, New Zealand and USA. Whenever possible, we preferred large-scale nationwide surveys that have been conducted within the last 10 years and included at least 100 individuals. Forty-six out of 48 values in Table 1 were based on studies that were conducted between 2003 and 2013. The remaining two studies (from Australia and Lithuania) were done between 1999 and 2001. In case we found two or more representative sources from this period, we preferred those with higher measured values. In general, information from the southeastern part of Europe was the most problematic, because large-scale, nationwide anthropometric research is often virtually non-existent. The only country from which we had data on less than 100 individuals was Georgia ($n = 69$).[2]

In seven cases, we found the most recent data only on local populations (Bosnia and Herzegovina, Georgia, Iceland, Latvia, Romania, Sweden and United Kingdom). The urban surveys from Iceland and Latvia may increase the real national mean, but the study from Iceland was undertaken in the greater area of Reykjavik that encompasses ~70% of the Icelandic population. The mean for the United Kingdom (177.7 cm) was computed from the average height in England, Scotland and Northern Ireland, weighted by the population size. A weighted average of six adult, non-university samples from Bulgaria was 175.9 cm ($n = 643$), which agrees with a rounded mean 176 cm ($n = 1204$) reported in the age category 25–34 years in a recent nationwide health survey CINDI 2007

[1] With regard to possible climatic factors, see the climatic deterioration between 1812 and 1917, documented in Prague Klementinum by average monthly temperatures for August between 1775 and 2013, http://www.infomet.cz/pix/pix1378445272-2.jpg.

[2] According to M. Kharabadze (pers. communication), median male height in a closely unspecified nationwide survey from Georgia was 176 cm.

Table 1
Average male height in European countries and nations of European descent.

Country/region	n	Age	Date	Height	Source
Herzegovina	819	17	2001–2003	185.2	Pineau et al. (2005) (pers. communication)
Netherlands	211	20–21	2009	183.8	Schönbeck et al. (2013)
Montenegro	710	18–19	2013	183.2	S. Popović–pers. communication
Iceland (Reykjavik area)	146	18	2008–2009	181.8	Arngrímsson et al. (2012) (pers. communication)
Sweden (Göteborg area)[a]	2408	17–20	2008–2009	181.4	Sjöberg et al. (2012)
Lithuania	195	18	2001	181.3	Tutkuviene (2005)
Czech republic	302	18–29	2011–2013	181.2	A survey of physical fitness conducted by the authors
Estonia[b,c]	603	20–25	2003–2005	180.9	Kaarma et al., 2008
Serbia	1187	20–29	2006	180.9	J. Grozdanov - pers. communication
Denmark	25,454	~18	2006	180.6	Denmark Statistical Yearbook 2007 (conscripts)
Croatia	358	18	2006–2008	180.5	Juresa et al. (2012)
Germany	317	18–24	2008–2011	180.2	DEGS1 (communication with authors)
Latvia (Riga)[b]	102	18–19	2005–2006	180.1	Céderštréma et al. (2006)
Norway		~18–19	2007	179.9	Statistics Norway 2007 (conscripts)
Slovenia	7033	21	2012	179.8	G. Starc–pers. communication
Austria		19	2009–2011	179.6 (m)	Gleiss et al. (2013)
Belgium		18	2005	179.5	DINBelg 2005
Australia (whites)	295	25–30	1999–2000	179.4	AusDiab survey (1999–2000) (S. Tanamas - pers. comm.)
Slovakia	823	18	2011	179.3	L. Ševčíková - pers. communication
USA (whites)	664	20–39	2003–2006	178.9	McDowell et al. (2008)
Bosnia (Tuzla)	88	18	2003	178.8	Hadžihalilović et al. (2006)
Finland	14,939	20	2011	178.6	M. Santtila–pers. communication
Ireland	162	18–29	2007	178.5	Harrington et al. (2008) (communication with authors)
Poland	846	18	2007–2009	178.5	Kułaga et al. (2010)
Northern Ireland	144	20–25	2010–2012	178.5	Northern Ireland Health Survey (comm. with authors)
Switzerland	29,707	18–22	2009	178.2	Staub et al. (2011)
Greece	3982	18–26	2006–2007	178.1	Papadimitriou et al. (2008)
Scotland	1231	20–29	2008–2011	178.0	Scottish Health Survey 2008-11 (comm. with authors)
France	110	18–29	2006	177.8	French nutrition and health survey (2006)
New Zealand (whites)	158	19–30	2008–2009	177.8	New Zealand Adult Nutrition Survey (2008–2009)
England	1084	25–34	2008	177.6	Health Survey for England, 2008
Hungary	890	18	2003–2006	177.5	Bodzsár et al. (2008)
Belarus	209	18	2005–2007	177.5	Tehako et al. (2008)
Macedonia[d]	596	18	2012	177.4	Gontarev et al. (2012)
Spain	1275	18–24	2000–2004	177.3	Carrascosa Lezcano et al. (2008)
Russia	1077	20–25	2004–2005	177.3	RLMS (http://www.cpc.unc.edu/projects/rlms-hse)
Italy		18	1999–2004	176.5	Cacciari et al. (2006)
Georgia (Kakheti region)	69	18	2012	176.3	Kharabadze et al. (2012) (pers. communication)
Romania[e]	>1259	18–20	1999–2006	176.0	An unweighted mean of 3 local studies
Bulgaria[f]	643	18–29	2003–2008	175.9	A weighted mean of 6 studies
Ukraine	208	17	2009	175.9	Platonova (2011)
Moldova[g]		20–24	2005	175.3	estimate (based on the Moldova DHS survey, 2005)
Cyprus	339	17.5–18.5	2006–2007	174.6	Photiou (2007)
Albania	649	20–29	2008–2009	174.0	Albania DHS survey (2008–2009) (comm. with authors)
Portugal	696	18	2008	173.9	Sardinha et al. (2010) (D. Santos–pers. communication)
Turkey	325	20–22	2007	173.6	Işeri and Arslan (2009) (comm. with authors)
Azerbaijan	341	20–24	2006	172.9	Azerbaijan DHS survey, 2006 (comm. with authors)
Armenia[g]		20–24	2005	171.9	Estimate (based on the Armenia DHS survey, 2005)

[a] Only men of Scandinavian origin.
[b] Computed by the authors of this study from means of age categories divided by 1 year, weighted by the sample size.
[c] Only ethnic Estonians, who make up ~70% of the population.
[d] Only ethnic Macedonians, who make up ~64% of the population.
[e] An unweighted mean of 3 local studies: Romanian Moldova, northeast (175.7 cm; Vasilov, 2001); the city of Bucharest, southeast (175.7 cm; Radu et al., 2006–2007); Timiş county, west (176.7 cm; M. Tarcea–pers. communication).
[f] A weighted mean of 5 studies (Baykova et al., 2004; Savov et al., 2007; Todorev et al., 2008; Galcheva et al., 2009; Stojanova et al., 2009; Tineshev and Nikolova, 2011).
[g] Estimates of male height from female DHS surveys. The Armenian female mean was obtained via personal communication.
(m) = median.
For more details on sources see Appendix.

(P. Dimitrov–pers. communication). In the case of Romania, we used an unweighted average of 3 local surveys (176.0 cm). Similarly, the average height in Bosnia and Herzegovina (182.0 cm) was computed as an unweighted mean of two local studies in the city of Tuzla, Northeastern Bosnia (178.8 cm), and in Herzegovina (185.2 cm), respectively. Because of the large (6+ cm) difference between these regions, this estimate must be considered only as very rough. However, considering that Herzegovinians used to be the tallest in the country and inhabitants of Tuzla the

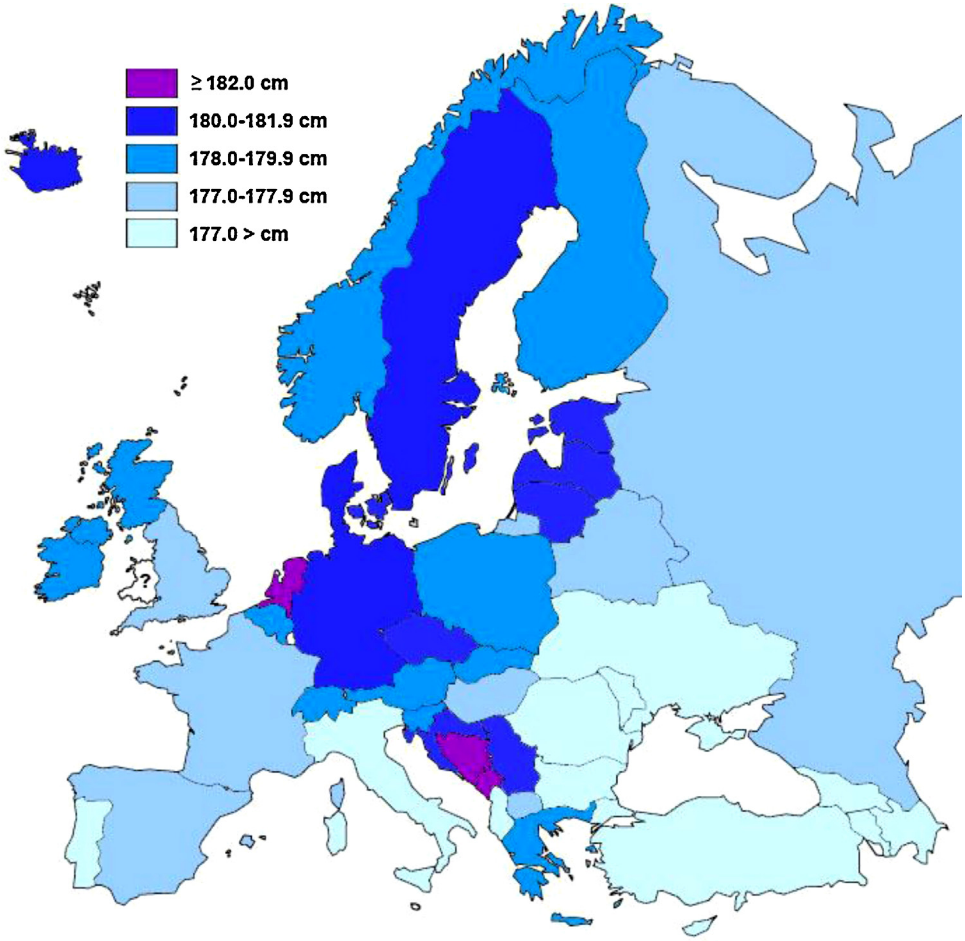

Fig. 1. Distribution of average male height in Europe. *Source:* See Table 1.

shortest (Coon, 1939), it appears reasonable.[3] The average of Herzegovina was further corrected by +1 cm for unfinished growth in 17-year olds, which increased the average of Bosnia and Herzegovina to 182.5 cm. The addition of +1 cm to the height of 17-year old Ukrainian boys increased the Ukrainian mean to 176.9 cm.[4]

In another two countries (Armenia and Moldova), male height was estimated, based on highly representative data of 20–24 year old women from demographic and health surveys (DHS): 159.2 cm for Armenia ($n = 1066$) and 162.3 cm for Moldova ($n = 1099$). These female means were multiplied by 1.08, which was the average ratio of male and female height in 36 countries, where data on both sexes were available from the same study. The obtained values—171.9 cm for Armenia and 175.3 cm for Moldova—appear reasonable, because male and female height in these 36 studies mutually highly correlated ($r = 0.91$; $p < 0.001$). No information on measured height was available from Luxembourg, Malta and Wales.

2.2. Exogenous and genetic variables

Data from these anthropometric surveys were subsequently used for a geographical comparison of European nations (Fig. 1) and for a detailed analysis of key factors that could potentially play a role in the current trends of male height in Europe, primarily with the help of statistics from the CIA World Factbook (the Gini index), FAOSTAT (food consumption) and especially the World Bank, which contained all other variables that we examine (GDP, health expenditure, children's mortality, total fertility, urbanization).[5] Since the

[3] This is also indicated by available surveys of university students: 181.3 cm in Zenica, a Muslim town center in Central Bosnia ($n = 176$), measured between 2010 and 2014 (A. Stanković—pers. communication), and 183.9 cm in Banja Luka in Northern Bosnia, the largest city of the Serb republic ($n = 178$), measured in 2013 (S. Popović—pers. communication). Besides that, a small sample ($n = 58$) of 18-year old students measured in 2010 at three gimnazije (elite high schools) in Tuzla reached 183.4 cm (M. Šabanović – pers. communication).

[4] Understandably, these corrections must be taken as arbitrary, but differences in height between 17 and 18 year olds in the Balkans are of a similar magnitude: +0.7 cm in Croatian boys (a reference growth curve in Jureša et al., 2012), +1.0 cm in Serbian boys from Vojvodina (R. Rakić—pers. communication), or even +1.5 cm in Northeastern Romanians (Vasilov, 2001).

[5] See the CIA World Factbook (https://www.cia.gov/library/publications/the-world-factbook/), FAOSTAT (http://faostat.fao.org/site/610/default.aspx#ancor), the World Bank (http://data.worldbank.org/topic).

final adult stature can be influenced by changes in living standards up to the cessation of growth, it was not surprising that long-term averages of these variables routinely produced higher correlation coefficients than data from the latest available year. However, data from all these sources were available only since 2000 and our analysis was therefore limited to long-term means from the period 2000–2012. The only exception was the Gini index (which was based on the latest available year from 1997 to 2011) and nutritional statistics (FAOSTAT 2000–2009), where the mean of Montenegro was computed only from the period 2006–2009.

Genetic profiles of European nations (the phenotypic incidence of lactose tolerance, Y haplogroup frequencies in the male population) were obtained from various available sources and the most numerous samples were always preferred. Only samples with at least 50 individuals were included (see Appendix Tables 3a–d). Frequencies of Y haplogroups (male genetic lineages) E-M96, G-M201, J-P209, R1a-M420 and I-M170 were available from 43 countries (with only Australia and New Zealand missing), but the information on R1b-U106 and R1b-S116 was more limited, because these two lineages were discovered relatively recently (Myres et al., 2011). Nevertheless, most of the missing information concerned the eastern and southeastern parts of Europe, where their frequency is often close to zero and thus largely unimportant for this study. A similar limitation applied for lactose tolerance, where we found data only from 27 countries.

2.3. Statistical analyses

The analysis of the data collected was performed by the software package Statistica 12. Statistical relationships between variables were first investigated via Pearson's linear correlation coefficients. Subsequently, we identified the most meaningful factors via a series of stepwise regression analyses.

3. Results and discussion

3.1. Distribution of average male height in Europe

The average height of 45 national samples used in our study was 178.3 cm (median 178.5 cm). The average of 42 European countries was 178.3 cm (median 178.4 cm). When weighted by population size, the average height of a young European male can be estimated at 177.6 cm. The geographical comparison of European samples (Fig. 1) shows that above average stature (178+ cm) is typical for Northern/Central Europe and the Western Balkans (the area of the Dinaric Alps). This agrees with observations of 20th century anthropologists (Coon, 1939; Coon, 1970; Lundman, 1977). At present, the tallest nation in Europe (and also in the world) are the Dutch (average male height 183.8 cm), followed by Montenegrins (183.2 cm) and possibly Bosnians (182.5 cm) (Table 1). In contrast with these high values, the shortest men in Europe can be found in Turkey (173.6 cm), Portugal (173.9 cm), Cyprus (174.6 cm) and in economically underdeveloped nations of the Balkans and former Soviet Union (mainly Albania, Moldova and the Caucasian republics).

If we also took single regions into account, the differences within Europe would be even greater. The first place on the continent would belong to Herzegovinian highlanders (185.2 cm) and the second one to Dalmatian Croats (183.8 cm).[6] The shortest men live in Sardinia (171.3 cm; Sanna, 2002). Large differences in height exist even within some countries. For example, the average height of Norwegian conscripts in the northern areas (the Finnmark county) is only 176.8 cm, but reaches 180.8 cm in the southern regions of Agder and Sogn og Fjordane,[7] which is a very similar value like in Denmark and Sweden. In Finland, recruits are 178.6 cm tall on average, but men from the southwest of the country reach 180.7 cm (Saari et al., 2010). Both in Norway and Finland, the national average is pulled down by the northernmost regions that are inhabited by the Saami and are usually characterized by below-average values around 177 cm. In Germany, the tallest men can be found in the northwest, in areas adjacent to the Netherlands and Denmark (~181 cm), while the shortest men come from the southeast, east and southwest (~179 cm) (Hiermeyer, 2009). Unusually large differences are typical for Italy, where we can detect a 6.6 cm gap between Sardinia and the northeastern region of Friuli-Venezia Giulia (Sanna, 2002). In the western Balkans, geographical changes in body size are similarly striking, especially in Bosnia and Herzegovina.

3.2. The current state of the height trend

The trend of increasing height has already stopped in Norway, Denmark, the Netherlands, Slovakia and Germany. In Norway, military statistics date its cessation to late 1980s. Since that time, the average height of Norwegian conscripts aged 18–19 years has fluctuated between 179.4 and 179.9 cm.[8] In Germany, the height of recruits has not changed since the mid-1990s, when it reached ~180 cm (J. Komlos–pers. communication). Denmark Statistical Yearbooks also show a stagnation of the height of conscripts throughout the 2000s.[9] In the Netherlands, national anthropometric surveys done in 1997 and 2009 documented the same height in young men aged 21 years (184.0 cm and 183.8 cm, respectively; Schönbeck et al., 2013). According to preliminary results of the Slovakian survey from 2011 (L. Ševčíková–pers. communication), the stature of Slovak males also remained the same, 179.4 cm in 2001 and 179.3 cm in 2011.

In contrast, the positive trend of height still probably continues in Sweden and Iceland. The stature of Swedish conscripts was growing throughout the 1990s and reached 180.2 cm in 2004, which was a 0.7 cm increase in comparison with 1994 (Werner, 2007). In 2008–2009, Swedish boys of Scandinavian origin aged 17–20 years ($n = 2408$) from the Göteborg area were 181.4 cm tall

[6] In both cases, the values were measured in 17-year old boys with unfinished growth (Pineau et al. 2005).
[7] Statistics Norway, http://www.ssb.no/a/samfunnsspeilet/utg/201101/08/tab-2011-02-28-01.html. See also Sunder (2003).
[8] https://www.ssb.no/a/histstat/tabeller/4-22.html.
[9] http://www.dst.dk/pukora/epub/upload/17957/01pop.pdf.

Table 2
Pearson linear correlations between male height and various enviromental factors. Statistically significant correlations ($p < 0.05$) are in bold.

	Mean	SD	*r*	i^2	*p*
GDP 2000–2012 (USD)	22,134.1	12,560.5	**0.38**	**0.14**	**0.011**
"West"	32,812.4	7772.3	**0.66**	**0.43**	**0.0009**
"East"	11,920.0	5897.2	**0.54**	**0.29**	**0.008**
HEALTH EXPENDITURE 2000–2011 (USD)	1948.9	1458.4	**0.35**	**0.12**	**0.018**
"West"	3134.1	1167.5	**0.56**	**0.31**	**0.007**
"East"	815.2	452.2	**0.59**	**0.35**	**0.003**
CHILDREN'S MORTALITY 2000–2011	10.1	8.7	**−0.61**	**0.37**	**0.00001**
"West"	5.8	4.1	**−0.48**	**0.23**	**0.022**
"East"	14.2	10.0	**−0.75**	**0.56**	**0.00004**
GINI INDEX	32.4	6.1	**−0.40**	**0.16**	**0.007**
"West"	31.5	5.7	**−0.52**	**0.27**	**0.013**
"East"	33.2	6.5	−0.30	0.09	0.16
% URBAN POPULATION 2000-2012	68.6	12.9	**0.30**	**0.09**	**0.046**
"West"	77.0	10.6	**0.55**	**0.31**	**0.007**
"East"	60.5	9.2	0.14	0.02	0.53
TOTAL FERTILITY 2000–2011	1.59	0.28	−0.11	0.01	0.47
"West"	1.72	0.28	0.12	0.01	0.60
"East"	1.46	0.21	**−0.47**	**0.22**	**0.024**

(Sjöberg et al., 2012). Although these results may not be perfectly comparable, it is noteworthy that the mean in the latter study would decrease to 180.8 cm, if we included boys with immigrant origin. These made up 13.4% of the whole sample and their mean height was only 177.7 cm. This observation can lead to a speculation that the marked deceleration of the height trend in some wealthy European countries may also be due to the growing population of short-statured immigrants. Unfortunately, precise information on the "immigration effect" is not routinely addressed in nationwide anthropometric studies. Nevertheless, population means from an English health survey (2004) allow us to estimate that immigrants and their descendants decreased the height of men in England by ca. −0.3 cm, from 177.5 to 177.2 cm.[10]

A certain stagnation or even a reversal of the height trend can also be observed in other parts of Europe, but considering that it concerns relatively less developed countries, with short population heights (e.g. Azerbaijan), it stems from momentary economical hardships. The onset of the economic recession in the early 1990s was particularly harsh in Lithuania, where it may have affected the youngest generation of adult men, but not women: While in 2001, the average height of 18-year olds was 181.3 cm in boys ($n = 195$) and 167.5 cm in girls ($n = 278$) (Tutkuviene, 2005), in 2008 the means in the same age category in the area of Vilnius were 179.7 cm in boys ($n = 250$) and 167.9 cm in girls ($n = 263$) (Suchomlinov and Tutkuviene, 2013). Since the economic situation in Lithuania has dramatically improved during the last ~15 years, the contemporary generation of teenage boys could potentially exceed the value from 2001.

In contrast, the fastest pace of the height increase (≥1 cm/decade) can be observed in Ireland, Portugal, Spain, Latvia, Belarus, Poland, Bosnia and Herzegovina, Croatia, Greece, Turkey and at least in the southern parts of Italy. Interestingly, the adult male population in the Czech Republic also continues to grow at a rate of ~1 cm/decade. Our own observations were supported by a recent cross-sectional survey of adolescents from Northern Moravia (Kutáč, 2013), in which 18-year old boys reached 181.0 cm ($n = 169$). In Estonia (Kaarma et al., 2008) and Russia (RLMS survey), the pace of height increments in males can be estimated at 0.5 cm/decade. In Slovenia, the upward trend in 21-year olds has been slowing down, from 0.5 cm during 1992–2002 to only 0.3 cm during 2002–2012 (G. Starc–pers. communication).

In many of the wealthiest countries (Austria, France, Switzerland, United Kingdom and USA) the increase is mostly steady, but slow. For example, the height of Austrian conscripts increased by 0.5 cm in the period between 1991–1995 and 2001–2005 (E. Schober–pers. communication). Similarly, the stature of Swiss conscripts increased by 0.6 cm between 1999 and 2009 (Staub et al., 2011). Approximately the same pace is typical for white American men (Komlos and Lauderdale, 2007). In England, the height of men aged 25–34 years stagnated at ~176.5 cm during the 1990s, but then started to grow again around 2000 and reached 177.6 cm in 2008–2009. Information from the southeastern part of Europe is much scarcer, but DHS surveys show a moderate upward trend (~0.8 cm/decade) in Albanian men (Albania DHS survey, 2008–2009) and about 0.5 cm/decade in women from Armenia (Armenia DHS survey, 2005) and Moldova (Moldova DHS survey, 2005).

3.3. *Positive relationship between GDP per capita and the height trend in Europe*

As expected, the large regional differences in male height outlined in the Section 3.1 correlated with average GDP per capita (in USD, by purchasing power parity) according to the World Bank (2000–2012) ($r = 0.38$; $p = 0.011$) (Table 2; Fig. 2). However, this moderately strong relationship actually consists of two far narrower correlation lines in the former communist "Eastern block" ($r = 0.54$; $p = 0.008$) and non-communist "Western countries" (including Cyprus and Turkey) ($r = 0.66$; $p < 0.001$).

[10] The average height of all non-English communities (including the Irish) was ca. 174.3 cm, from 169.8 cm in the Bangladeshi to 177.3 cm in Afro-Carribean men (http://www.natcen.ac.uk/media/460320/c78191bb-1c0d-4e18-9eaf-db6b8035647d.pdf, Table 6.3).

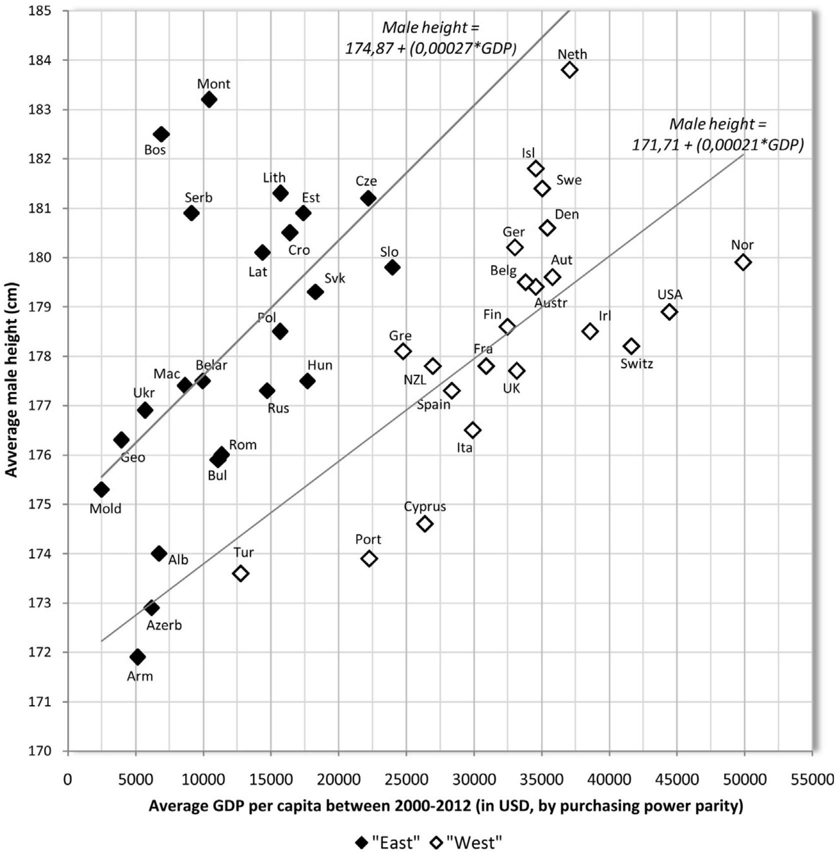

Fig. 2. Relationship between average GDP per capita (current international USD, by purchasing power parity; 2000–2012) and male height ($r = 0.38$; $p = 0.011$). The correlation would reach $r = 0.66$ ($p < 0.001$) in the "West" and $r = 0.54$ ($p = 0.008$) in the "East".
(*Source:* The World Bank. http://data.worldbank.org/indicator/NY.GDP.PCAP.PP.CD (GDP per capita. by purchasing power parity).)

The difference between them is about 20 000 USD. In other words, some of the former "Eastern" countries reach the same height like former "Western countries" despite ~20,000 USD lower GDP and at the same level of GDP, they are ca. 3 cm taller. These facts could imply that the trend of increasing height in Europe continued uninterrupted on both sides of the "Iron curtain", irrespectively of the increasing gap in national wealth, and today's differences in height were largely determined by regional differences existing in Europe at the end of the 19th century.

To test this hypothesis, we compared documented averages of young males from the end of the 19th century with present values in 21 countries/regions (Fig. 3). This comparison shows that the height of males in the eastern half of Europe (and even in Southern Europe and the Netherlands) grew much faster than in the highly industrialized Western Europe. For example, since the 1880s male height has increased by ca. 11 cm in Great Britain and France, by 7.4 cm in Australia and by 8.1 cm in USA. In contrast, the height of Czech and Dutch men has increased by 16.6 cm, Slovak men by 16.7 cm, Slovenian men by 17.2 cm, Polish men by 17.5 cm and Dalmatian men by at least 18.3 cm. Furthermore, the height of young men in these countries is currently higher than in Western Europe, often very markedly. Apparently, this phenomenon can't be explained by any economic statistics.

A very eccentric example emerged especially in former Yugoslavia, where Bosnia and Herzegovina, Montenegro and Serbia reach much higher values of mean height than their GDP would predict. After the exclusion of 6 successor states of former Yugoslavia, the correlation with GDP per capita in the remaining 39 countries would steeply increase to $r = 0.58$ ($p < 0.001$) and it would even reach $r = 0.80$ ($p < 0.001$) in 17 countries of the former "Eastern block". Remarkably, the huge decrease of height across the border of Montenegro and Albania (at least -9 cm), at similar values of GDP per capita, has hardly any parallel in other parts of the world, except a similar difference across the borders of malnourished North Korea/South Korea (Kim et al., 2008; Pak, 2010) and USA/Mexico (Del-Rio-Navarro et al., 2007; McDowell et al., 2008). Again, this points to the strong role of some specific local factors.

A very different situation can be observed in former "Western" countries like Norway and Switzerland that have a much higher GDP per capita than we would assume on the basis of the correlation line. Interestingly, the same applies for the white population of USA, which is a phenomenon that is discussed (Komlos and Lauderdale, 2007). It seems that economic growth in these countries

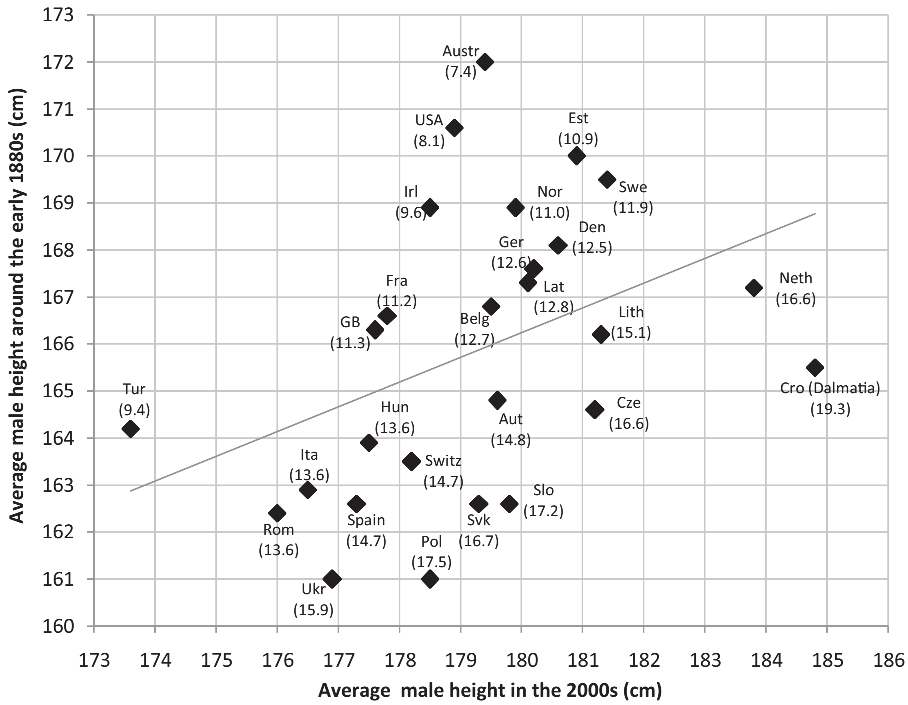

Fig. 3. Relationship between average male height at the end of the 19th century and the most recent anthropometric surveys (the increase of height in centimeters is in parantheses) ($r = 0.40$; $p = 0.036$).
(*Source:* Hatton and Bray, 2010 (birth cohorts 1861–1865 for Belgium, Denmark, France, Germany, Great Britain, Ireland, Italy, Netherlands, Norway, Spain, Sweden), Komlos, 2007 (birth cohort 1863 for Austria, Czech lands, Dalmatian Croatia, Hungary, Poland, Romania, Slovakia), Steckel, 2001 (Australia, 1860–1890), Zehetmeyer, 2011 (USA, birth cohort 1860–1864), Gerhards, 2005 (Latvia, 1874–1875), Kasmel et al., 2008 (Estonia, 1890), Tutkuviene, 2005 (Lithuania, 1882), Özer, 2008 (Turkey, 1891), Staub et al., 2011 (Switzerland, 1884). For more details on sources see Appendix.)
Note: The data for Poland and Ukraine encompass only the territory of the Austro-Hungarian empire. Lintsi and Kaarma (2006) list average height only 165.9 cm in 17-year old Estonian boys from Tartu/Dorpat (in 1886). The height of 17-year old Dalmatian Croats (183.8 cm; J.-C. Pineau–pers. communication) was corrected by +1 cm for unfinished growth.

must have outpaced the positive height trend, but this fact still cannot explain, why the trend remains quite slow or non-existent during the last decades.

3.4. Health expenditure

Besides GDP per capita, another moderately significant relationship ($r = 0.35$; $p = 0.018$) was found between height and average health expenditure per capita (in USD, by purchasing power parity) according to the World Bank (2000–2011). The general pattern was very similar to that in Fig. 2, with two parallel and much stronger lines of correlation consisting of the former "Eastern" ($r = 0.59$; $p = 0.003$) and "Western" ($r = 0.56$; $p = 0.007$) countries (Fig. 4). Wealthy countries spend more money on healthcare than poorer countries, and USA is an anomaly in this regard. Relatively low expenditures on healthcare are typical for the Balkans, Caucasian republics, the Mediterranean and former USSR republics.

3.5. Children's mortality under 5 years

A closely related factor, average children's mortality under 5 years (per 1000 live births; according to the World Bank, 2000–2012), showed the highest impact on physical growth out of all examined socioeconomic variables ($r = -0.61$; $p < 0.001$) that would persist even after the exclusion of an outlier—Azerbaijan ($r = -0.58$; $p < 0.001$) (Fig. 5). Indeed, Hatton (2013) found that children's mortality (or a disease-free environment, respectively) has had a far bigger influence on the positive height trend in Europe since the mid-19th century than GDP per capita and other socioeconomic stats. Our data nevertheless indicate that in contemporary Europe, children's mortality is a serious issue only in some regions of the former USSR and the Balkans (mainly Azerbaijan, Georgia, Turkey, Moldova, Armenia, Albania and Romania). When the death rate falls below 10 cases per 1000 live births, this factor loses its predictive power, as shown by the sharp difference between correlation coefficients in the former "Eastern" block ($r = -0.75$; $p < 0.001$) and "Western" countries ($r = -0.48$; $p = 0.022$).

3.6. Gini index

The Gini index of social inequality (the latest available year after the CIA World Factbook, 1997–2011) also appeared to be a significant, negative variable ($r = -0.40$; $p = 0.007$) (Fig. 6). The lowest values of the

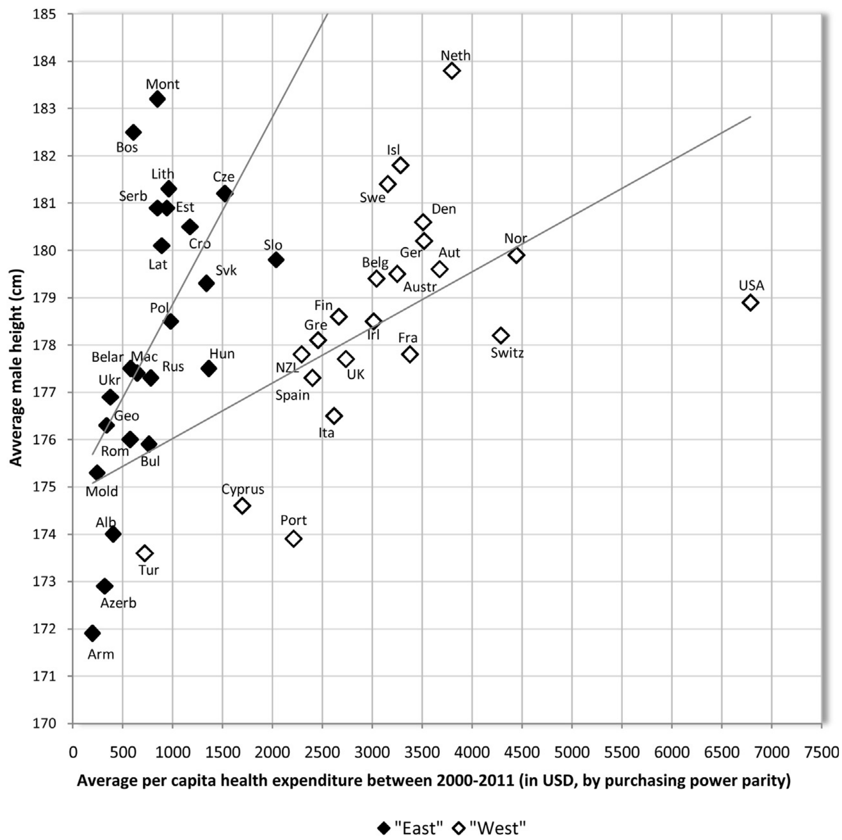

Fig. 4. Relationship between average per capita health expenditure (constant 2005 international USD, by purchasing power parity; 2000–2011) and male height ($r = 0.35$; $p = 0.018$). The correlation would reach $r = 0.56$ ($p = 0.007$) in the "West" and $r = 0.59$ ($p = 0.003$) in the "East".
(*Source:* The World Bank. http://data.worldbank.org/indicator/SH.XPD.PCAP.PP.KD (health expenditure per capita. by purchasing power parity).)

Gini index (i.e. the highest levels of social equality) are typical for Northern/Central Europe, while the highest Gini indices (the biggest social differences) can be found mainly in the Balkans, former USSR, and also in the United Kingdom and USA. A higher Gini average (33.2) indicates that social differences in countries of the former "Eastern block" are somewhat more accentuated, but they have no relationship to male stature ($r = -0.30$; $p = 0.16$), most probably because of outliers in the least developed regions, where the Gini index recedes to the background at generally high levels of poverty. In contrast, the Gini index in "Western" countries is lower on average (31.5), but it does play some role in this regard ($r = -0.52$; $p = 0.013$), mainly because of the wide polarity between egalitarian societies of Northern/Central Europe on one hand, and more socially stratified countries like USA, UK, Portugal and Turkey on the other hand. In general, social inequality tended to increase with decreasing GDP per capita ($r = -0.31$; $p = 0.038$) and it also correlated with higher children's mortality rates ($r = 0.39$; $p = 0.008$).

It is understandable that when lower social classes suffer from an uneven distribution of wealth, they are likely to reach lower height on average and pull the national mean down. A huge role of socioeconomic differences can be demonstrated on some examples from the Balkans, where it concerns mainly the contrast between urban and rural populations. For example, male height in Romania can range from 168.2 cm in rural areas of Suceava county up to 179.5 cm in middle-sized towns of the same region (Vasilov, 2001). Nevertheless, male height in Lithuania, Latvia and Bosnia and Herzegovina is still above-average, despite rather high Gini indices.

3.7. Urbanization (% urban population)

The effect of urbanization (measured as the proportion of the urban population according to the World Bank, 2000–2012) was quite low ($r = 0.30$; $p = 0.046$), when Europe is viewed as a whole, but its role increases dramatically, when only former "Western countries" are taken into account ($r = 0.55$; $p = 0.007$), or when former Yugoslavia is excluded ($r = 0.56$; $p < 0.001$) (Appendix Fig. 1). This is also reflected by the high association between urbanization and GDP per capita ($r = 0.69$; $p < 0.001$) (Appendix Table 1). In the former "Eastern block", urbanization in the above mentioned period was much lower (60.5% vs. 77.0% in the "West") and has no relationship to stature ($r = 0.14$; $p = 0.53$). Based on our data, it seems that the level of urbanization starts to affect stature only after more than ~70% population is concentrated in cities.

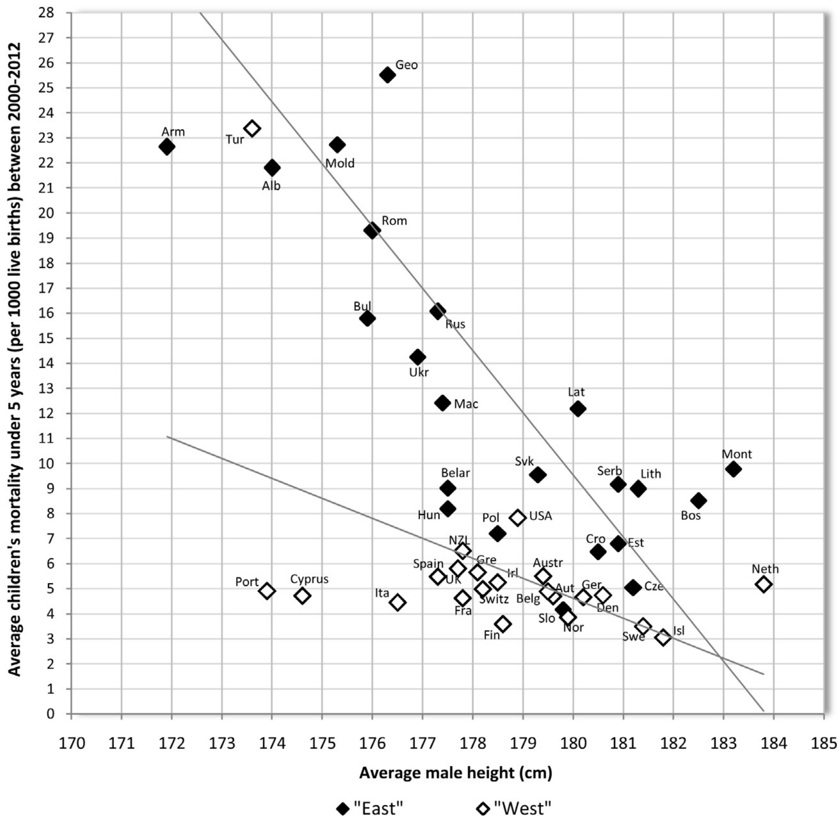

Fig. 5. Relationship between average children's mortality under 5 years (per 1000 live births) between 2000 and 2012 and male height ($r = -0.61$; $p < 0.001$). The correlation would reach $r = -0.48$ ($p = 0.022$) in the "West" and $r = -0.75$ ($p < 0.001$) in the "East".
(*Source:* The World Bank. http://data.worldbank.org/indicator/SH.DYN.MORT/countries (mortality rate under 5 years per 1.000 live births). *Note:* The outlier value of Azerbaijan (50.3) was omitted.)

3.8. *Total fertility*

The analysis of fertility (total number of children per woman) was based on the statistics from the World Bank (2000–2011). The presumption is that if the number of children is low, the expenditure of parents per a child can increase, and hence living conditions for its development improve. This factor apparently played an important role in the acceleration of the height trend in Europe in the past (Hatton and Bray, 2010), but this does not seem to be the case in contemporary Europe ($r = -0.11$; $p = 0.47$) and especially in "Western" countries ($r = 0.12$; $p = 0.60$) (Appendix Fig. 2). The correlation coefficient was medium high only in former "Eastern" countries ($r = -0.47$; $p = 0.024$), largely due to higher birth rates in economically disadvantaged regions of the Balkans and former USSR. Considering that birth rates are already very low in all regions of Europe, height differences among nations are unlikely to be influenced by this variable. To the contrary, it is possible that in the future, height will correlate positively with higher fertility, as indicated by the positive relationship of fertility with GDP per capita ($r = 0.33$; $p = 0.025$), health expenditure ($r = 0.36$; $p = 0.016$) and urbanization ($r = 0.40$; $p = 0.006$) (Appendix Table 1).

3.9. *Nutrition*

The available data on protein consumption from the FAOSTAT database (2000–2009) show that male stature generally correlates positively with animal proteins ($r = 0.41$; $p = 0.005$), particularly with proteins from milk products in general ($r = 0.47$; $p = 0.001$), cheese ($r = 0.44$; $p = 0.002$), pork meat ($r = 0.42$; $p = 0.004$) and fish ($r = 0.33$; $p = 0.028$).[11] In plant proteins, the effect was clearly negative ($r = -0.50$; $p < 0.001$), and was particularly strong in proteins from wheat ($r = -0.68$; $p < 0.001$) (Fig. 7) and cereals in general ($r = -0.59$; $p < 0.001$), but partly even in rice ($r = -0.38$; $p = 0.01$) and vegetables ($r = -0.35$; $p = 0.017$) (Table 3). Total protein consumption is quite an insignificant dietary indicator, because its

[11] The lack of correlation between height and whole milk may seem contradictory at first glance, but whole milk is nowadays consumed mainly in less developed countries like Albania and Romania. Furthermore, it has only a weak relationship to the total consumption of milk proteins ($r = 0.28$; $p = 0.06$) that is primarily linked to the consumption of cheese ($r = 0.68$; $p < 0.001$). The exact meaning of the term "whole milk" in the FAOSTAT database is uncertain, but some available national statistics clearly show that it may include all types of liquid milk, not only whole fat milk.

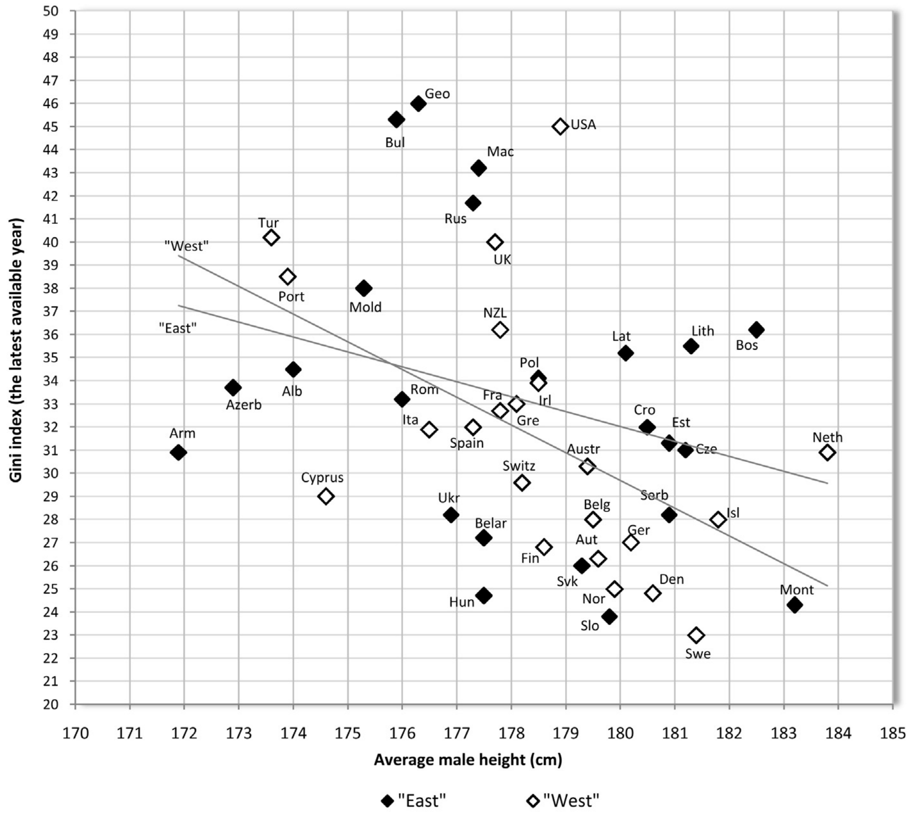

Fig. 6. Relationship between the Gini index of social inequality (the latest available year from the period 2005–2011; 1997 for New Zealand) and male height ($r = -0.40$; $p = 0.007$). High Gini indices betray high social inequality. The correlation would reach $r = -0.52$ ($p = 0.013$) in the "West" and $r = -0.30$ ($p = 0.16$) in the "East". (*Source:* CIA World Factbook. https://www.cia.gov/library/publications/the-world-factbook/fields/2172.html (Gini indices).)

relationship to male stature is very weak ($r = 0.19$; $p = 0.20$).

When we combined the intake of proteins with the highest *r*-values, the correlation coefficients further increased, as evidenced by the relationship betwen height and the total consumption of proteins from milk products and pork meat ($r = 0.55$; $p < 0.001$), or from milk products, pork meat and fish ($r = 0.56$; $p < 0.001$) (Fig. 8). All these comparisons still failed to explain the extreme height of the Dutch. The secret of the tall Dutch stature emerged only after we plotted the total consumption of proteins from milk products, pork meat and fish against the consumption of wheat proteins. This "protein index" was the strongest predictor of male height in our study, when all 45 countries were included ($r = 0.72$; $p < 0.001$) (Fig. 9).[12] Without former Yugoslavia, the correlation further increased to $r = 0.77$. The ratio between milk and wheat proteins gave almost the same result ($r = 0.71$; $p < 0.001$).

These findings are logical, because according to the amino acid score (AAS, the proportion of the worst represented amino acid), wheat contains one of the poorest proteins among all kinds of food due to a severe deficit of lysine, whereas animal proteins contain one of the very best proteins (see Appendix Table 2 and further e.g. Milford, 2012; FAO Expert Consultation, 2013). Furthermore, the digestibility of protein from plant foods is between 80% and 90%, while the digestibility of animal protein is higher, usually ~95%, and can reach 100% in boiled meat.[13] Therefore, the PDCAAS (Protein Digestibility Corrected Amino Acid Score, i.e. true protein quality) of plant proteins is even lower and it is mainly the ratio between the best and worst proteins that determines the overall level of the diet.[14]

[12] The correlation would change only marginally to $r = 0.73$ ($p < 0.001$), if we used a more rigorous approach and excluded 4 countries with estimated data (Armenia, Bosnia and Herzegovina, Moldova, Ukraine). A minor difference (decrease) would be observed even in other factors such as GDP per capita ($r = 0.35$; $p = 0.024$), health expenditure ($r = 0.33$; $p = 0.037$), children's mortality ($r = -0.57$; $p < 0.001$) and total fertility ($r = -0.08$; p=0.63). The r-values would differ (increase) somewhat more in % urban population ($r = 0.36$; $p = 0.022$) and the Gini index ($r = 0.48$; $p = 0.002$).

[13] See http://www.fao.org/docrep/005/ac854t/AC854T68.htm#chII.I.

[14] This does not exclude the possibility that some other, non-protein food sources can also influence physical growth, as shown by the significant relationship between male stature and the consumption of beer ($r = 0.46$; $p = 0.002$), bananas ($r = 0.47$; $p = 0.001$) and especially coffee ($r = 0.63$; $p < 0.001$). Although the role of coffee and beer in the physical growth of male youth makes little sense at first glance, these food items remained among the most significant factors even in a multiple regression analysis and showed a very remarkable relationship to various health indicators. The possible explanations for these findings should be addressed by our next special paper dealing with human height and nutrition.

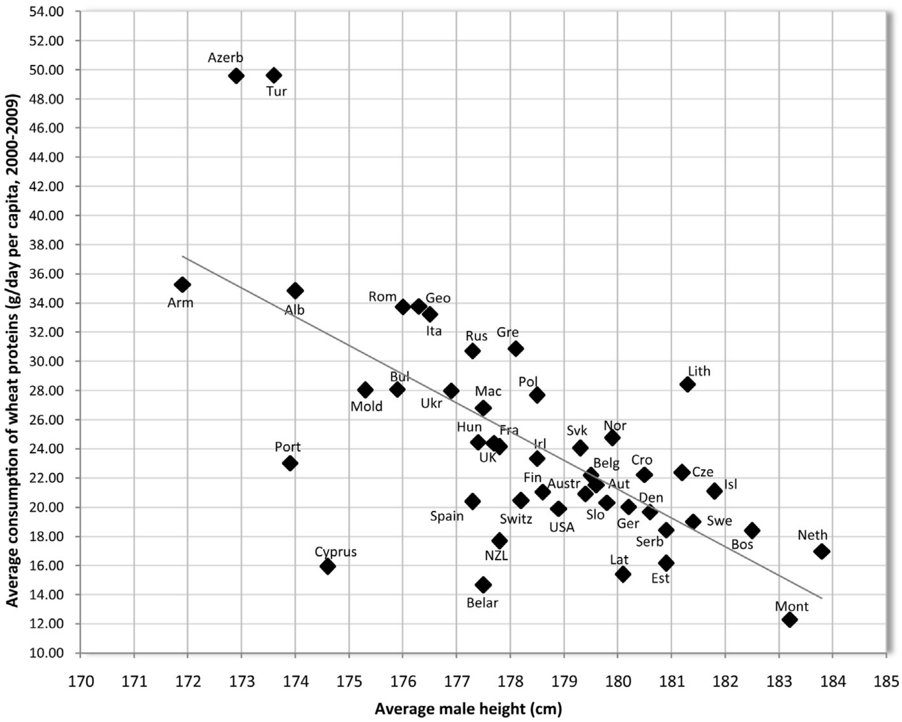

Fig. 7. Relationship between the average consumption of wheat proteins (g/day per capita; for 2000–2009) and male height ($r = -0.68$; $p < 0.001$). (*Source:* http://faostat.fao.org/site/610/DesktopDefault.aspx?PageID=610#ancor (average food consumption between 2000 and 2009).)

Table 3
Pearson linear correlations between male height and average protein consumption (g/day per capita; after FAOSTAT 2000–2009), sorted by *r*-values. Statistically significant correlations ($p < 0.05$) are in bold. Only food items with consumption rates above 0.5 g/day were included.

Protein (g/day)	Mean	SD	r	r^2	p
Milk products total	19.0	5.8	**0.467**	**0.218**	**0.001**
Cheese	7.3	4.9	**0.440**	**0.194**	**0.002**
Pork meat	8.1	4.5	**0.422**	**0.178**	**0.004**
ANIMAL PROTEIN	53.1	16.4	**0.408**	**0.166**	**0.005**
Fish total[a]	3.1	2.4	**0.328**	**0.108**	**0.028**
Meat total	23.2	8.8	0.289	0.083	0.054
Pelagic marine fish	2.1	2.2	0.279	0.078	0.06
Crustaceans	0.5	1.0	0.263	0.069	0.08
Fish & seafood	5.6	5.0	0.243	0.059	0.11
Freshwater fish	0.7	0.8	0.241	0.058	0.11
TOTAL PROTEIN	96.3	14.9	0.166	0.028	0.28
Eggs	3.2	1.0	0.161	0.026	0.29
Offals	1.8	1.0	0.138	0.019	0.36
Beef meat	6.0	3.1	0.123	0.015	0.42
Oilcrops	0.9	0.6	0.123	0.015	0.42
Potatoes	3.2	1.4	0.111	0.012	0.47
Poultry	7.0	3.3	0.042	0.002	0.79
Treenuts	0.6	0.4	0.035	0.001	0.82
Fruits	1.2	0.5	0.007	0.000	0.96
Legumes	1.7	1.4	−0.067	0.004	0.66
Whole milk	9.1	4.6	−0.068	0.005	0.66
Mutton and goat meat	1.3	1.9	−0.090	0.008	0.56
Vegetables total[b]	3.7	1.3	**−0.354**	**0.125**	**0.017**
Rice	0.9	0.5	**−0.381**	**0.145**	**0.0098**
PLANT PROTEIN	43.3	8.4	**−0.497**	**0.247**	**0.0005**
Cereals total	29.3	7.9	**−0.590**	**0.348**	**0.00002**
Wheat	24.5	7.9	**−0.684**	**0.468**	**0.000000**

[a] Includes freshwater fish, pelagic marine fish and other (unspecified) species of marine fish.
[b] Vegetables include mushrooms, but not potatoes.
Source: http://faostat.fao.org/site/610/DesktopDefault.aspx?PageID=610#ancor (average food consumption 2000–2009).

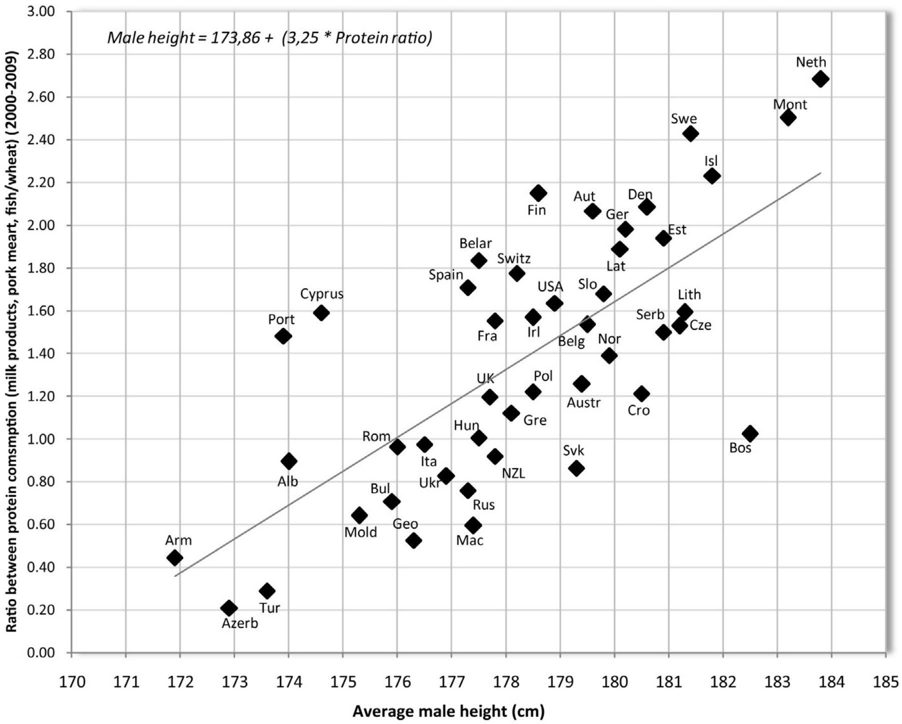

Fig. 8. Ratio between the average consumption of high-quality proteins (milk products, pork meat, fish) and low-quality proteins (wheat) (for 2000–2009) and its relationship to male height ($r = 0.72$; p ? 0.001).
(*Source:* http://faostat.fao.org/site/610/DesktopDefault.aspx?PageID=610#ancor (average food consumption between 2000 and 2009).)

3.10. Implications for rational nutritional programs

The fundamental role of nutrition among exogenous variables influencing male stature has very important implications. While many economic and social factors are usually beyond an individual's direct control (personal income, total fertility and living in urban areas being rather exceptions), nutrition is a matter of personal choice. It is true that the accessibility of certain foodstuffs is limited by national wealth (GDP per capita), but the relationship is not as high as we would expect. GDP per capita has the most direct influence on the total consumption of animal protein ($r = 0.82$), meat ($r = 0.78$), cheese ($r = 0.75$) and exotic fruits like pineapples, oranges and bananas ($r \geq 0.67$), but not so much on the "protein index" ($r = 0.57$; $p < 0.001$). This shows that nutrition in all countries could be significantly improved via rational dietary guidelines, irrespectively of economic indicators.

In this context, it should be noted that the quality of proteins (expressed as the "protein index") in the wealthiest nations of European descent has a tendency to deteriorate during the last 2–3 decades (Fig. 9 and Appendix Fig. 3). This trend is characterized by a partial decrease in the consumption of milk products, beef and pork meat, and increasing consumption rates of cheese, poultry and cereals. In contrast, the quality of nutrition in the Mediterranean and some countries of the former Eastern block has been improving (Appendix Fig. 4). In the light of these findings, it is understandable, why other wealthy nations haven't reached the height standard seen in the Netherlands and why their positive height trend slowed down or stopped.

We suspect that these negative tendencies are due to the combination of the inadequate "fast-food" nutrition with some misguided dietary guidelines such as "modern healthy eating plates" of the Harvard School of Public Health. These are currently promoted by certain public initiatives in Czech schools and empasize vegetables and whole grains at the expense of animal proteins, while recommending to limit milk intake.[15] Although some of these recommendations could certainly improve overall health in adults, our calculations based on the FAOSTAT data show that they should be viewed as detrimental for the healthy development of children. The possible health risks of a diet based on high-quality animal proteins seem to be exaggerated as well and we intend to address all important issues related to height and nutrition in a more detailed paper, based on our own research using actual statistics of the incidence/prevalence of cancer and cardiovascular diseases in Europe and long-term averages of FAOSTAT data (1993–2009).

[15] http://www.hsph.harvard.edu/nutritionsource/healthy-eating-plate/.

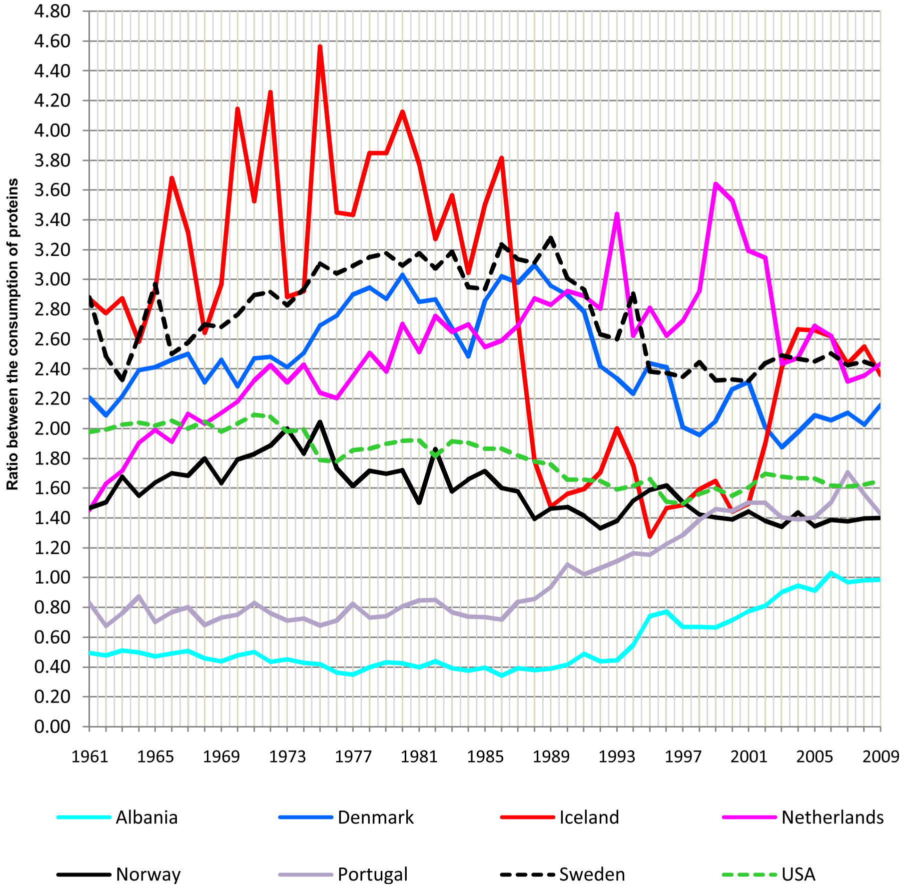

Fig. 9. Ratio between the consumption of high-quality proteins (milk products, pork meat and fish) and low-quality proteins (wheat) in selected countries since 1961.
(*Source:* http://faostat.fao.org/site/610/DesktopDefault.aspx?PageID=610#ancor (average food consumption between 1961 and 2009).)

3.11. Y haplogroups I-M170 and R1b-U106: possible genetic determinants of extreme tallness in Europe

Although the documented differences in male stature in European nations can largely be explained by nutrition and other exogenous factors, it is remarkable that the picture in Fig. 1 strikingly resembles the distribution of Y haplogroup I-M170 (Fig. 10a). Apart from a regional anomaly in Sardinia (sub-branch I2a1a-M26), this male genetic lineage has two frequency peaks, from which one is

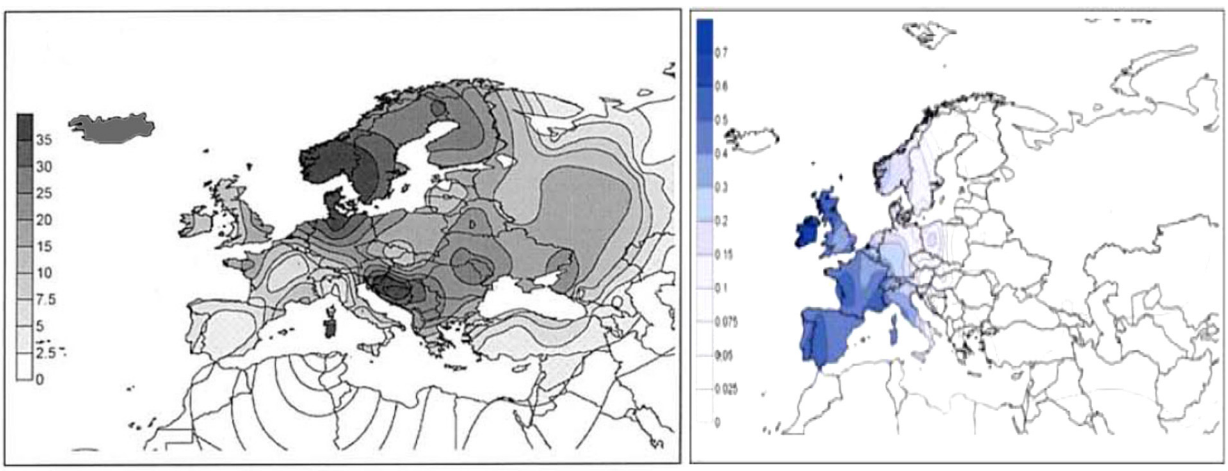

Fig. 10. (a) Distribution of Y haplogroup I-M170 in Europe. (*Source:* Rootsi et al. (2004).) (b) Distribution of Y haplogroup R1b-S116 in Europe. (*Source:* Myres et al. (2011).) *Note:* The frequency of I-M170 in Iceland was supplemented by the authors.

Table 4
Pearson linear correlations between male height and various genetic factors. Statistically significant correlations ($p < 0.05$) are in bold.

Variable 1	Variable 2	n	r	r^2	p
Male height	I-M170	43	**0.65**	**0.42**	**0.000003**
Male height	I-M170[a]	43	**0.67**	**0.45**	**0.000001**
Male height	R1a-M420	43	0.19	0.04	0.21
Male height	R1a-M420[a]	43	0.25	0.06	0.11
Male height	R1a-M420 + I-M170	43	**0.52**	**0.27**	**0.0003**
Male height	R1a-M420[a] + I-M170[a]	43	**0.55**	**0.31**	**0.0001**
Male height	R1b-U106	34	**0.49**	**0.24**	**0.003**
Male height	R1b-U106[b]	19	**0.60**	**0.36**	**0.007**
Male height	R1b-S116	31	−0.12	0.02	0.51
Male height	R1b-S116[b]	17	**−0.48**	**0.23**	**0.049**
Male height	R1b-U106 + R1b-S116	31	0.08	0.01	0.65
Male height	I-M170 + R1b-U106	34	**0.75**	**0.56**	**0.000000**
Male height	I-M170[a] + R1b-U106[a]	34	**0.78**	**0.60**	**0.000000**
Male height	I-M170 + R1b-U106 + R1a-M420	34	**0.59**	**0.35**	**0.0002**
Male height	I-M170 + R1b-U106 + R1b-S116	31	**0.43**	**0.18**	**0.017**
Male height	I-M170[a] + R1b-U106[a] + R1b-S116[a]	31	**0.45**	**0.20**	**0.011**
Male height	E-M96 + G-201 + J-P209	43	**−0.64**	**0.41**	**0.000004**
Male height	Lactose tolerance	27	**0.71**	**0.50**	**0.00004**
Lactose tolerance	I-M170	26	**0.66**	**0.43**	**0.0003**
Lactose tolerance	I-M170[a]	26	**0.62**	**0.39**	**0.0007**
Lactose tolerance	R1a-M420	26	−0.10	0.01	0.62
Lactose tolerance	R1a-M420[a]	26	−0.09	0.01	0.67
Lactose tolerance	R1a-M420 + I-M170	26	0.23	0.06	0.25
Lactose tolerance	R1a-M420[a] + I-M170[a]	26	0.22	0.05	0.28
Lactose tolerance	R1b-U106	23	**0.65**	**0.43**	**0.0007**
Lactose tolerance	R1b-U106[b]	17	**0.60**	**0.36**	**0.010**
Lactose tolerance	R1b-S116	21	0.33	0.11	0.14
Lactose tolerance	R1b-S116[b]	15	0.12	0.01	0.67
Lactose tolerance	R1b-U106 + R1b-S116	21	**0.57**	**0.32**	**0.007**
Lactose tolerance	I-M170 + R1b-U106	23	**0.74**	**0.55**	**0.00005**
Lactose tolerance	I-M170[a] + R1b-U106[a]	23	**0.75**	**0.56**	**0.00004**
Lactose tolerance	I-M170 + R1b-U106 + R1a-M420	23	**0.43**	**0.18**	**0.042**
Lactose tolerance	I-M170 + R1b-U106 + R1b-S116	21	**0.78**	**0.60**	**0.00003**
Lactose tolerance	I-M170[a] + R1b-U106[a] + R1b-S116[a]	21	**0.80**	**0.63**	**0.00002**
Lactose tolerance	E-M96 + G-201 + J-P209	26	**−0.73**	**0.53**	**0.00002**

[a] After the exclusion of N1c-M46 in Estonia, Finland, Latvia and Lithuania.
[b] Without Eastern and Southeastern Europe.

located in Scandinavia and northern Germany (I1-M253 and I2a2-M436), and the second one in the Dinaric Alps in Bosnia and Herzegovina (I2a1b-M423).[16] In other words, these are exactly the regions that are characterized by unusual tallness. The correlation between the frequency of I-M170 and male height in 43 European countries (including USA) is indeed highly statistically significant ($r = 0.65$; $p < 0.001$) (Fig. 11a, Table 4). Furthermore, frequencies of Paleolithic Y haplogroups in Northeastern Europe are improbably low, being distorted by the genetic drift of N1c-M46, a paternal marker of Ugrofinian hunter-gatherers. After the exclusion of N1c-M46 from the genetic profile of the Baltic states and Finland, the r-value would further slightly rise to 0.67 ($p < 0.001$). These relationships strongly suggest that extraordinary predispositions for tallness were already present in the Upper Paleolithic groups that had once brought this lineage from the Near East to Europe.

The most frequent Y haplogroup of the western and southwestern part of Europe is R1b-S116 (R1b1a2a1a2-S116) that reaches maximum frequencies in Ireland (82%), Britain, France and on the Iberian peninsula (~50%), and is in all likehood tied with the post-glacial expansion of the Magdalenian culture from the glacial refugium in southern France/Cantabria (Fig. 10b).[17] As already mentioned, Mesolithic skeletons in Western Europe were typically petite (~163 cm) (Formicola and Giannecchini, 1999), which could imply that this haplogroup would be connected with below average statures. When we omitted 14 countries of Eastern and Southeastern Europe, where the frequencies of R1b-S116 are mostly close to zero, the relationship between R1b-S116 and male height reached statistical significance ($r = -0.48$; $p = 0.049$) (Appendix Fig. 5). Therefore, the frequency of R1b-S116 may limit the future potential of physical stature.

A related branch, R1b-U106 (R1b1a2a1a1-U106), apparently has a very different history and is typical for Germanic speaking nations, with a frequency peak in Friesland (~43%). Its correlation with male height in 34 European countries was rather moderate ($r = 0.49$; $p = 0.003$), but increased to 0.60 ($p = 0.007$) without Eastern and Southeastern Europe. Visually, the distribution of this

[16] Y-DNA Haplogroup I and its Subclades—2014, http://www.isogg.org/tree/ISOGG_HapgrpI.html.

[17] In this place, we consider as highly unlikely the view of Myres et al. (2011), who suggest that R1b-S116 and R1b-U106 spread with the advance of Neolithic farmers from Asia Minor, based primarily on notoriously unreliable coalescence times. Such a scenario would require a virtually complete deletion of local Mesolithic lineages in a vast space between Spain and the British Isles.

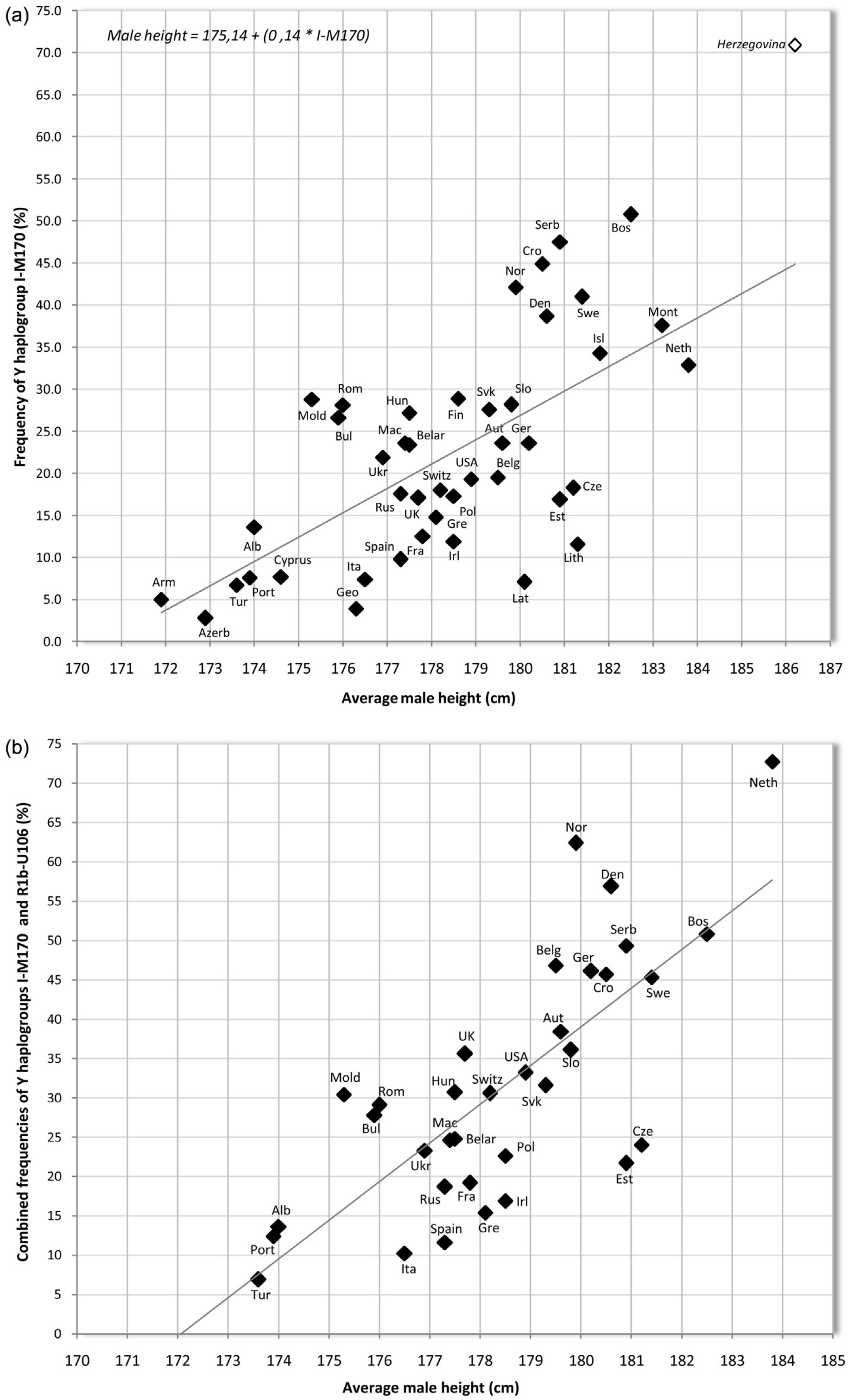

Fig. 11. (a) Relationship between the frequency of Y haplogroup I-M170 and average male height in Europe ($r = 0.65$; $p < 0.001$) (43 countries). A separate regional sample of Herzegovina (70.9% I-M170; after Peričić et al., 2005) was added for an additional comparison. (b) Relationship between combined frequencies of Y haplogroups I-M170 + R1b-U106 and male height ($r = 0.75$; $p < 0.001$) (34 countries).

Table 5a
Multiple regression analysis examining the relationship between male height (43 countries) and 17 meaningful variables significantly ($p < 0.05$) correlating with male stature in this study ($R = 0.93$, adj. $R^2 = 0.76$, $p = 0.000001$). Statistically significant correlations ($p < 0.05$) are in bold.

	b^*	Partial correlation	R^2	Tolerance	p-Value
Plant protein	**1.502**	**0.503**	**0.979**	**0.021**	**0.007**
Cheese	**0.459**	**0.495**	**0.780**	**0.220**	**0.009**
Vegetables total	**−0.521**	**−0.487**	**0.837**	**0.163**	**0.010**
Cereals total	**−1.414**	**−0.447**	**0.982**	**0.018**	**0.019**
I-M170	**0.265**	**0.427**	**0.546**	**0.454**	**0.026**
Animal protein	−0.470	−0.305	0.934	0.066	0.122
GDP 2000–2012	−0.340	−0.189	0.954	0.046	0.346
E + G + J	−0.123	−0.174	0.704	0.296	0.385
Milk products total	0.200	0.166	0.899	0.101	0.408
Protein index	0.294	0.148	0.963	0.037	0.461
Fish total	0.106	0.126	0.794	0.206	0.531
% urban population 2000–2012	−0.076	−0.109	0.705	0.295	0.589
Wheat	−0.188	−0.092	0.965	0.035	0.647
Gini index	0.056	0.087	0.651	0.349	0.666
Health expenditure 2000-2011	0.088	0.055	0.944	0.056	0.786
Children's mortality 2000–2011	0.023	0.016	0.929	0.071	0.937
Pork meat	−0.001	−0.001	0.859	0.141	0.996

haplogroup resembles that of I1-M253 and I2a2-M436 in Northern and Central Europe, which would indicate that they shared a common local history, very different from R1b-S116. This assumption is also supported by the fact that out of all examined genetic lineages in Europe, combined frequencies of R1b-U106 and I-M170 have the strongest relationship to male stature ($r = 0.75$; $p < 0.001$ in 34 countries) (Fig. 11b and Appendix Fig. 6).

The fourth most important Y haplogroup endogenous to Upper Paleolithic Europe, R1a-M420, is typical for Slavic nations (with ~50% frequency in Belarussians and Ukrainians, and 57% in Poles) and has a steeply curvilinear relationship with height that peaks in the case of Poland (178.5 cm) and then abruptly decreases, largely due to a rising proportion of I-M170 in the genetic pool of tall nations. As a result, it is not a good predictor of male height ($r = 0.19$; $p = 0.21$) (Appendix Fig. 7), but combined frequencies of I-M170 and R1a-M420 reach statistical significance ($r = 0.52$; $p < 0.001$) (Appendix Fig. 8). After the exclusion of N1c-M46, the frequency of R1a-M420 in the Baltic states would rise above neighbouring Slavic nations (up to 66.5% in Latvia), but its predictive power still would lag behind I-M170 ($r = 0.25$; $p = 0.11$). Such a result implies that this lineage may have a moderate position in Europe, as for genetic predispositions for height.

Y haplogroups E-M96, G-M201 and J-P209 represent the most important non-indigenous, post-Mesolithic lineages that spread to Europe mainly during the Neolithic expansion from the Near East (6th millenium BC). Expectably, their combined frequencies are the highest in the southeastern part of Europe (>40%) and decrease below 5% in the most remote areas of the continent such as Ireland, Scotland and the Baltic region (Appendix Fig. 9). Their relationship to male stature was markedly negative ($r = -0.64$; $p < 0.001$) (Appendix Fig. 10) and remained significant even after an adjustment for GDP ($r = -0.57$; $p < 0.001$) or the "protein index" ($r = -0.40$; $p = 0.009$). This result indicates that the extremely small statures of early agriculturalists stemmed both from severe undernutrition and genetics.

3.12. Multiple regression analyses of socioeconomic, nutritional and genetic data

Considering that data on the frequencies of I-M170, R1a-M420 and three post-Mesolithic lineages (E-M96, G-M201 and J-P209) were available from 43 countries (except Australia and New Zealand), we included these 43 countries into a series of multiple regression analyses. When we examined the relationship between male height and 6 socioeconomic variables previously discussed above, a forward multiple regression identified children's mortality and the Gini index as the only factors contributing to a fully saturated model ($R = 0.63$, adj. $R^2 = 0.37$; $p < 0.001$). Nutritional factors included into a forward stepwise regression consisted of the "protein index" and 9 significant ($p < 0.05$) protein sources with a daily intake higher than 3.0 g protein per capita (see Table 3). Except pork meat, all of them played an important role ($R = 0.89$, adj. $R^2 = 0.73$; $p < 0.001$). Among three genetic factors, only two (I-M170 and E + G + J) turned out to be meaningful ($R = 0.76$, adj. $R^2 = 0.56$; $p < 0.001$).

Subsequently we made a standard regression analysis that included all 17 meaningful variables significantly related to stature ($p < 0.05$): two genetic factors (I-M170, E + G + J), five socioeconomic factors and 10 nutritional factors. Here, five variables turned out to be statistically significant (Table 5a), but the low values of tolerance indicated a very high degree of multicollinearity. A simpler, fully saturated model based on a forward stepwise regression ($R = 0.89$, adj. $R^2 = 0.75$, $p < 0.001$) consisted of eight variables (Table 5b).[18] The "protein index" deter-

[18] If Armenia, Bosnia and Herzegovina, Moldova and Ukraine were excluded, the forward stepwise regression with 39 countries would include 7 factors ($R = 0.88$; adj. $R^2 = 0.73$; $p < 0.001$). The "protein index" and Y haplogroup I-M170 would again be the most important. The most marked difference would lie in the much higher significance of Y haplogroups E + G + J ($p = 0.006$) that would follow in the third place, and a smaller importance of the Gini index ($p = 0.11$). Besides that, children's mortality and health expenditure would be substituted by % urban population.

Table 5b
Forward stepwise regression analysis examining the relationship between male height (43 countries) and 17 meaningful variables significantly ($p < 0.05$) correlating with male stature in this study ($R = 0.89$, adj. $R^2 = 0.75$, $p < 0.000001$). Statistically significant correlations ($p < 0.05$) are in bold.

	b^*	Partial correlation	R^2	Tolerance	p-Value
Protein index	**0.645**	**0.623**	**0.689**	**0.311**	**0.00005**
I-M170	**0.357**	**0.519**	**0.411**	**0.589**	**0.001**
Cheese	**0.373**	**0.409**	**0.706**	**0.294**	**0.013**
Animal protein	**−0.416**	**−0.368**	**0.816**	**0.184**	**0.027**
Gini index	**0.230**	**0.353**	**0.454**	**0.546**	**0.035**
E + G + J	**−0.233**	**−0.351**	**0.473**	**0.527**	**0.036**
Children's mortality 2000–2011	−0.164	−0.220	0.614	0.386	0.198
Health expenditure 2000–2011	−0.158	−0.192	0.688	0.312	0.261

mined in this study was by far the most important, followed by Y haplogroup I-M170 and cheese (the source of the most concentrated milk proteins).[19] Interestingly, this model also explained the seemingly outlier position of the Dinaric countries and the most important factor here was the inclusion of the genetic component (I-M170) (Appendix Table 4 and Fig. 11).

When examining the causes of the unexpected gap in height between "Eastern" and "Western" countries in Fig. 2, we observed that out of all variables examined in this study, Y haplogroup I-M170 and the "protein index" had the most marked effect on the increase of R-values (to $R = 0.71$, adj. $R^2 = 0.48$ and $R = 0.73$, adj. $R^2 = 0.50$, respectively) and hence a narrowing of this gap, when added as independent variables into a multiple regression that incorporated male height and GDP per capita. In other words, the tallest countries of the former Eastern block enjoy a relatively high level of nutrition that is often better than in "Western" countries with similar or higher GDP values. In addition, their means of male height are further elevated due to genetic factors, which especially applies for former Yugoslavia.

3.13. The role of lactose tolerance: another possible genetic predictor of height in Northern and Central Europe?

The fundamental role of milk in the nutrition of European nations stems from the high prevalence of lactose tolerance—a very valuable genetic trait allowing a sufficient intake of milk even during adulthood. Although many scientists are still not certain about the evolutionary role of lactose tolerance in Europe, the findings of this study show that the ability to consume milk must have been a tremendeous advantage, because it opened up an additional source of nutrition that not only guaranteed survival in the periods of food shortage, but contained nutrients right of the highest natural quality. Interestingly, the correlation of lactose tolerance with the consumption of whole milk ($r = 0.10$; $p = 0.62$) and milk products in general ($r = 0.59$; $p = 0.001$) was weaker than that between lactose tolerance and male height ($r = 0.71$; $p < 0.001$) (Fig. 12). This is the exact opposite of what we would expect. Considering that lactose tolerance is a genetic trait, it is possible that it may correlate with certain genes that determine tall stature.

When examining the relationship between lactose tolerance and frequencies of Y haplogroups, we noticed a very high association of lactose tolerance with the combined frequency of I-M170 and R1b-U106 ($r = 0.74$; $p < 0.001$ in 23 countries) (Appendix Fig. 12). The correlation coefficient further increased to $r = 0.78$ ($p < 0.001$, 21 countries), when R1b-S116 was added, although it overestimated lactose tolerance in R1b-S116-rich areas such as the British Isles, France, Spain and Italy (Appendix Fig. 13 and 14). Based on these results, we hypothesize that the spread of lactose tolerance started from the Northwest

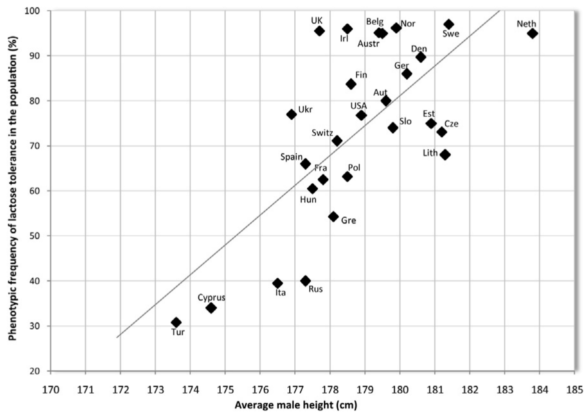

Fig. 12. Relationship between the phenotypic frequency of lactose tolerance in the examined populations and average male height ($r = 0.71$; $p < 0.001$) (27 countries).
(*Sources:* Global Lactase persistance Association Database (weighted means; http://www.ucl.ac.uk/mace-lab/resources/glad/LP_phenotype_frequencies_YI_April-2012.xls), suppplemented by data from Flatz and Rotthauwe (1977), Sahi (2001), Ingram et al. (2009), Wilt et al. (2010), Farup et al. (2004). For more details on sources see Appendix.)
Note: The data on the lactose tolerance in USA and Australia refer to the white (European) population. When only a certain range of data was available in Sahi (2001) (e.g. 92–98% for the Dutch), we opted for the median value (95%). Methodologically dubious results (Belarus, Ukraine) from the same review were excluded. Although the used value for Ukraine (from Kiev, 77%; A. Kozlov–pers. communication, after Gromashevskaya et al., 1991) doesn't deviate fundamentally from the correlation line, it is almost certainly exaggerated, as evidenced by much lower frequencies in Poland and Hungary, and by genotypic testing done in Ukraine (58.2%).

[19] A backward stepwise regression had a smaller power ($R = 0.83$, adj. $R^2 = 0.66$, $p < 0.001$) based on 4 variables (cereals, I-M170, plant protein, vegetables).

European territory between Belgium and Scandinavia, which is the presumed area of origin of the Funnelbeaker culture during the 4th millenium BC (Appendix Fig. 15a). These populations probably carried Y haplogroups I-M170 (I1-M253 and I2a2-M436), R1b-U106 and partly R1b-S116. The successor Corded Ware populations most likely expanded from present-day Poland during the 3rd millenium BC and their genetic composition may have been somewhat different. In any case, contrary to some assumptions, which are also based on limited archeogenetic data (Haak et al., 2008), the distribution of lactose tolerance does not seem to be related to Y haplogroup R1a-M420 ($r = -0.10$; $p = 0.62$ in 26 countries), and this picture would hardly change even when missing data from Latvia and Belarus were added. Obviously, if Corded Ware populations consisted of R1a-M420 males, they were not closely related to the earliest carriers of the lactose tolerance genes. Alternatively, they may have belonged to some minor subbranches of R1a-M420.[20] Besides that, the spread of lactose tolerance in Western Europe and in the British Isles must have been tied with some other cultural circle, perhaps the Bell-Beaker culture during the second half of the 3rd millenium BC (Appendix Fig. 15b). Similarly, lactose tolerance can't be connected with Near Eastern agriculturalists, i.e. Y haplogroups E-M96, G-M201 and J-P209 ($r = -0.73$; $p < 0.001$), despite computer simulations showing that genes of lactose tolerance were originally acquired from agricultural populations in Central Europe (Itan et al., 2009).

4. Conclusion

The dramatic increase of height in Europe starting during the late 19th century is closely linked with the beneficial effect of the industrial revolution. Our comparisons show that this effect is manifested in generally higher standards of living, better healthcare, lower children's mortality, lower fertility rates, higher levels of urbanization, higher social equality and access to superior nutrition containing high-quality animal proteins. In the past, some of these factors may have been more important for a healthy physical growth than they are today and some of them are important only in certain regions, but in general, the most important exogenous factor that impacts height of contemporary European nations is nutrition. More concretely, it is the ratio between proteins of the highest quality (mainly from milk, pork meat and fish) and the lowest quality (i.e. plant proteins in general, but particularly wheat proteins). Besides that, we discovered a similarly strong connection between male height and the frequency of certain genetic lineages (Y haplogroups), which suggests that with the gradual increase of living standards, genetic factors will increasingly be getting to the foreground. Even today, many wealthy nations of West European descent are ca. 3 cm smaller than much poorer countries of the former Eastern block with the same nutritional statistics. Another evidence for this genetic hypothesis recently appeared in the study of Turchin et al. (2012), who found systematically higher presence of alleles associated with increased height in US whites of North European ancestry than in Spaniards.

Remarkably, the quality of nutrition in the wealthiest countries shows signs of a marked deterioration, as indicated by the decreasing values of the "protein index". This can illuminate the recent deceleration/cessation of the positive height trend in countries like USA, Norway, Denmark or Germany, which was routinely explained as the exhaustion of the genetic potential. In our opinion, this assumption is still premature and with the new improvement of nutritional standards, some increase still can be expected.

A very specific case is that of Dinaric highlanders, who are as tall or even taller than the wealthiest nations, in spite of considerably lower living and nutritional standards. However, their seemingly outlier position can be explained by strong genetic predispositions. In the near future, we want to focus on this problem in detail via our planned field project directly in the Dinaric Alps, in collaboration with the University of Montenegro.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ehb.2014.07.002.

[20] According to data listed by Underhill et al. (2014), the most likely candidates are R1a-Z284 and R1a-M417*. Both are more or less associated with lactose tolerance and combined frequencies of I-M170 and R1b-U106, but the examined samples are still too small to allow any meaningful conclusions. Remarkably, these haplogroups don't show any geographical relationship to three other European R1a subbranches tested by Underhill et al. Among these, R1a-M558 is the most frequent and typical for West and East Slavic nations, and has the most negative relationship to lactose tolerance ($r = -0.33$; $p = 0.16$).

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