Annals of
Human Biology
Journal of the Society for the Study of Human Biology

http://informahealthcare.com/ahb
ISSN: 0301-4460 (print), 1464-5033 (electronic)

Ann Hum Biol, Early Online: 1–6
 DOI: 10.3109/03014460.2014.902993

informa
healthcare

RESEARCH PAPER

Digit ratio (2D:4D) as an indicator of body size, testosterone concentration and number of children in human males

Magdalena Klimek[1], Andrzej Galbarczyk[1], Ilona Nenko[1,2], Louis Calistro Alvarado[3], and Grazyna Jasienska[1]

[1]*Department of Environmental Health, Faculty of Health Sciences, Jagiellonian University Medical College, Krakow, Poland,* [2]*Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK, and* [3]*Department of Anthropology, University of New Mexico, Albuquerque, NM, USA*

Abstract

Objectives: The 2nd to 4th digit ratio (2D:4D) is thought to reflect exposure to androgens during foetal development. This study examined the relationship between low (more masculine) and high (more feminine) 2D:4D and body size at different stages of the life course, adult testosterone levels and number of children among males.
Methods: Five hundred and fifty-eight men from rural Poland at the Mogielica Human Ecology Study Site participated in this study. Life history data and anthropometric measurements were collected. Salivary morning and evening testosterone levels among 110 men from the same population were measured.
Results: Low 2D:4D was related to higher birth weight ($p = 0.04$), higher birth length ($p = 0.01$), higher body mass during childhood and adolescence ($p = 0.01$), higher BMI (borderline significance, $p = 0.06$), higher number of children among fathers ($p = 0.04$) and higher testosterone levels during adulthood ($p = 0.04$).
Conclusions: This study shows, for the first time in a single population, that digit ratio is related to sub-adult body size at different stages of the life course, adult testosterone levels and number of children. The observed results suggest that digit ratio might be a valuable predictor of male body size and reproductive characteristics.

Keywords

2D:4D, body size, number of children, rural population, testosterone

History

Received 23 October 2012
Revised 27 January 2014
Accepted 16 February 2014
Published online 28 April 2014

Introduction

Pre-natal testosterone concentration may play a significant role in programming the future biological condition of males, including body size and reproductive success (Fink et al., 2003; Manning & Fink, 2008). A number of researchers have suggested that 2nd to 4th digit ratio (2D:4D) might be a marker of pre-natal androgens concentration in the womb (i.e. Manning & Bundred, 2000). 2D:4D is defined as a proportion between the length of the index and ring fingers and is determined during early foetal development, around the 13th week of gestation (Manning et al., 1998). Higher concentration of pre-natal testosterone (in relation to oestrogen) may be indicated by longer ring finger than index finger and is defined as low digit ratio. In contrast, high 2D:4D potentially indicates a greater early oestrogen exposure (in relation to testosterone) (Manning & Bundred, 2000). The relationship between pre-natal sex hormone concentration and finger lengths was supported by a study that shown that males with congenital adrenal hyperplasia (CAH) – a disease related to high pre-natal levels of androgens – had lower values of 2D:4D (Brown et al., 2002), similarly to males with 21-hydroxylase deficiency (responsible for developing CAH) (Ökten et al., 2002). It is also hypothesized that 2D:4D is genetically determined due to the presence of variant rs314277 located within intron 2 of the LIN28B gene (Medland et al., 2010) and expression of Hoxa or Hoxd genes. These Hox genes are responsible for differentiation of both the digits and the urinogenital system simultaneously (Manning et al., 2003), although this hypothesis still requires confirmation (Medland et al., 2010).

Digit ratio (as a possible marker of pre-natal sex hormone levels) has been reported to correlate with male birth size (Danborno et al., 2010; McIntyre et al., 2006; Ronalds et al., 2002), adult body size (Fink et al., 2003; Van Dongen, 2009) and family size (Manning et al., 2003). However, some other studies have not confirmed these relationships (for a review see: Putz et al., 2004). Additionally, there are some suggestions that digit ratio predicts adult testosterone concentrations (Garcia-Cruz et al., 2012), including patients of infertility clinics (Manning et al., 2004), but this association was questioned by meta-analytic review (Honekopp et al., 2007), which did not prove a statistically significant relationship between 2D:4D and adult circulating sex hormone levels.

Testosterone is related to body size and body composition in males. The impact of pre-natal and post-natal testosterone concentration on body composition may be 2-fold. High testosterone concentration is associated with higher lean body mass (Schroeder et al., 2012), while lower testosterone levels are related to increased fat mass (Vermeulen et al., 1999).

Correspondence: Magdalena Klimek, Institute of Public Health, Jagiellonian University Medical College, Grzegorzecka 20, 31–531 Krakow, Poland. Tel: +48 12 43 32 842. Fax: +48 12 421 7447. E-mail: magdalenaannaklimek@gmail.com

This is a possible consequence of the multifunctional effects of testosterone (i.e. induction of muscular hypertrophy, increased lipid uptake and higher fatty acid mobilization from adipose tissue) (i.e. Vermeulen et al., 1999). It should also be noted that high testosterone levels may accelerate foetal growth and, thus, result in higher birth weight and length, but the positive role of oestrogen also should be taken into account (Danborno et al., 2010; Frank, 2003). Moreover, a relationship between 2D:4D and birth size can also be expected, since it is hypothesized that both these traits are pre-natally programmed (Voracek, 2009). 2D:4D may also predict family size (i.e. number of children) since it is related to mating and reproductive preferences and sexual behaviour (i.e. Manning & Fink, 2008), although not all studies have confirmed such associations (Manning et al., 2000; Sorokowski et al., 2012).

In this study we tested relationships between 2D:4D and birth size, body size during childhood and adulthood, number of children and testosterone concentration among men from a traditional, rural population from Southern Poland. We hypothesized that more masculine digit ratio (low 2D:4D), indicating higher exposure to pre-natal androgens, will predict larger body size, higher testosterone levels and a higher number of children.

Materials and methods

The study was conducted in a village with a high birth rate, which is a part of the Mogielica Human Ecology Study Site, located in Southern Poland (for description of the study site see Jasienska & Ellison (2004) and Jasienska (2013)). Two groups of men were studied. Group 1 consisted of 558 males who participated in the study between years 2003–2009. This group was divided into two sub-groups: Group 1A: Children and adolescents (3–22 years old) and Group 1B: Fathers (23–89 years old). Data on demographic, anthropometric and family characteristics were collected. Participants' birth weight and length were obtained from personal health records. Body weight, body height, right and left hand finger digits were measured. Body weight, body height and BMI for each child and adolescent were individually compared to WHO Child Growth Standards (2006) and calculated as a z-score. Finger lengths were measured directly on the ventral surface of the palm by a trained assistant, using a manual calliper. The measurements of second and fourth finger length in both hands were taken from proximal finger crease to the distal tip of the finger, according to a previously published procedure (i.e. Manning et al., 1998), but to the nearest 0.1 cm. Participants with arthritis or finger injury (i.e. due to manual labour) were excluded from the study.

Group 2: Testosterone Study consisted of 110 men surveyed in 2011, aged 18–78 (mean = 39.5, SD = 17.82) from the same village. Saliva samples for testosterone assessment were self-collected by participants in polypropylene tubes and frozen within 8 hours of collection. Each participant took two saliva samples: in the morning, shortly after waking up and at night, just before going to bed. Saliva was analysed for testosterone at the Hominoid Reproductive Ecology Laboratory, University of New Mexico, using an enzyme immunoassay kit manufactured by Salimetrics (State College, PA; Kit No. 1-2402).

Table 1. Characteristics of study groups (mean and standard deviation).

	Mean	SD
Group 1A: Children and adolescents, $n = 320$		
Right hand 2D:4D	0.97	0.05
Left hand 2D:4D	0.97	0.05
Age (years)	10.8	6.69
Birth weight (g)	3423.6	539.21
Birth length (cm)	55.4	3.21
Body mass (z-score)	0.43	1.177
Body height (z-score)	0.16	1.091
BMI (z-score)	0.23	1.136
Group 1B: Fathers, $n = 238$		
Right hand 2D:4D	0.97	0.05
Left hand 2D:4D	0.97	0.05
Age (years)	51.9	15.92
Body mass (kg)	78.6	14.19
Body height (cm)	171.1	6.74
BMI (kg/m^2)	23.4	4.22
Number of children	3.7	2.27
Group 2: Testosterone Study, $n = 110$		
Right hand 2D:4D	0.97	0.04
Left hand 2D:4D	0.97	0.04
Age (years)	39.5	17.82
Testosterone levels (pmol/L)	270.3	100.22

Statistical analysis

Participants from both groups (1 and 2) were further divided into two groups based on digit ratio value: low 2D:4D (2D:4D $<$ 1) or high 2D:4D (2D:4D $\geq$ 1), following previously published studies (i.e. Bang et al., 2005; Seo et al., 2010). Differences between groups with low and high 2D:4D in birth weight, birth length, body weight, body height, BMI during childhood and adolescence and testosterone concentration were tested by Student's t test or Mann–Whitney U test (depending on whether a particular variable had a normal distribution or not). Differences in body weight, body height, BMI and the number of children in adulthood were tested by analysis of covariance (ANCOVA), with age as a potential confounder. Additionally, all analyses were repeated with right- and left-hand 2D:4D as a continuous variable in regression analysis. Simple or multiple (including participant's age) regression analyses were performed. Statistical analyses were conducted in Statistica package version 9.0. An alpha of 0.05 was set to determine statistical significance.

Results

Means (SD) of 2D:4D in both hands, age and anthropometric measures of studied groups (Group 1A, Group 1B and Group 2) are presented in Table 1 and means (SD) of 2D:4D in groups with high and low digit ratio in both hands are presented in Table 2. Groups of men with low and high digit ratio differed in size at birth and childhood body size, number of children and mean testosterone levels (Table 3). Among children and adolescents, a group with low right-hand 2D:4D had higher birth weight ($p = 0.04$) and higher birth length ($p = 0.01$). In this group, boys with low right-hand 2D:4D had higher body mass (when compared to norms published by the World Health Organization (2006) and calculated as z-scores)

Table 2. Characteristics of low and high 2D:4D (mean and standard deviation) among study groups.

	Low right 2D:4D	High right 2D:4D	Low left 2D:4D	High left 2D:4D
	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)
Group 1A: Children and adolescents	0.95 (0.36)	1.02 (0.03)	0.95 (0.03)	1.02 (0.03)
Group 1B: Fathers	0.95 (0.04)	1.03 (0.04)	0.94 (0.04)	1.03 (0.05)
Group 2: Testosterone Study	0.95 (0.03)	1.01 (0.02)	0.95 (0.03)	1.01 (0.01)

than boys with high 2D:4D ($p = 0.01$). We observed a difference in BMI (borderline significance, $p = 0.06$) – boys with low right-hand 2D:4D had higher BMI than boys with high 2D:4D, when also calculated as *z*-scores. In addition, we found no difference between groups of children and adolescents with low and high right-hand 2D:4D in body height ($p = 0.36$).

Fathers had between 1–12 children (mean = 3.69, SD = 2.27). Fathers with low right-hand 2D:4D had a higher number of children relative to the high 2D:4D group, after controlling for age ($p = 0.04$, Table 3). No statistically significant differences were observed among fathers in body mass ($p = 0.36$), body height ($p = 0.34$) or BMI ($p = 0.36$). Furthermore, among participants from Group 2: Testosterone Study, mean testosterone concentration (calculated as a mean of morning and evening values) was 270.6 [pmol/L] (SD = 100.22). Men with low right-hand digit ratio had higher testosterone concentrations than those with high right-hand 2D:4D ($p = 0.04$) and these participants did not differ in mean age ($p = 0.1$, for both hands). All tested differences between groups with low and high digit ratio were not statistically significant for the left hand (Table 3).

When we re-ran all analyses with 2D:4D as a continuous variable in simple or multiple regression models some of the results remained statistically significant. We observed that right hand 2D:4D is negatively related to body mass ($r = -0.18$, $p = 0.01$) and to BMI during childhood and adolescence ($r = -0.14$, $p = 0.02$), when body weight and BMI were calculated as *z*-scores. Additionally, we observed results with borderline statistical significance: negative relationship between left-hand digit ratio and birth weight ($r = -0.08$, $p = 0.08$), right-hand 2D:4D and birth length ($r = -0.11$, $p = 0.08$) and left-hand digit ratio and number of children among fathers ($r = -0.09$, $p = 0.09$), when participants age was included to the model.

Discussion

This study, for the first time, documents that men's digit ratio (a putative measure of prenatal androgen concentration) is associated with several life history traits in a single population. We show that low right-hand 2D:4D was related to larger size at birth, higher body mass during childhood and adolescence, higher testosterone levels and higher number of children. This indicates a possible long-term effect of pre-natal androgens on male life history. However, some of the results obtained in group comparisons were not confirmed when regression models were used. The statistical approach of group comparison was chosen to compare participants with low more masculine and high more feminine 2D:4D. Since body size, testosterone levels and fertility are influenced by many factors we did not expect to find strong, linear correlations with 2D:4D. We rather hypothesized that there are differences between groups of men who are more or less ''masculine'' (based on their foetal hormonal exposure).

Our results, based on analysing 2D:4D in groups with high and low digit ratio, show that a low digit ratio is related to a larger birth size in males. A similar relationship was shown in a sample of British men among whom low 2D:4D was related to higher birth length (Ronalds et al., 2002) and in a sample of Nigerian men where low 2D:4D was related to higher birth weight (Danborno et al., 2010). This may be due to a role of testosterone in determining body composition, especially its positive impact on somatic growth (Danborno et al., 2010) and development of lean body mass (Schroeder et al., 2012). Higher body mass and higher BMI (calculated as *z*-score) among children and adolescents with low 2D:4D (borderline significance for BMI) was observed. However, adult body size was no longer predicted by 2D:4D. Results of previous studies investigating the relationship between adult body size and 2D:4D were inconclusive. For example, Barut et al. (2008) and Danborno et al. (2008) did not observe statistically significant relationships, while other studies documented either a positive relationship between 2D:4D and adult body size—heavier males tended to have a lower digit ratio (i.e. Van Dongen, 2009; Almasry et al., 2011) or a negative impact of pre-natal testosterone on body mass—heavier males had a higher digit ratio (i.e. Fink et al., 2003). Such discrepancies between our results and some of the previous findings may occur because of inter-population variation in nutritional and behavioural factors that influences body composition and size throughout the lifespan. Moreover, pre-natal testosterone concentration is more likely to influence birth size and body size in childhood (due to the shorter period of time elapsing since pre-natal exposure) than body size in adulthood, when many different factors have been influencing growth. This is exactly the pattern that we observed in the studied population. It is also likely that in adults other traits are better markers of adult body composition than body weight or BMI. For example, 2D:4D correlated with waist-to-hip ratio (Manning, 2002) and hand grip strength (a proxy of muscular strength) (Fink et al., 2006; Hone & McCullough 2012; Zhao et al., 2012) among males and with waist-to-chest ratio (Fink et al., 2003) among females. Analyses of the 2D:4D relationship and body composition using different pointers should be taken into account in future studies.

Our study also shows that men with low 2D:4D have a higher number of children. Similar findings were reported in other studies assessing the relation between digit ratio and males' fertility (Manning et al., 2000; Manning & Fink, 2008; Voracek et al., 2010). Despite the fact that there are many cultural and behavioural factors which may affect males'

Table 3. Differences between groups with low and high, right- and left-hand 2D:4D in birth size, body size in childhood and adulthood, testosterone levels and number of children. p Value was derived from Student's t test, Mann–Whitney U test or analysis of covariance.

	Right 2D:4D					Left 2D:4D				
	Low 2D:4D Mean (SD)	High 2D:4D Mean (SD)	t/F^a	df	p	Low 2D:4D Mean (SD)	High 2D:4D Mean (SD)	t/F^a	df	p
Group 1A: Children and adolescents	$n=179$	$n=113$				$n=196$	$n=128$			
Birth weight (g)	3482 (469)	3352 (599)	1.98	267	0.04	3369 (505)	3358 (583)	1.7	297	0.09
Birth length (cm)	55.87 (2.95)	54.88 (3.58)	2.47	250	0.01	55.60 (2.94)	55.22 (3.59)	0.91	275	0.3
Body mass in childhood and adolescence z-score[b]	0.60 (1.17)	0.14 (1.15)	2.56	178	0.01	0.47 (1.20)	0.35 (1.17)	0.70	178	0.4
Body height in childhood and adolescence z-score[b]	0.19 (1.07)	0.08 (0.98)	0.92	289	0.3	0.14 (1.07)	0.17 (0.99)	0.26	288	0.7
BMI in childhood and adolescence z-score[b]	0.33 (1.28)	0.08 (1.06)	1.84	287	0.06	0.26 (1.19)	0.21 (1.08)	0.40	286	0.7
Group 1B: Fathers	$n=129$	$n=74$				$n=134$	$n=76$			
Body mass in adulthood (kg)	78.39 (13.54)	80.16 (15.54)	0.85	199	0.3	77.46 (15.30)	81.00 (12.31)	3.13	207	0.07
Body height in adulthood (cm)	171.44 (6.47)	170.60 (7.35)	0.90	201	0.3	170.92 (7.04)	171.24 (6.28)	0.27	208	0.6
BMI in adulthood (kg/m^2)	23.33 (3.90)	23.86 (4.62)	0.85	199	0.3	23.05 (4.55)	24.10 (3.66)	3.13	207	0.08
Number of children	3.8 (2.42)	3.2 (2.01)	4.45	200	0.04	3.8 (2.21)	3.4 (2.38)	2.15	207	0.1
Group 2: Testosterone study	$n=77$	$n=31$				$n=77$	$n=33$			
Testosterone levels (pmol/L)	283.17 (106)	239.9 (89.4)	1.99	106	0.04	275.77 (91.95)	258.50 (123)	0.81	48	0.4

t coefficient corresponds with student's t test or Mann–Whitney U test. F coefficient corresponds with analyses of covariance.
[a]Depending on the type of analysis.
[b]Calculated according to World Health Organization norms.

reproductive success, pre-natal hormonal environment (reflected in 2D:4D value) seems to play a role as well. Variables associated with male fertility such as sperm number (Manning et al., 1998), sex drive, level of sexual excitement (Manning & Fink, 2008), number of sexual partners per individual (Honekopp et al., 2006) and age at first marriage (Sorokowski et al., 2012) were all related to 2D:4D. These results might suggest that digit ratio might be widely associated with traits related to male reproductive strategy.

We also show that pre-natal testosterone levels (reflected in 2D:4D values) predict adult testosterone concentration. In previous studies, in males referred for prostate biopsy, those with high 2D:4D had lower testosterone serum levels (Garcia-Cruz et al., 2012) and patients attending infertility clinics tended to have 2D:4D (Manning et al., 2004). However, the majority of other studies did not detect statistically significant relationships between 2D:4D and testosterone levels (i.e. Bang et al. 2005; Honekopp et al., 2007; Muller et al., 2011). We previously demonstrated a relationship between pre-natal characteristics and adult sex-hormone levels in Polish women (Jasienska et al., 2006a,b) and results of the present study suggest that pre-natal environment may influence levels of male sex hormones as well.

It is also worth mentioning that all our results are significant only for right-hand digit ratio. It is likely that pre-natal testosterone (early developmental masculinization) influences a delay of development of left side of the body traits (Geschwind & Galaburda, 1985) and may also lead to stronger expression of sexually dimorphic traits on the right side of the body (Tanner, 1990). Furthermore, a meta-analysis of 116 studies suggested that right-hand digit ratio might be a more suitable marker of pre-natal sex hormones exposure than left-hand (Honekopp & Watson, 2010).

Several limitations of our study should be taken into account. First, our results should be replicated in a study in which assessment of adult testosterone levels would be based on a higher number of samples for each participant, since testosterone levels can be influenced by many physiological and behavioural factors, i.e. stress level, sexual relationships, parenting or male competition (Gray & Campbell, 2009; Jasienska et al., 2012) and thus frequent sampling would lead to more reliable results. Second, due to the study protocol and long-term duration of the study, finger measurements were conducted only once for each participant and participants taking part in a study in different years were measured by different study assistants. However, we did not observe any differences in mean finger lengths among years of study for: right-hand index finger $F_{6,539}=0.28$, $p=0.95$, right-hand ring finger $F_{6,534}=0.20$, $p=0.97$, left-hand index finger $F_{6,540}=0.13$, $p=0.99$ and left-hand ring finger $F_{6,542}=0.10$, $p=0.99$ in ANOVA analyses. This suggests high reliability of measurements. Finally, further studies are needed in order to determine at what age effects of pre-natal environment on body size are no longer significant. It can be hypothesized that this occurs around puberty, but our sample size did not allow for testing of this hypothesis.

Conclusion

In conclusion, 2nd to 4th digit ratio, a potential biomarker of pre-natal testosterone exposure, is related to birth size and subsequent sub-adult body size, adult testosterone levels and number of children among men. This indicates a long-term effect of pre-natal androgens on male life history.

Acknowledgements

We are grateful to Michal Jasienski, Ludwik Odrzywołek, Reverend Jan Gniewek, Reverend Stanisław Krzywonos (Słopnice Parish, Poland), Janusz Dziedzic, MD, research assistants and to our study participants. We also thank Melissa Emery Thompson and the Hominoid Reproductive Ecology Laboratory, University of New Mexico, for assistance with hormone analysis. We are grateful to two anonymous reviewers for comments that helped to improve the manuscript.

Declaration of interest

The authors report no conflicts of interest. The authors alone are responsible for the content and writing of the paper.

This study was supported by grants from the National Science Centre (grant no. N N404 273440) and Ministry of Science and Higher Education (grant no. IdP2011 000161), *Salus Publica* Foundation the Foundation for Polish Science (I.N.) and Yale University Program in Reproductive Ecology.

References

Almasry SM, El Domiaty MA, Algaidi SA, Elbastawisy YM, Safwat MD. 2011. Index to ring digit ratio in Saudi Arabia at Almadinah Almonawarah province: a direct and indirect measurement study. J Anatom 218:202–208.

Bang AK, Carlsen E, Holm M, Petersen JH, Skakkebaek NE, Jørgensen N. 2005. A study of finger lengths, semen quality and sex hormones in 360 young men from the general Danish population. Hum Reprod 20: 3109–3113.

Barut C, Tan U, Dogan A. 2008. Association of height and weight with second to fourth digit ratio (2D:4D) and sex differences. Percept Motor Skills 106:627–632.

Brown WM, Hines M, Fane BA, Breedlove SM. 2002. Masculinized finger length patterns in human males and females with congenital adrenal hyperplasia. Horm Behav 42:380–386.

Danborno B, Adebisi SS, Adelaiye AB, Ojo SA. 2008. Sexual dimorphism and relationship between chest, hip and waist circumference with 2D, 4D and 2D:4D in Nigerians. Internet J Biol Anthropol 1:2.

Danborno B, Adebisi SS, Adelaiye AB, Ojo SA. 2010. Relationship between digit ratio (2D:4D) and birth weight in Nigerians. Anthropologist 12:127–130.

Fink B, Neave N, Manning JT. 2003. Second to fourth digit ratio, body mass index, waist-to-hip ratio, and waist-to-chest ratio: their relationships in heterosexual men and women. Ann Hum Biol 6:728–738.

Fink B, Thanzami V, Seydel H, Manning JT. 2006. Digit ratio and handgrip strength in German and Mizos men: cross-cultural evidence for an organizing effect of prenatal testosterone on strength. Am J Hum Biol 18:776–782.

Frank GR. 2003. Role of estrogen and androgen in pubertal skeletal physiology. Med Pediatr Oncol 41:217–221.

García-Cruz E, Huguet J, Piqueras M, Ribal MJ, Alcaraz A. 2012. Second to fourth digit ratio, adult testosterone level and testosterone deficiency. BJU Int 109:266–271.

Geschwind N, Galaburda AM. 1985. Cerebral lateralization: biological mechanisms, associations and pathology: II. A hypothesis and a program for research. Arch Neurol 42:521–552.

Gray PB, Campbell BC. 2009. Human males testosterone, pair-bonding, and fatherhood. In: Ellison PT, Gray PB, editors. Endocrinology of social relationships. Cambridge, MA: Harvard University Press. p 270–293.

Hone LSE, McCullough ME. 2012. 2D:4D ratios predict hand grip strength (but not hand grip endurance) in men (but not in women). Evol Hum Behav 33:780–789.

Honekopp J, Bartholdt L, Beier L, Liebert A. 2007. Second to fourth digit length ratio (2D:4D) and adult sex hormone levels: new data and a meta-analytic review. Psychoneuroendocrinology 32:313–321.

Honekopp J, Voracek M, Manning JT. 2006. 2nd to 4th digit ratio (2D:4D) and number of sex partners: evidence for effects of prenatal testosterone in men. Psychoneuroendocrinology 31:30–37.

Honekopp J, Watson S. 2010. Meta-analysis of digit ratio 2D:4D shows greater sex difference in the right hand. Am J Hum Biol 22:619–630.

Jasienska G. 2013. The fragile wisdom. An evolutionary view on women's biology and health. Cambridge, MA: Harvard University Press.

Jasienska G, Ellison PT. 2004. Energetic factors and seasonal changes in ovarian function in women from rural Poland. Am J Hum Biol 16: 563–580.

Jasienska G, Jasienski M, Ellison PT. 2012. Testosterone levels correlate with the number of children in human males, but the direction of the relationship depends on paternal education. Evol Hum Behav 33: 665–671.

Jasienska G, Thune I, Ellison PT. 2006a. Fatness at birth predicts adult susceptibility to ovarian suppression: an empirical test of the ''Predictive Adaptive Response'' hypothesis. PNAS 34:12759–12862.

Jasienska G, Ziomkiewicz A, Lipson SF, Thune I, Ellison PT. 2006b. High ponderal index at birth predicts high estradiol levels in adult women. Am J Hum Biol 18:133–140.

Manning JT. 2002. Digit ratio: a pointer to fertility, behavior and health. New Brunswick, NJ: Rutgers University Press.

Manning JT, Barley L, Walton J, Lewis-Jones DI, Trivers RL, Singh D, Thornhill R, et al. 2000. The 2nd:4th digit ratio, sexual dimorphism, population differences, and reproductive success. Evidence for sexually antagonistic genes? Evol Hum Behav 21:163–183.

Manning JT, Bundred PE. 2000. The ratio of 2nd to 4th digit length: a new predictor of disease predisposition? Med Hypoth 54:855–857.

Manning JT, Fink B. 2008. Digit Ratio (2D:4D), dominance, reproductive success, asymmetry, and sociosexuality in the BBC Internet Study. Am J Hum Biol 20:451–461.

Manning JT, Henzi P, Venkatramana P, Martin S, Singh D. 2003. Second to fourth digit ratio: ethnic differences and family size in English, Indian and South African populations. Ann Hum Biol 30:579–588.

Manning JT, Scutt D, Wilson J, Lewis-Jones DI. 1998. The ratio of 2nd to 4th digit length: a predictor of sperm numbers and concentrations of testosterone, luteinizing hormone and oestrogen. Hum Reprod 13:3000–3004.

Manning JT, Wood S, Wang E, Walton J, Bunded PE, van Heyningen C, Lewis-Jones DI. 2004. Second to fourth digit ratio (2D:4D) and testosterone in men. Asian J Androl 6:211–215.

McIntyre MH, Cohn BA, Ellison PT. 2006. Sex Dimorphism in digital formulae of children. Am J Phys Anthropol 129:143–150.

Medland SE, Zayats T, Glaser B, Nyholt DR, Gordon SD, Wright M, Montgomery GW. 2010. A variant in LIN28B is associated with 2D:4D finger-length ratio, a putative retrospective biomarker of prenatal testosterone exposure. Am J Hum Genet 86:519–525.

Muller DC, Giles GG, Bassett J, Morris HA, Manning JT, Hopper JL, English DR, Severi G. 2011. Second to fourth digit ratio (2D:4D) and concentrations of circulating sex hormones in adulthood. Reprod Biol Endocrinol 9:57.

Ökten A, Kalyoncu M, Yariş N. 2002. The ratio of second- and fourth-digit lengths and congenital adrenal hyperplasia due to 21-hydroxylase deficiency. Early Hum Develop 70:47–54.

Putz DA, Gaulin SJC, Sporter RJ, McBurney DH. 2004. Sex hormones and finger length. What does 2D:4D indicate? Evol Hum Behav 25: 182–199.

Ronalds G, Phillips DI, Godfrey KM, Manning JT. 2002. The ratio of second to fourth digit lengths: a marker of impaired fetal growth? Early Hum Dev 68:21–26.

Schroeder ET, He J, Yarasheski KE, Binder EF, Kawakubo M, Roubenoff R, Azen SP, Sattler FR. 2012. Value of measuring muscle performance to assess changes in lean mass with testosterone and growth hormone supplementation. Eur J Appl Physiol 112: 1123–1131.

Seo H, Kim KY, Rho J. 2010. Is the index finger and ring finger ratio (2D: 4D) reliable predictor of semen quality? Korean J Urol 51: 208–211.

Sorokowski P, Sorokowska A, Danel D, Mberira ML, Pokrywka L. 2012. The second to fourth digit ratio and age at first marriage in semi-nomadic people from Namibia. Arch Sex Behav 41: 703–710.

Tanner JM. 1990. Foetus into man: physical growth from conception to maturity. Cambridge, MA: Harvard University Press.

Van Dongen S. 2009. Second to fourth digit ratio in relation to age, BMI and life history in a population of young adults: a set of unexpected results. J Neg Res Ecol Evol Biol 6:1–7.

Vermeulen A, Goemaere S, Kaufman JM. 1999. Testosterone, body composition and aging. J Endocrinol Invest 22:110–116.

Voracek M. 2009. Who wants to believe? Associations between digit ratio (2D:4D) and paranormal and superstitious beliefs. Pers Individ Diff 47:105–109.

Voracek M, Pum U, Dressler SG. 2010. Investigating digit ratio (2D:4D) in a highly male-dominated occupation: the case of fire-fighters. Scand J Psychol 51:146–156.

WHO Multicentre Growth Reference Study Group. 2006. WHO Child Growth Standards: Length/height-for-age, weight-for-age, weight-for-length, weight-for-height and body mass index-for-age: methods and development. Geneva: World Health Organization. Available online at: http://www.who.int/childgrowth/publications/technical_report_pub/en/ (accessed 23 September 2013).

Zhao D, Li B, Yu K, Zheng L. 2012. Digit ratio (2D:4D) and handgrip strength in subjects of Han ethnicity: impact of sex and age. Am J Phys Anthropol 149:266–271.