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Digit length ratio (2D:4D) and variation in key life-history traits and fitness in contemporary Finnish women

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The ratio of second-to-fourth digit length (2D:4D) has been suggested to reflect prenatal steroid levels, which likely bear important consequences for vertebrate adult-age physiology, behavior, and reproductive success. The evidence for 2D:4D being related to individual fitness comes largely from studies in humans. These studies have not, however, been conclusive as important confounding factors affecting completed family size (e.g., socioeconomic status) have not been accounted for and the vast majority of the participants examined have not yet ended their reproductive careers. In addition, the life-history traits generating such fitness differences have received less attention in the literature. We studied whether 2D:4D was associated with several life-history traits (probability of reproducing, adulthood height, ages at first and last reproduction, and interbirth intervals) and fitness (the number of offspring raised to adulthood) in postreproductive Finnish women, while controlling for education and spatio-temporal variation of traits. We found no association between 2D:4D and the life-history traits studied and fitness among these Finnish women. These results thus cast doubts to the claim that 2D:4D predicts female life histories and evolutionary fitness in humans. *Key words:* age at first reproduction, age at last reproduction, birth spacing, digit ratio (2D:4D), stature, prenatal steroids, testosterone. *[Behav Ecol 21:1061–1066 (2010)]*

Recent decades have witnessed a growing understanding of the importance of prenatal programming on individual's subsequent physiology, behavior, phenotype, and ultimately on reproductive success (Lindström 1999; Lummaa and Clutton-Brock 2002; Gluckman and Hanson 2005) that may last over generations (Pembrey et al. 2006). For example, in humans low birth weight for gestational age and prematurity at birth have both been associated with increased mortality and impaired reproductive success in adulthood, leading to reduced long-term individual fitness (Swamy et al. 2008; Goodman and Koupil 2009). Prenatal steroids have also been considered to play a role in the programming of later-life reproductive performance (Cohen-Bendahan et al. 2005). Such effects are, however, inherently difficult to study and manipulate in most vertebrate species, particularly in humans due to ethical issues. Therefore, most of our current understanding on the effects of prenatal steroids (mainly testosterone) on later-life performance in humans comes from indirect observations. For example, congenital adrenal hyperplasia (CAH), a medical disorder causing elevated testosterone levels during prenatal development, has been shown to impair growth and fertility in both women and men (New 2004; Merke and Bornstein 2005).

One noninvasive retrospectively available measure, the ratio of second-to-fourth digit lengths (2D:4D), has been highlighted as a potentially useful phenotypic marker of steroid exposure in utero in vertebrates (Manning 2002, 2008; McIntyre 2006). Although the underlying causal connections remain still elusive (Forstmeier et al. 2008), it is generally postulated that the lower the individual 2D:4D, the higher testosterone but the lower estrogen levels experienced during fetal life. In humans, the evidence for this hypothesis comes from studies showing that 2D:4D is sexually dimorphic with lower ratios among males than females from the end of the first trimester of fetal development onwards (Manning et al. 1998; Peters et al. 2002; Malas et al. 2006; Galis et al. 2010) and that 2D:4D does not markedly change from childhood to adulthood (McIntyre et al. 2005; Trivers et al. 2006). Furthermore, CAH, which leads to excessive prenatal androgen production, has been shown to be related to low 2D:4D in both sexes (Brown et al. 2002; Ökten et al. 2002; Ciumas et al. 2009). Similarly, women with polycystic ovarian syndrome (PCOS) that presumably relates to increased prenatal testosterone level have lower than normal 2D:4D (Cattrall et al. 2005). In addition, women from the opposite-sex twin pairs have also been reported to show masculinized 2D:4D (van Anders et al. 2006; Voracek and Dressler 2007). Most importantly, 2D:4D has been found to negatively relate to the ratio of fetal testosterone to estrogen levels measured by amniocentesis (Lutchmaya et al. 2004).

Variation in 2D:4D has been suggested to have evolutionary relevance because of its associations with fitness components. At the phenotypic level, evidence for an association between 2D:4D and reproductive success comes from few studies in humans, provided mainly by Manning and his coworkers (Manning et al. 2000, 2003; Manning and Fink 2008). Using data from 8 countries and including childless individuals and adjusting for participant age, they reported that in men 2D:4D was negatively related to the number of children born in 3 countries, whereas in women 2D:4D was positively related to the number of children born in 4 countries (Manning et al. 2000, 2003). In one country, South Africa, women showed a men-type association, that is, a negative association between 2D:4D and family size (Manning et al. 2003). Furthermore, Voracek et al. (2010) recently reported a negative correlation between 2D:4D and family size in male fire fighters. Sample sizes in these correlations were moderate, ranging from 27 to 214 participants aged at least 18 years. Manning and Fink (2008) using global data from the BBC Internet Study found that in 83 681 at least 18-year-old men self-measured 2D:4D

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was negatively related to the number of children born, whereas in 69 173 same-age women 2D:4D was positively related to the number of children born. The explanatory power of 2D:4D has, however, been extremely low in these studies. For example, in the BBC Internet Study, 2D:4D explained less than 0.03% of variation of family size. In addition, previous studies have likely used inaccurate proxies of the evolutionary fitness of individuals as they have not measured their completed reproductive output by including postreproductive individuals (just adjusted for participant age) and not taken offspring survival into account.

Fitness-related life-history traits in relation to 2D:4D have not been extensively examined either. An exception to this is adulthood height. The results have, however, been conflicting as some studies have reported no correlation between 2D:4D and adult height (Manning et al. 1998; Fink et al. 2003; Neave et al. 2003; Rahman et al. 2005), whereas some have found lower 2D:4D among taller individuals (Hurd and van Anders 2006; Tester and Campbell 2007; Barut et al. 2008) or just the opposite (Lippa 2003). Moreover, in the BBC Internet Study, women with high 2D:4D started reproducing at an earlier age (Manning and Fink 2008). Most importantly, there is recent evidence that the gene associated with height and age at menarche in women is also associated with 2D:4D (Medland et al. 2010). To our knowledge, no study has yet looked at other life-history traits, like age at last reproduction and birth spacing in women. All the above-mentioned life-history traits have been suggested to be related to fitness in women, also in contemporary populations (e.g., Kirk et al. 2001; Nettle 2002; Helle et al. 2005; Pettay et al. 2007; Byars et al. 2010).

The aim of this study was to investigate the associations between 2D:4D and key life-history traits and fitness in contemporary postreproductive Finnish women. The current analysis advances the field by studying women who have ended their reproductive careers, making it possible to estimate their lifetime reproductive success, and by accounting for variation in life histories arising from socioeconomic and spatio-temporal differences. First, we examine the association of 2D:4D on whether these women reproduced during their lifetime. Second, among those women who reproduced at least once, we examine how the variation in life-history traits, including adulthood height, ages at first and last reproduction and interbirth intervals, and fitness relates to women's 2D:4D.

MATERIALS AND METHODS

Participants

Data on completed lifetime reproductive history including lifetime reproductive success and the right and left hand 2D:4D of women ($n = 312$) born in years 1946–1958 in Finland were collected by questionnaires during 2006 (Helle and Lilley 2008). These women are presumably a random sample of approximately 50-, 55- and 60-year-old voluntaries that participated in Finnish national screening program of cervical cancer in year 2006. The relatedness of these women is unknown but is must be rather negligible because these women represent a geographically diverse sample from Finland (Helle and Laaksonen 2009). The women studied were largely born during the "baby boom" period that followed the end of the Second World War. From the 1960s onwards, when the earliest cohort of the women studied started to reach sexual maturity, Finnish women generally made use of modern contraceptive methods (78% of the women included in this study reported that they have used contraceptives during their lifetime). Life-history variables recorded for the purposes of the current study were adulthood height, ages at first and last reproduction, mean interbirth interval and fitness. For those women

Table 1
Summary statistics of the variables studied

	n	Mean (±SD)	Minimum	Maximum
Right hand 2D:4D	303	0.978 (±0.031)	0.900	1.076
Left hand 2D:4D	307	0.972 (±0.033)	0.886	1.076
Age at first reproduction (year)	267	24.16 (±4.55)	16	43
Age at last reproduction (year)	267	28.91 (±5.21)	17	43
Adult height (cm)	305	164.2 (±5.67)	149	193
Mean interbirth interval (year)	267	1.91 (±1.80)	0	10
Lifetime reproductive success	312	1.75 (±1.04)	0	5

who gave birth to one child during their lifetime, the mean interbirth interval was set to zero in order to avoid the deletion of these women from the regression analyses. We used lifetime reproductive success, the total number of offspring raised to age 18, as a fitness-measure because it has been shown to be in good accordance with the long-term individual contribution to the future gene pool (Brommer et al. 2004). We also recorded women's birth area (classified to born in North-, South-, or West-Finland or born abroad), birth cohort (1946–1947, 1951–1952, or 1956-58), and their education (elementary school, secondary school, or university degree), which is an important determinant of family size in modern populations (e.g., Kravdal and Rindfuss 2008).

Digit ratio measurements

During the collection of questionnaires, both of the women's hands were scanned (Canon Canoscan D66OU) for 2D:4D measurements. The digits were measured from the tip of the finger to the crease proximal to the palm with computer program Image-J (http://rsb.info.nih.gov/ij/) by one person. Sixty randomly selected hands were measured twice by the same person in order to estimate repeatability (i.e., intraclass correlation coefficient) of 2D:4D measurements using one-way analysis of variance (Lessells and Boag 1987). The 2D:4D measurements showed a repeatability of 0.79 ($F_{1,59} = 8.44$, $P = 0.0052$). There was also no difference between the mean right and left hand 2D:4D among these women (paired t-test, $t_{301} = 0.07$, $P = 0.94$). The 2D:4D of both hands were, however, included in the analyses (and not, e.g., their mean) because the 2D:4D of both hands have been used in previous studies investigating 2D:4D and reproductive success and because the associations studied may show side-specificity (Manning 2008) because the sex difference is more elaborated in the right hand 2D:4D (Hönekopp and Watson, forthcoming).

Statistical analysis

Summary statistics of the variables studied are given in Table 1. Prior to the analyses, we checked for the potential nonlinearity of associations between 2D:4D (separately for both hands) and female life history. Second-order polynomials were considered only because if 2D:4D works as a fitness component in women then the plausible polynomials we would expect to find are either convex (disruptive selection) or concave (balancing selection) associations (Travis 1989). However, we found no clear evidence for nonlinearity ($F_{2,229} < 1.2$, $P > 0.31$); in the case of age at last reproduction and the left hand 2D:4D only, there was a marginal association

($F_{2,229} = 2.9$, $P = 0.06$). We therefore restricted the analyses to linear associations. We started by examining how 2D:4D was related to whether women ($n = 265$) had any children during their lifetime (9.9% remained childless) using logistic regression with binomial errors and logit link function (Allison 1999). The right and left hand 2D:4D were both simultaneously included into the model, but we first tested whether their joint influence showed statistical significance. After this, among the women who reproduced ($n = 240$), we studied the association between the right and left hand 2D:4D and women's height, ages at first and last reproduction, mean interbirth interval, and fitness using general multivariate linear regression model with exact tests (Knattree and Naik 2003). The primary aim of the model was to test the hypothesis that the life histories studied are neither related to the right nor left hand 2D:4D. If this hypothesis is rejected, more specific analyses investigating which hand 2D:4D relates to which female life-history traits are warranted. All the models controlled for women's birth area, birth cohort, and educational level. Correlations among response variables varied between $|r| = 0.04$–0.61. In order to obtain more biologically interpretable parameter estimates, both the right and left hand 2D:4D were standardized to zero mean and 1 standard deviation (SD). Therefore, the parameter estimates represent how the change of 1 SD in the 2D:4D measures related to women's life-history traits and fitness. Collinearity among digit ratios was assessed with variance inflation factors. The largest variance inflation factor was 1.65, suggesting no such problems. Multivariate regression assumes multinormally distributed residuals, which was visually confirmed to hold (after mean interbirth interval by adding a constant was log-transformed) by using multivariate chi-square plot (Knattree and Naik 2003). The most robust multivariate test, Pillai's trace, was used for statistical inference (Knattree and Naik 2003). The heteroskedasticity of the model residuals was assessed according to White (1980) and found to be homoskedastic ($\chi^2 > 9.6$, $P > 0.09$). All analyses were conducted with SAS statistical software version 9.2 (SAS Institute Inc, Cary, NC).

RESULTS

We found that 2D:4D was not associated with the probability of women having at least one child during their lifetime ($\chi^2_2 = 2.48$, $P = 0.29$). Moreover, multivariate linear regression analysis provided no evidence for a statistical association between 2D:4D and the life-history traits studied and fitness (Pillai's trace = 0.026, $P = 0.81$). Therefore, no detailed analyses investigating whether the right or left hand 2D:4D relates to specific female life-history traits were statistically justified. In addition, the 2D:4D explained only up to 0.9% of variation in the response variables studied.

Figure 1 shows scatter plots for these response variables in relation to 2D:4D and their corresponding regression coefficients with 95% confidence intervals. These confidence intervals define the range of parameters supported by the data, and they show that in each case the influence of 2D:4D on the response clearly includes the value of the null hypothesis of no association between 2D:4D and female life history. Furthermore, the maximum upper and lower limits regarding the association between 2D:4D and fitness, for example, suggest that an increase of 1 SD in left hand 2D:4D was related to 0.18 more adult offspring, whereas 1 SD increase in right hand 2D:4D was related to 0.16 adult offspring less in these women. In other words, a difference of one adult offspring would have required an increase of almost 6 SD units in the left hand 2D:4D—a value out of the range recorded for these women (Table 1).

DISCUSSION

Recent acknowledgment of the importance of early programming on adult phenotype and behavior has generated a wide interest on 2D:4D as a potential noninvasive indicator of prenatal steroid exposure in vertebrates. In humans, this interest is evidenced as a large number of articles published between 1998 and 2009 relating 2D:4D to the various aspects of adulthood life in both sexes (Voracek and Loibl 2009). From an evolutionary point of view, perhaps the most relevant result yet has been the potential association between 2D:4D and reproductive success documented in some human populations. These studies have provided some indication that low and high 2D:4D in men and women, respectively, might pinpoint their higher evolutionary success (Manning et al. 2000, 2003; Manning and Fink 2008; Voracek et al. 2010). However, the current data on postreproductive Finnish women provide no evidence for an association between 2D:4D and fitness. The only agreement with the current data and the previous ones is the extremely low explanatory power of 2D:4D in predicting reproductive success in humans. In these Finnish women, the right and left hand 2D:4D together explained less than 0.2% of variation in fitness only. This together with the estimated maximum effect sizes here gives little support to the claims that 2D:4D explains any biologically meaningful variation of human fitness. In this population, 2D:4D seemed to be unrelated to women's life histories as well. These findings thus also contrast, for example, those studies reporting association between 2D:4D and adulthood stature (Lippa 2003; Hurd and van Anders 2006; Tester and Campbell 2007; Barut et al. 2008) and age at first reproduction (Manning and Fink 2008) in humans.

The failure to replicate the previous findings of statistically significant associations between 2D:4D and the outcome of interest are unfortunately common in the field of 2D:4D research. Publication bias may not be an unfamiliar phenomenon in this field either (Voracek and Loibl 2009), which suggests that we may have currently overestimated some of the associations studied. However, recent meta-analyses have suggested only moderate publication bias at best among studies relating 2D:4D to athletic prowess and those examining sex difference in 2D:4D (Hönekopp and Schuster 2010; Hönekopp and Watson, forthcoming). Difficulties in repeating previously published results concern also the measures of fertility that may underlie some of the variation in female life-history traits included in this study. For example, age at menarche was initially reported to correlate with women's 2D:4D (Matchock 2008), but similar results were not found in subsequent attempts to establish such an association (Lujan et al. 2009; Helle 2010). Similarly, preliminary associations reported between 2D:4D and fertility-related female sex hormones were not supported by a recent meta-analysis (Hönekopp et al. 2007). Nevertheless, there is recent genetic evidence that the gene related to delayed age at menarche and increased height may also be associated with increased 2D:4D in women (Medland et al. 2010), but with respect to 2D:4D these associations do not correspond to those suggested at the phenotypic level (see above). Therefore, there is yet no convincing evidence to suggest that the life history of women reflects their 2D:4D.

Apart from this, the fundamental paradigms of the 2D:4D theory remains still far from resolved. One of the major shortcomings of the theory is that there is very little direct evidence that digit ratios respond to prenatal steroid concentrations and if they do, what are the actual causal connections behind such links (Forstmeier et al. 2008). In humans, this is not surprising given the inability to manipulate steroid levels during prenatal development. Perhaps the most convincing evidence to date

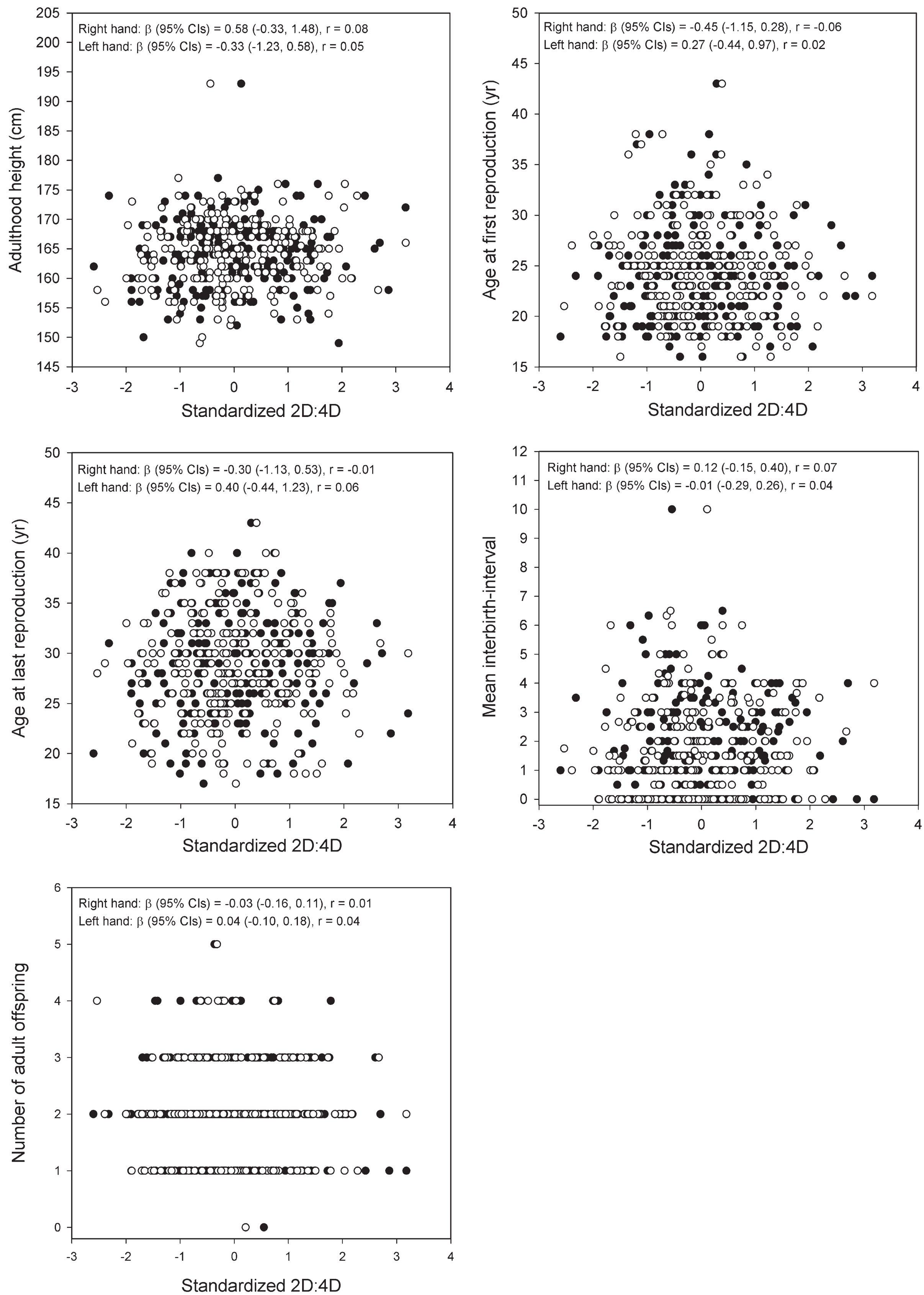

Figure 1
Scatter plots of the right (filled circles) and left (blank circles) hand 2D:4D on the female life-history traits and fitness studied. In the upper left-hand corner of the panels are shown standardized regression coefficients and their 95% confidence intervals (CIs), adjusted for women's educational level, birth area, and birth cohort, followed by zero-order Pearson correlation coefficients.

for the 2D:4D theory in humans comes from "natural experiments" that are associated with increased androgen exposure during gestation. Women diagnosed for CAH have lower, more male-like 2D:4D (Brown et al. 2002; Ökten et al. 2002; Ciumas et al. 2009), whereas genetic XY-males lacking prenatal testosterone exposure due to complete androgen insensitivity syndrome have instead higher, more female-like 2D:4D (Berenbaum et al. 2009). These studies are corroborated by the finding that testosterone-receptor sensitivity negatively correlates with 2D:4D (Manning et al. 2003). Moreover, women having PCOS also show lowered 2D:4D (Cattrall et al. 2005). However, these findings have not been successfully replicated in all studies (see Buck et al. 2003 for CAH and Lujan et al. 2009 for PCOS).

Animal models have also been applied to examine this question. In studies of birds, Romano et al. (2005) and Saino et al. (2007) showed that experimental elevation of egg yolk steroids affected digit ratios in captive strains of pheasants (*Phasianus colchicus*), but these results differed with respect to sex and the digit ratio measure used (2D:3D vs. 2D:4D). In mammals, Talarovičová et al. (2009) found that experimentally elevated levels of maternal testosterone decreased offspring 2D:4D in rats. However, this result was based only on 3 manipulated females and their 8 pups for digit ratio measurements, and Lilley et al. (2010) failed to find a phenotypic correlation between maternal testosterone level and offspring 2D:4D in field voles. In contrast, anogenital distance, a well-known marker of prenatal androgen exposure in rodents, does not seem to correlate with 2D:4D in mice (Hurd et al. 2008; Manno 2008).

All the above-mentioned experimental studies have manipulated the amount of maternally derived steroid concentrations. It is likely that some, if not the majority, of the steroid exposure for digit development comes from the embryo itself (Manning 2002; McIntyre 2006; Forstmeier et al. 2008). If the steroids of embryonic origin play a more important role in affecting digit ratios than the maternal ones, avian models may not have that much relevance here unless there is a link from maternal to embryonic steroid concentrations (see Forstmeier et al. 2008). In mammals, however, the placental enzyme aromatase generally buffers the embryo from high levels of maternally exposed testosterone (Cohen-Bendahan et al. 2005). Manipulating the steroid concentrations produced by the embryo itself might unfortunately turn out to be a really daunting task. More experimental research using suitable animal models are therefore needed to examine the future potential of digit ratios as retrospective markers of prenatal programming.

In conclusion, these results suggest that women's life history and fitness were unrelated to their 2D:4D in this contemporary Finnish population. It is not straightforward to put these findings into context because we do not currently know whether digit ratios indicate what they are generally expected to indicate or whether these contrasting findings should be considered an anomaly rather than a rule in the current literature. In addition, several points in this study, as in many previous reports, may have affected the ability to establish associations between 2D:4D and female life history. For example, we cannot exclude the possibility of 2D:4D-related selective mortality during the reproductive lifespan that might have had some bearing on the results because 2D:4D may be associated with the earlier onset of breast cancer and higher mortality from breast and ovarian cancers in women (Manning 2008). Assortative pairing by 2D:4D, that is, a tendency of presumably high-fertility women having high 2D:4D to marry low fertility having high 2D:4D (Voracek et al. 2007), may have also masked the associations examined here. Moreover, the indirect measurements of 2D:4D used here are shown to produce lower mean 2D:4D than direct measurements (Allaway et al. 2009) and may have reduced our ability to detect association between the traits studied if weak (Manning et al. 2010).

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