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### **Differential investment in body girths by sex: evidence from 3D photonic scanning in a Thai cohort**



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## **ABSTRACT**

**Objectives**: Life history trade-offs may manifest between competing organs and tissues in the body. Sexual dimorphism in tissue investment is well-established in humans, with sexassociated body shape differences linked to natural and sexual selection. This study uses threedimensional (3D) photonic scanning to test whether males and females differentially invest energy in various body regions in relation to two independent proxies of growth.

**Materials and Methods**: Body shape data (multiple girths) came from a Thai cohort (n=11,610; 53% female; age range 21-88 years). Weight was considered a proxy for recent energy acquisition. Stature represented completed growth, a proxy for energy acquisition earlier in life. The data were analyzed using growth-proxy by sex interaction log-log regression models adjusting for age, salary and number of children.

**Results**: For a given percentage increase in weight, females showed greater percentage increases than males in girths of the arm, chest, hip, thigh, knee and calf (*p* < .001), whilst males exceeded females in head and waist girths (also *p* < .001). For a given percentage increase in height, weight and all girths showed greater proportional changes in males than females (*p* < .001).

**Discussion**: These results indicate sex-specific life history strategies wherein the direction and timing of energy investment in girths varies between the sexes. The results add to literature suggesting that sexual dimorphism in body morphology is not a fixed trait; rather, differential energy allocation to specific body regions appears to be a plastic strategy adjusted in relation to energy acquisition across the life course.

### **Introduction**

Life history theory predicts that organisms use energy captured from the environment in ways which promote survival and reproduction. Assuming energy is finite, the optimization of energy investment strategies is characterized by a series of trade-offs, where resources used for one function are unavailable for allocation to others (Stearns, 1992; Hill, 1993; Ellison, 2003). In contemporary human populations, rising levels of overweight and obesity indicate that many individuals do not overtly lack energy; nevertheless, how energy is allocated for functional purposes may still reflect trade-offs that evolved in past environments.

Energy trade-offs have largely been examined in the anthropological literature in relation to essential functions like growth, reproduction, maintenance and immune defense (Kirkwood and Rose, 1991; Hill and Kaplan, 1999; Charnov, 2001; Tracer, 2002). However, trade-offs may also manifest in the construction of the body, for example between competing organs and tissues, and these trade-offs may vary based on environmental conditions and across the life course (see Aiello and Wheeler, 1995; Isler and van Schaik, 2006; Wells, 2010, 2013; Pomeroy et al., 2012; Kotrschal et al., 2013). It is well-established that mammals demonstrate sexual dimorphism in tissue investment, yet humans appear to do so in a manner different to other animals, including their close primate relatives (Pond, 1978, 1998; Norgan, 1997; Wells, 2007). Marked contrasts are apparent in human body shape due to variation in the deposition of fat and lean tissues, even when BMI is similar (e.g. Wells et al., 2007).

Explanations for human body shape dimorphism, which are not mutually exclusive, include the differential exposure of the sexes to natural selective pressures, and sexual selection (Darwin, 1871; Lande, 1980; Gaulin and Sailer, 1984; Fairbairn, 1997; Olsson et al., 2002; Plavcan, 2001, 2012; Wells, 2007). Zillikens et al. (2008) identified genetic differences between males and females for body composition variables including percentage fat and lean mass. Waist-to-hip ratio (WHR), an index of fat distribution that is heritable independently of BMI, also

demonstrates sex-specific effects at a number of loci (Heid et al., 2010; Shungin et al., 2015). At the same time, core genes controlling growth are shared by males and females, and the sexes' ontogenetic divergence in morphology may principally arise through sex-specific gene expression (Badyaev, 2002). The characteristics of dimorphism can vary over time and in association with cultural preferences or ecological conditions, indicating that phenotypic plasticity is also relevant (Norgan, 1990; Holden and Mace, 1999; Teder and Tammaru, 2005; Deaton, 2008; Guntupalli and Moradi, 2008; Wells, 2012; Freedman and Ford, 2015).

At birth, human females have on average slightly less lean mass (here used synonymously with fat-free mass) and slightly more fat than males (Tanner, 1990; Rodriguez et al., 2004; Andersen et al., 2013). Whilst males continue to accrete lean tissue through to early adulthood (Marshall and Tanner, 1968; Maynard et al., 2001, Wells et al., 2012a), from puberty females preferentially invest in peripheral adipose tissue, a strategy attributed to their primary role in funding reproduction and lactation (Rebuffé-Scrive et al., 1985; Foley and Lee, 1991; Lee, 1996; Dufour and Sauther, 2002; Ellison, 2003; Lassek and Gaulin, 2006, 2009).

Gonadal steroid hormones and growth hormone are central to the sexually dimorphic distribution of adipose tissue, whilst testosterone is especially important in males' accretion of lean mass in adolescence (Tanner, 1965; Martin and Daniel, 1993; Bogin, 1999; Rogol et al., 2002). Hormones and transcription factors may interact at sexually-dimorphic loci, like those described above for WHR, to differentially impact on the regulation of gene activity (Shungin et al., 2015). Regional variability in the action of the enzyme lipoprotein lipase may also be important for sex-specific fat distribution on the body (Norgan, 1997).

That males demonstrate greater overall lean mass than females has been shown in diverse populations (Immink et al., 1992; Deurenberg et al., 1995, 2001; Deurenberg-Yap et al., 2000; Maynard et al. 2001), and this investment strategy may have been shaped by aggressive male:male competition for mates (Trivers, 1972; Pagel, 1994; Hawkes, 2004; Dixson, 2009; Lassek and Gaulin, 2009; Puts, 2010; Plavcan, 2012). In an examination of data across several populations, males on average had 18% greater lean mass than females, who in contrast had 34% more fat mass than males, after adjusting for height (Wells, 2006). Unlike in females, sex steroid hormones in males mediate increased fat storage on the trunk (Norgan, 1997; Santosa and Jensen, 2014) where it may promote immune function (Gabrielsson et al., 2003; Wells and Cortina Borja, 2013).

Sexual dimorphism likewise extends to skeletal morphology. From puberty, sex hormones drive differential skeletal development in males and females, and bone mineral content, size and mass are often increased in males, resulting in relatively larger skeletal elements and overall body size compared to females (Riggs et al., 2002; Wells, 2007). However, certain aspects of skeletal growth, for example in the pelvis, are greater in females than males (Schultz, 1949; Tague, 2005).

These components of dimorphism likely have two main implications for fitness: they allow the sexes to prioritize different physiological functions, especially regarding reproduction, and they also allow them to signal in different ways to the opposite sex. Females may signal their capacity to nourish offspring via both quantity and pattern of fat deposition. Muscle mass might signal a male's capacity to attract mates and produce offspring with similar reproductive potential (Zaadstra et al., 1993; Singh, 1993; Norgan, 1997; Ellison, 2003; Wells, 2006; Lassek and Gaulin, 2008, 2009).

The extent to which sexual dimorphism arises through genetic mechanisms or plastic responses to ecological circumstances at different life stages is still inadequately understood. Rather than dimorphism being 'fixed' at adulthood, there is evidence that it continues to change through adult life (Gallagher et al., 1997; Wells et al., 2007, 2008; Shen et al., 2009). It is therefore especially informative to consider dimorphism in tissue trade-offs as a function of energy acquisition at different points in the life course.

On this basis, we hypothesize that the two sexes invest in body girths differently, in association with energy acquired relatively recently (proxied by current weight) or during development (proxied by stature, representing completed linear growth). Given the evidence for shape dimorphism described above, we hypothesize that males preferentially invest energy in building a bigger body overall, in particular during early development when fat-free mass is most readily accreted. In contrast, we hypothesize that females preferentially invest in reproductive fat stores, especially during adolescence and adulthood. During adult life, fat is relatively more plastic than lean. We therefore expect associations between girths and height to be stronger in males, and those between girths and weight to be stronger in females.

To test these hypotheses, we used body shape data derived from three-dimensional (3D) photonic scanning. Previous analysis of a large British cohort found contrasting associations between body girths and height in men and women (Wells et al., 2007). Here, we use similar 3D scan data from the Thai National Sizing Survey, and include an interaction term in multivariable regression analyses to further elucidate patterns of sexual dimorphism in association with energy supply at different life course stages. To our knowledge, this is the first study to investigate in men and women the potential statistical interaction of sex and height, and also sex and weight, on various girths of both the trunk and limbs.

#### **MATERIALS AND METHODS**

The Size Thailand survey was conducted in Thailand from 2006-2007 (Charoensiriwath and Tanprasert, 2010) to obtain information on body size and shape in the Thai population. The data and methods have been described previously (e.g. Wells et al., 2011, 2012b). Briefly, data were collected using a single  ${[TC]}^2$  body scanner (Cary, North Carolina, USA; www.tc2.com) transported between five geographical regions (Bangkok, North, South, Northeast and Central). Individuals from 74 of 76 Thai provinces ultimately took part. No information on ethnicity was recorded, although participants were required to show proof of Thai nationality in order to participate.

Recruitment utilized quota sampling based on age, gender and geographical region, and reached potential participants through advertisements including flyers, websites, and TV and radio interviews. Transport was provided from rural areas to scanning sites, where data collection centers were set up. A minimum number of males and females were recruited within set age cells: 17-25, 26-35, 36-45, 46-59 and 60+ years, with an age range of 17-88 years. Information on number of children, medical history, and salary was collected via questionnaire. Salaries ranged from 5,000 baht (USD  $^{\sim}140$ ) to >40,000 baht (USD  $^{\sim}1140$ ) per month. Exclusion criteria included pregnancy, disabilities, and lack of proof of Thai nationality. Participants gave written consent for their data to be analyzed and published in anonymized form.

Participants were scanned in a standardized position, with feet shoulder-width apart and arms held out from the sides of the body at a 45° angle. They wore tight-fitting underwear to avoid artefacts of bulky clothing. The scanner projects strips of safe, white light onto the body, and computer algorithms reconstruct skin surface topography from a raw point cloud of photonic data (Douros et al., 1999; Treleaven, 2004). [TC]<sup>2</sup> Body Measurement System Software version 5.3 was used to automatically extract a number of measurements, with technical precision within 0.5 cm, from each scan. Those used in this analysis were girths of the head, mid-upper arm, chest, waist (taken at the level of the small of the back), hip, mid-thigh, knee and calf, along with manually measured weight and height. Limb measurements were on the right-hand side.

Compared to manual anthropometry, 3D scans tend to overestimate girths due to differences in the manner of acquisition and the location of landmarks (Wells et al., 2007). However, epidemiological analyses are unlikely to be confounded by this problem, as previous studies have reported high correlations and excellent consistency in ranking between the two techniques (Wang et al., 2006; Wells et al., 2011, 2012b).

#### **STATISTICS**

Body girths, height and weight were natural log transformed to capture the allometric relationships between the variables. Correlations were calculated between the girths, weight and height in each sex. The data were plotted to visualize sex differences in the associations of each girth with weight or height.

Two sets of multivariable regression models were fitted, with each body girth as a separate outcome. The first set included as covariates sex, height and their interaction, while the second set included sex, weight and their interaction. Weight was also analyzed as an outcome in the first set of models. Weight and height were mean-centered prior to analysis, to ensure that their main effects did not confound the interaction term. Due to the log transformations, the interaction terms tested for differences between males and females in the percentage difference in each girth associated with a one percent difference in height or weight. In the presence of the interaction term, the corresponding main effect coefficient for height or weight corresponded to that for females.

In addition, the models controlled for age, salary and fertility as potential confounders. Age was analyzed as a continuous variable; salary was coded as a binary variable designating two groups: ≤10,000 or >10,000 baht/month, and fertility was based on the number of children categorized as 0, 1, 2, 3 or 4 children in both sexes, and additionally, 5 and 6+ children in women, or 5+ children in men.

Statistical analyses were carried out using SPSS (IBM SPSS Statistics for Macintosh, Version 24.0) and the R language and environment for statistical computing (Version 1.0.136), with two-tailed tests for significance at an alpha level of 0.05.

### **RESULTS**

Analyses were conducted on 11,610 individuals (53% female). Those <21 years old (n= 774, 48% female) and possibly not yet at final height were excluded, hence the age range for analysis was 21 to 88 years (females: range=21-88, median=41, IQR=30-54; males: range=21-88, median=40.5, IQR=30-52). Raw values for body size and shape outcomes are shown in Table 1. Means and standard deviations for height, weight, BMI and eight girths stratified by sex and six age categories are given in Table 2.

### [Table 1 and 2 near here]

Correlations of weight and height with body girths are shown in Table 3. Head girth, unlike the other girths, was only weakly correlated with weight in both sexes, while hip had the strongest relationships with weight.

## [Table 3 near here]

Girth-height correlations were generally weaker than girth-weight correlations in both sexes. In males, waist was most weakly correlated with height ( $r = 0.13$ ), while in females, waist girth ( $r =$ -0.04) and chest girth (r = 0.04) were both very weakly correlated. In general, the girth-height correlations were more sexually dimorphic than the girth-weight correlations.

Plots of height versus body girths illustrate the sex differences, with males having steeper slopes than females for all girths (Fig. 1, and Supporting Information).

### [Figure 1 near here]

Plots for weight and body girths are more mixed, with interactions evident for some girths, but not others. Where the interactions are apparent, they are smaller than for height. Head-weight and waist-weight plots demonstrate steeper slopes for males, whilst male and female slopes in the calf-weight plot are virtually identical (see Supporting Information). For arm, chest, and

knee plots, slopes are steeper for females than males to varying degrees (Fig. 2, and Supporting Information). Hip and thigh plots show relatively consistent sex differences across the whole range of weight, whereas the slopes show very little contrast between the sexes (Fig. 2).

### [Figure 2 near here]

Table 4 shows multivariable log-log regression models of body girth, and also weight, on the interaction between sex and height, adjusting for sex, height, age, number of children, and salary. (Fuller results including the age, salary and fertility variables are available online as Supporting Information, Table S1). In each model, the interaction term tested for sexdependent variation in the relationship between the girth (or weight) and height. This term was positive and highly significant in every model (*p* < .0001). Thus, males demonstrated a larger percentage difference in every girth and in weight for a given percentage difference in stature, compared to females. The largest interaction coefficients were for arm and waist, and the smallest for head and knee.

### [Table 4 near here]

Table 5 (and Supporting Information, Table S2) shows similar models for body girths on sexweight interactions, controlling for sex, weight, age, number of children and salary. Again, all the interaction terms were highly significant ( $p < .0001$ ). For head and waist the terms were positive, indicating that males had a larger percentage difference for a given percentage difference in body weight, compared to females. For the other girths the interactions were negative and the reverse was true. Arm and knee girth had the largest interactions, and hip girth the smallest.

[Table 5 near here]

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Adding to the models information on salary and number of children did not appreciably alter the coefficients for the other variables, including the interaction term, and  $R^2$  values remained largely unchanged. Thus, these variables are not interpreted further. For information, unadjusted values are given online for weight, height, BMI, and all shape variables stratified by sex and number of children (Supporting Information, Table S3), along with unadjusted values for the same variables stratified by sex and salary (Supporting Information, Table S4).

#### **DISCUSSION**

Optimized reproduction is the fundamental factor in any organism's successful life history strategy (Ellison, 2003), and male/female dimorphism in the amount and distribution of fat and lean tissue is functionally relevant to mating and producing offspring (Norgan, 1997; Wells, 2010). Consistent with this, dimorphism becomes distinctly more marked from puberty, remains highly pronounced throughout the reproductive years (Boot et al., 1997; Norgan, 1997; Maynard et al., 2001; Nindl et al., 2002; Wells, 2006, 2007), and then declines in old age (Wells et al., 2008). This pattern is evident across ethnic and cultural groups (Immink et al., 1992; Deurenberg et al., 1995, 2001; Deurenberg-Yap et al., 2000; Maynard et al. 2001). Previous analyses of British 3D scan data reported significant sex-differences in body shape, indicating strategic, sex-specific investment in different tissues (Wells et al., 2007).

With the incorporation of interaction terms in regression analyses, we were able to investigate statistically whether, as hypothesized, the relationship between a given girth and height or weight differs in a sex-dependent manner (Aiken and West, 1991). Our results constitute evidence for such sex-interactive effects with both height and weight on girth outcomes. These findings support the notion of distinct life history strategies in males and females, wherein both the direction and timing of investment in body girths differs between the sexes.

Individuals demonstrate a wide scatter about the regression lines, particularly in girth-height plots (Fig. 1), within which we focus on average male and female effects. In Figure 1, it appears that investment in the arm and chest is similar for shorter and taller women, in comparison to starker differences between shorter and taller men. Taller men have larger waists than shorter

men, but for women the reverse is true. Regression analysis reveals that for a given percentage increase in height, a proxy for energy acquisition in early life, males invest in girths and overall weight to a greater degree than females. This is consistent with males' differential accretion of lean tissue during development (Marshall and Tanner, 1968; Maynard et al., 2001), through which they may increase muscle mass and body size to facilitate successful competition for mates in adulthood (e.g. Hawkes, 2004; Lassek and Gaulin, 2009; Puts, 2010).

Muscle mass is increased in males relative to females (Fuller et al., 1992; Shih et al., 2000; Abe et al., 2003), most notably in the upper body. Evidence suggests the combination in males of a broad chest, wide shoulders and narrow waist enhances females' perception of male attractiveness (Maisey et al., 1999; Fan et al., 2005), although this may vary between urban and rural populations (Swami and Tovée, 2005). This was reflected in our sex-height interaction analyses, where weight as an outcome demonstrated the largest coefficient, followed by upperbody girths including the arm and chest, along with the thigh.

In contrast, in association with a given percentage increase in weight, Thai females appear to invest more than males in all girths except the head and waist. Here, we considered weight a proxy for more recent energy acquisition, more likely to represent an increase in adipose tissue. Fat is clearly essential to both sexes as an energy store, and a central component of immune function (Gabrielsson et al., 2003; Fantuzzi, 2005; Wells and Cortina-Borja, 2013). However, for both its overall amount and regional distribution, fat appears to be a key sexually-selected trait in females, in contrast to the greater lean mass favored in males (Singh, 1993; Lassek and Gaulin, 2008; 2009). Beyond other functions, fat provides energy for reproductive women, especially during lactation (Clutton-Brock et al., 1989; Dufour and Sauther, 2002).

Several maternal fat depots (e.g. girths of the chest, arm, thigh and calf) have been linked with offspring birth weight, indicating that energy stores throughout the body may benefit reproductive investment (Neggers et al., 1995; Gupta et al., 2001). Females in our sample appear to favor several body girths for a given increase in weight relative to males, with the

greatest effect for the arm, followed by the knee and thigh. However, interaction coefficients in the sex-weight models are smaller than those in the sex-height models.

Females demonstrate preferential deposition of fat around the hips, buttocks and thighs, referred to as gluteofemoral fat (Lassek and Gaulin, 2006, 2008), although males have relatively larger hip bones and bi-iliac breadth (Kurki, 2011). Contrary to expectations, we did not find that females invest relatively more in hip and thigh girths in association with increasing weight. Rather, we observed a relatively fixed degree of dimorphism in these girths across the whole of the weight range, as shown by the large coefficients for male sex in the models. For the hip in particular, this may relate both to preferential fat deposition by females, and also to larger pelvic canal dimensions (Tague, 1992; Kurki, 2011). Since males showed greater investment in hip girth than females in association with height, this may indicate that greater female investment in pelvic dimensions occurs during/after puberty, consistent with evidence that pelvic dimensions of women continue to increase through this period (see Moerman, 1982).

In the sex-weight models, most interaction coefficients indicated a larger proportional increase in a given girth for females, relative to males. However, the interaction coefficient in the waist girth model showed the reverse. This result is inconsistent with the notion of sexual selection for an 'inverted triangle' shape (broad chest and shoulders, narrow waist) in males (Maisey et al., 1999; Fan et al., 2005; Swami and Tovée, 2005). Instead, it suggests sex differences in the distribution of fat tissue. Studies indicate that visceral adipose tissue (VAT) increases in both sexes with age, but beyond this males have greater VAT depots compared to females (Lemieux et al., 1993; He et al., 2004; Kuk et al., 2005; Shen et al., 2009).

We incorporated in our models a fertility variable principally to control for the confounding effects of parity on females, in whom associations between shape and parity have been demonstrated (Lassek and Gaulin, 2006; Wells et al., 2010; Wells et al., 2011). Similar associations have not been found for males, although evidence suggests that the hormone testosterone is lower in married fathers (Berg and Wynne-Edwards, 2001; Gray et al., 2002; Gray et al., 2006; Gettler et al., 2011). Testosterone impacts on tissue distribution (Norgan, 1997), thus it is not unreasonable that fatherhood could impact on shape (Wells et al., 2011), although further data are needed to elucidate these possible effects.

The large sample size is a principal strength of this study; statistical power to detect interaction effects is smaller than for main effects (McClelland and Judd, 1993; Brookes et al., 2004; Durand, 2013). The data were collected using a single scanner following a standardized protocol. Limitations include the cross-sectional nature of the data; for example, a proxy for energy acquisition in early life was used in the absence of available body shape data from adolescent individuals who would have been experiencing developmental trade-offs in real time. We were unable to address potential mechanisms that might underlie tissue trade-offs (e.g. the action of hormones). Additionally, with this methodology we were not able to attribute energy investment specifically to fat, lean, or other tissues, or investigate potential differences in investment related to BMI. These represent outstanding questions for future work.

In conclusion, our findings of sex-interactive effects with height and weight on body girths indicate that males and females invest energy differently across competing parts of the body at different points in the life course. The present results are consistent with the notion that sexual dimorphism is a plastic strategy varying in association with developmental experience and ecological conditions. Further studies are required in additional populations in order to elucidate these findings in more detail.

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Figure 1 254x254mm (300 x 300 DPI)

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254x254mm (300 x 300 DPI)



Figure 1. Arm, chest, waist, and hip girths plotted against height in males and females. Females are dark blue, males are red-orange. Males demonstrate steeper slopes compared to females.

Figure 2. Arm, chest, hip and thigh girths plotted against weight in males and females. Females are dark blue, males are red-orange. Interaction effects are evident for arm and chest girths on weight. Similar effects are less apparent for hip and thigh plots, wherein relatively consistent sex differences are seen across the range of weight.



### Table 1. Raw anthropometric and shape statistics for males and females

# Table 2. Raw anthropometric and shape statistics ( $\bar{x}$  ± SD) stratified by sex and age



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Males: n=5486; females: n=6124

All data log-transformed; all correlations significant at  $p \leq 0.002$ 

 Table 4. Multivariable log-log regression analysis of girths on height, sex, and sex-height interaction, adjusted for age, salary and number of children



n=11610 (f=6124)

Girths and height are mean-centered and natural log-transformed

 See Supporting Information online for table including outcomes for age, salary and number of children *p*-value for 'Male sex' coefficient in calf model non-significant; all other coefficients highly significant at *p* < 0.0001 With the interaction term included, 'Height' effect is for females; the sum of 'Height' and 'Male sex-height interaction' is the height effect for males

Table 5. Multivariable log-log regression analysis of girths on weight, sex, and sex-weight interaction, adjusted for age, salary and number of children



n=11610 (f=6124)

Girths and weight are mean-centered and natural log-transformed

See Supporting Information online for table including outcomes for age, salary and number of children

All coefficients highly significant at *p* < 0.0001

 With the interaction term included, 'Weight' effect is for females; the sum of 'Weight' and 'Male sex-weight interaction' is the weight effect for males