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Waist-hip ratio and cognitive ability: is gluteofemoral fat a privileged store of neurodevelopmental resources?

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Abstract

Upper-body fat has negative effects and lower-body fat has positive effects on the supply of long-chain polyunsaturated fatty acids that are essential for neurodevelopment. Thus, waist-hip ratio (WHR), a useful proxy for the ratio of upper-body fat to lower-body fat, should predict cognitive ability in women and their offspring. Moreover, because teenage mothers and their children compete for these resources, their cognitive development should be compromised, but less so for mothers with lower WHRs. These predictions are supported by data from the Third National Health and Nutrition Examination Survey. Controlling for other correlates of cognitive ability, women with lower WHRs and their children have significantly higher cognitive test scores, and teenage mothers with lower WHRs and their children are protected from cognitive decrements associated with teen births. These findings support the idea that WHR reflects the availability of neurodevelopmental resources and thus offer a new explanation for men's preference for low WHR.

Keywords: Waist-hip ratio; Cognition; Mate preferences; Fatty acids; Neurodevelopment

1. Introduction

Compared with men and other female primates in the wild (Dufour & Slather, 2002), women have substantially more total body fat; the effect size (*d*) for the human sex difference is 2.6 at the end of puberty (Boot, Bouquet, de Ridder, Krenning, & de Muinck Keizer-Shrama, 1997). Body fat *distribution* is also highly dimorphic, with women having more gluteofemoral fat and less abdominal and visceral fat than men, resulting in lower waist-hip ratios (WHRs), with an effect size of 1.7 (Tichet, Vol, Balkau, Le Clesiau, & D'Hour, 1993).

1.1. Female WHR, body mass index, and male preferences

Dimorphic body fat distribution, as reflected in WHR, seems to be an important dimension of female attractiveness. Many studies have shown that men in Western countries prefer women with both a low WHR (0.6–0.7) and a low body mass index (BMI; 17–20) (Singh, 1993; Sugiyama, 2005; Tovee, Maisey, Emery & Cornelisson, 1999; Wilson, 2005). For women who are considered to be highly attractive, the mean WHR and BMI were 0.68±0.04 and 18.09±1.21, respectively, in 300 *Playboy* models (Tovee et al., 1997), and 0.68±0.04 and 18.4±1.3, respectively, in 129 female adult film stars (Voracek & Fisher, 2006).

Several studies in non-Western populations also show a preference for low WHRs, even in some cases where heavier figures are preferred. A sample of Japanese men showed a *stronger* preference for low WHR then men in Britain (Swami, Caprario, Tovee, & Furnham, 2006), and men in a Chinese study showed a preference for a WHR of 0.6 (Dixson, Dixson, Li, & Anderson, 2007). Furnham, Moutafi, and Baguma (2002) found that male Ugandan students preferred a WHR of 0.5 while preferring heavier body weight. Furnham, McClelland, and Omer (2003) found that young men in Kenya also preferred figures with a narrow waist, as did Sugiyama (2004) for the Shiwiar of Ecuador. More systematically, using data for 58 cultures in the Human Area Relations Files, Brown and Konner (1987) found that fatter legs and hips in females were valued in 90%.

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Males in two isolated populations have shown a preference for larger WHRs. Using frontal views, Marlowe and Wetsman (2001) and Wetsman and Marlowe (1999) found that Hadza men preferred women with wider WHRs. Also using frontal views, Yu and Shepard (1998) found that men in an isolated Matsigenka village in Peru ranked an overweight figure with a WHR of 0.9 as most attractive, but noted that this WHR was characteristic of young women in the village before their first pregnancy. In contrast, they found that Matsigenka men in less isolated villages were indistinguishable from American men in their WHR preference. Neither of these studies tested for preference for larger buttocks in lateral views, which Goodwin (2001) found were preferred by African Americans. But in a later Hadza study (Marlowe, Apicella, & Reed, 2005), compared to American men, Hazda men showed a stronger preference for low WHR in lateral views, suggesting that the earlier studies may have overestimated the difference between American and Hadza men's WHR preferences.

In contrast to a fairly widespread preference for lower WHRs, cross-cultural studies have not supported a universal male preference for women with low BMIs. Furnham and Baguma (1994) found that Ugandan men rated obese figures as more attractive than British men. Furnham et al. (2002) found that male Ugandan students also preferred a heavier to a lighter figure (but rated women with a WHR of 0.5 as most attractive). Jackson and McGill (1997) found that most African-American men preferred women of "average" weight (136 lb), while a majority of white males preferred women who were thinner than average. Wetsman and Marlowe (1999) found that Hadza men preferred women with heavier figures, and Shiwar men in Ecuador also preferred heavier women within their population (Sugiyama, 2004, 2005). Men in Gambia also preferred heavier women compared to African Americans and white Americans (Siervo, Grey, Nyan, & Prentice, 2006). Perhaps most tellingly, Brown and Konner (1987) found that people in 81% of 58 cultures valued plump or moderately fat women versus 19% preferring thin women. Hungry men also prefer heavier women (Swami & Tovee, 2006).

Precisely what proportion of the variance in female bodily attractiveness is explained by low BMI or low WHR is the subject of ongoing debate (Singh & Randall, 2007; Tovee, Hancock, Mahmoodi, Singleton, & Cornelissen, 2002; Tovee, Maisey, Emery, & Cornelissen, 1999; Yu & Shepard, 1998). This issue is complicated both by the fact that the two parameters naturally covary and by the possibility that one or both of the preferences may differ among populations either adaptively (e.g., related to the risk of food shortage; Sugiyama, 2004; Swami & Tovee, 2006) or nonadaptively (e.g., "fashion"; Kowner, 2002). Regardless, a preference for low WHR seems widespread and strong enough to warrant questions about its possible adaptive bases.

1.2. What information might WHR contain?

Preferences often evolve when a perceptual signal is correlated with an underlying fitness-enhancing trait (Andersson, 1994). What might a low WHR signal? Arguments to date have focused mainly on the possibility that WHR may be correlated with fertility and/or health (Marlowe et al., 2005; Pawlowski & Dunbar, 2005; Singh, 1993; Sugiyama, 2005), but both of these assertions rest on evidence that is either limited or of questionable relevance.

Some studies of in vitro fertilization show that women with a WHR of <0.80 have a higher probability of "conceiving" (Imani, Eijkemans, te Velde, Habbema, & Fauser, 2002; Van Noord-Zaadstra, Seidell, Vrieswijk, & Van Noord, 1991; Wass, Waldenstrom, Rossner, & Hellberg, 1997; Zaadstra et al., 1993), but a similar study failed to find any relationship between a woman's WHR and her likelihood of conceiving with vaginal insemination (Eijkemans, Imani, Mulders, Habbema, & Fauser, 2003). Indirect support for the fertility hypothesis is provided by evidence that women with very high WHRs (>0.85) have more anovulatory cycles (Moran et al., 1999). Similarly, another study showed higher levels of estradiol and progesterone with low WHR, but only in those with larger breast size (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004). Many of these studies fail to control for BMI, which covaries with WHR (Tovee et al., 1999), so they likely include obese women with polycystic ovarian syndrome (PCOS), many of whom have lower hormone levels and impaired fertility (Pasquali, Gambineri, & Pagotto, 2006). However, normal-weight PCOS patients may have enhanced fertility (Gleicher & Barad, 2006), and there is no difference in primary family size between PCOS patients and controls (Pall, Stephens, & Azziz, 2006).

Regardless of the relation with PCOS, several studies suggest that WHR does not identify young women with menstrual disorders linked to infertility. In a study of 22,480 adolescents aged 15–16 years, there was no difference in WHR between those with regular cycles and those with oligomenorrhea or irregular menses (van Hooff, Voorhorst, Kaptein, & Hirasing, 1999), and the same was true in two other independent studies of young women aged 16–17 and 15–18 years (van Hooff et al., 2000a, 2000b).

There has also been little discussion of any *pathway* through which a low WHR might enhance fertility. Some suggest that fat stores help supply the energy needs of pregnancy and lactation (Cant, 1981; Frisch, 1980; Sugiyama, 2005), but women with lower WHRs usually have *lower* total fat stores (Yang et al., 2006; see below). Moreover, this view does not explain why fat would be preferentially stored on the hips and thighs, nor why similar sex differences in body fat are not generally found in mammals (Lassek & Gaulin, 2007).

It has also been suggested that a low WHR signals better health (Marlowe et al., 2005; Pawlowski & Dunbar, 2005; Singh, 1993; Sugiyama, 2005). This claim is supported by abundant evidence indicating that higher WHRs are associated with increased morbidity and mortality (Bjorntorp, 1988). However, this finding is based on relatively affluent *postmenopausal* women who are most commonly afflicted with chronic diseases that were probably rare during the Paleolithic (Eaton, Eaton, & Konner, 1997). "Thrifty genes" promoting abdominal obesity may also have had survival value in populations subject to nutritional stress (Groop, 2000), but which only recently have become responsible for many of the adverse effects associated with high WHRs. Thus, it is not clear whether, over most of human evolution, low- and high-WHR females would have differed in survival during their reproductive years.

1.3. WHR and neurodevelopmental resources

If WHR is not a reliable predictor of fertility or survival during the reproductive years, are there other reasons why it evolved as a criterion of male mate choice and why females preferentially store fat in the gluteofemoral depot? We have been pursuing the hypothesis that gluteofemoral fat and abdominal fat have opposite effects on the availability of essential fatty acids needed for fetal and infant brain development, with lower-body fat increasing the supply of these neurodevelopment resources and with upper-body fat inhibiting their availability, as discussed below. If this is correct, male preference for lower WHRs would likely spread in a species undergoing rapid brain expansion and, hence, increased demand for brain-building resources.

Storing gluteofemoral fat is a high priority during human female development. Most of the 10–20 kg of fat stored during a female's childhood and puberty is gluteofemoral fat (Fredriks, van Buuren, Fekkes, Verloove-Vanhorick, & Wit, 2005; Hammer et al., 1991). Importantly, menarche is accelerated by a greater proportion of gluteofemoral fat and is *slowed* by higher levels of abdominal fat (Lassek & Gaulin, 2007). Moreover, even with restricted food intake, gluteofemoral fat is metabolically protected from use until late pregnancy and lactation (the period of maximal infant brain growth) when it is selectively mobilized (Rebuffe-Scrive, 1987; Rebuffe-Scrive et al., 1985).

Gluteofemoral fat is the main source of long-chain polyunsaturated fatty acids (LCPUFAs), especially the omega-3 docosahexaenoic acid (DHA), that are critical for fetal and infant brain development, and these LCPUFAs make up approximately 20% of the dry weight of the human brain (Del Prado et al., 2000; Demmelmair, Baumheuer, Koletzko, Dokoupil, & Kratl, 1998; Fidler, Sauerwald, Pohl, Demmelmair, & Koletzko, 2000; Hachey et al., 1987). A recent meta-analysis estimates that a child's IQ increases by 0.13 point for every 100-mg increase in daily maternal prenatal intake of DHA (Cohen, Bellinger, Connor, & Shaywitz, 2005), and a recent study in England shows a similar positive relationship between a mother's prenatal consumption of seafood (high in DHA) and her child's verbal IQ (Hibbeln et al., 2007).

Gluteofemoral fat is richer than abdominal and visceral fat in essential LCPUFAs (Phinney et al., 1994; Pittet, Halliday, & Bateman, 1979; Shafer & Overvad, 1990), and a lower WHR is associated with higher DHA levels in the blood (Decsi, Molnar, & Koletzko, 1996; Garaulet et al., 2001; Karlsson et al., 2006; Klein-Platat, Davis, Oujaa, Schleinger, & Simon, 2005; Seidell, Cigolini, Deslypere, Charzewska, & Ellsinger, 1991). In contrast, abdominal fat decreases the amount of the enzyme Δ-5 desaturase, which is rate limiting for the synthesis of neurologically important LCPUFAs from dietary precursors (Fuhrman et al., 2006; Phinney, 1996), and higher WHRs decrease DHA production (Decsi et al., 2000; Hollmann, Runnebaum, & Gerhard, 1997). Studies using isotope-labeled fatty acids show that 60–80% of LCPUFAs in human breast milk come from maternal fat stores, rather than from the mother's current dietary intake (Del Prado et al., 2000; Demmelmair et al., 1998; Fidler et al., 2000; Hachey et al., 1987), presumably because of the rapid rate of infant brain development relative to limited dietary supplies of LCPUFAs.

Each cycle of pregnancy and lactation draws down the gluteofemoral fat store deposited in early life; in many poorly nourished populations, this fat is not replaced, and women become progressively thinner with each pregnancy, which is termed "maternal depletion" (Lassek & Gaulin, 2006). We have recently shown that even well-nourished American women experience a relative loss of gluteofemoral fat with parity (Lassek & Gaulin, 2006). In parallel, parity is inversely related to the amount of DHA in the blood of mothers and neonates (Al, van Houwelingen, & Hornstra, 1997).

That critical fatty acids are depleted with parity is also consistent with studies showing that cognitive functioning is impaired with parity. IQ is negatively correlated with birth order (Downey, 2001), and twins have decreased DHA (McFadyen, Farquharson, & Cockburn, 2001) and compromised neurodevelopment compared to singletons (Ronalds, De Stavola, & Leon, 2005). The mother's brain also typically decreases in size during pregnancy (Oatridge et al., 2002).

Women who become pregnant while they are still growing have a three-way conflict over nutritional resources that are needed to develop their own brains, nutritional resources that are to be stored for future pregnancies, and the needs of the current fetus; as a result, cognitive development in their offspring is often impaired (Furstenberg et al., 1987).

Only two previous studies have explored the relationship between WHR and cognitive ability, and they have shown that, in older men and women, higher WHRs are associated with poorer cognitive performance and detrimental changes in the brain (Jagust, Harvey, Mungas, & Haan, 2005; Waldstein & Katzel, 2006).

Taken altogether, these facts suggest that the unusual fattiness and fat deposition patterns of reproductive-aged women may be the result of natural selection for the ability to

Table 1
NHANES III subsamples used in analysis and mean values for age, education, and parity

Subsamples	*n*	Age (years)	Education	Parity
1. Mother–child	1933	35.1±7.1	11.0±3.5	2.9±1.8
1a. Mother–child–father	1019	35.3±7.7	10.7±3.9	3.0±1.9
2. Children aged 6–16 years	2563	11.1±2.6		
2a. Teens aged 12–16 years	859	14.0±1.4		0.04±0.22
2b. Teens aged 14–16 years	597	15.0+0.8		0.05±0.30
3. Women aged 18–49 years	5134	32.7±8.5	11.7±3.3	1.9±1.7
3a. With cognitive data	2259	33.1±8.2	12.1±3.1	1.9±1.7

support fetal and infant neurodevelopment—a selection pressure that was much weaker in our close primate relatives. This hypothesis thus unites two derived (evolutionarily novel) features of *Homo sapiens*: sexually dimorphic fat distributions and large brains. On this view, a low WHR signals the availability of critical brain-building resources and should therefore have consequences for cognitive performance.

Three predictions follow:

(a) A woman's WHR should be negatively correlated with her offspring's cognitive abilities.
(b) Because mothers pass both DHA and genes affecting LCPUFA metabolism (and hence WHR) to their (female) offspring and because WHR reflects the availability of LCPUFA, a woman's WHR should also be negatively correlated with her own cognitive abilities.
(c) Since mothers and offspring will be in competition for LCPUFAs and since this competition will be more intense while she is still growing her own brain and when her own LCPUFA reserves are low, cognitive development should be impaired in women whose first birth occurred early and in the resulting offspring, but lower WHRs, indicating larger LCPUFA stores, should be significantly protective for both.

We tested these predictions using anthropometric, demographic, and cognitive data from the Third National Health and Nutrition Examination Survey (NHANES III), which was conducted by the US National Center for Health Statistics from 1988 to 1994.

2. Methods

The NHANES III sample included 16,325 females aged 0–90 years (mean age, 29.9±25.8 years), with 38% non-Hispanic whites, 29% non-Hispanic blacks, 28% Hispanics, and 5% other. Anthropometric data included waist and hip circumferences, WHR, BMI, and total body fat estimated from bioelectrical impedance (Chumlea, Guo, Kuczmarski, Flegal, & Johnson, 2002). Sociodemographic data included years of education, race/ethnicity, and family income.

We analyzed data from seven subsamples:

1. 1933 mothers (regardless of age) matched with their youngest child with cognitive data;
1a. 1019 mother–child pairs matched to the father;
2. 2563 children aged 6–16 years with data from four cognitive tests;
2a. 859 teens aged 12–16 years from Sample 2;
2b. 597 teens aged 14–16 years from Sample 2a;
3. 5134 women aged 18–49 years;
3a. 2259 women from Sample 3 with data for two cognitive tests.

Some characteristics of these samples are given in Table 1.

In Sample 1, mothers were first matched to their youngest child with data from four cognitive tests using family number and age, yielding 1933 mother–child pairs. For Sample 1a, husbands were then matched to these mother–child pairs in 1019 cases using family number and marital status. The average age of the child was 10.3±2.7 years in Sample 1a. The four cognitive tests given to children aged 6–16 years in the NHANES III sample were the math and reading tests from the Wide Range Achievement Test—Revised, and the Digit Span and Block Design tests from the Wechsler Intelligence Scale for Children—Revised. The mean scaled score for the four tests in the 1019 matched children was 7.9±2.7 of 16. This same scaled score was available for teenaged women in Subsamples 2a and 2b.

In the adult subsample (Subsample 3a), scores were available for the Serial Digit Learning Test and the Serial Digit Substitution Test. The sum of these scores was converted to a *z*-score, with higher *z*-scores representing better performance. In adults, "years of education" was used as a second measure of cognitive ability on the assumption that, all other things being equal, those with higher cognitive ability will reach higher levels of educational achievement.

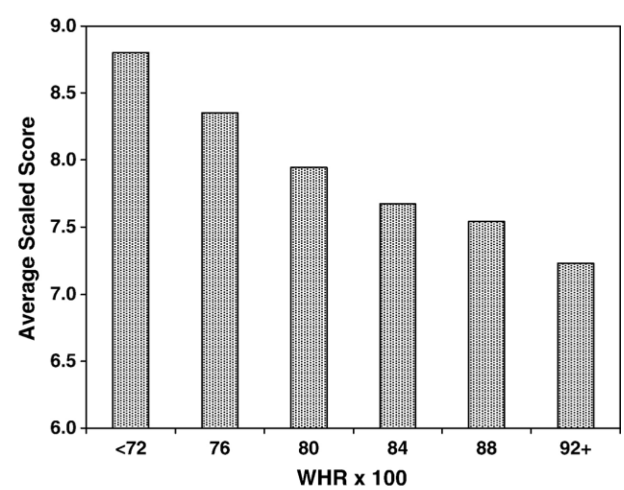

Fig. 1. Child's average scaled score on four cognitive tests versus mother's WHR for 1933 matched mother–child pairs: Sample 1a.

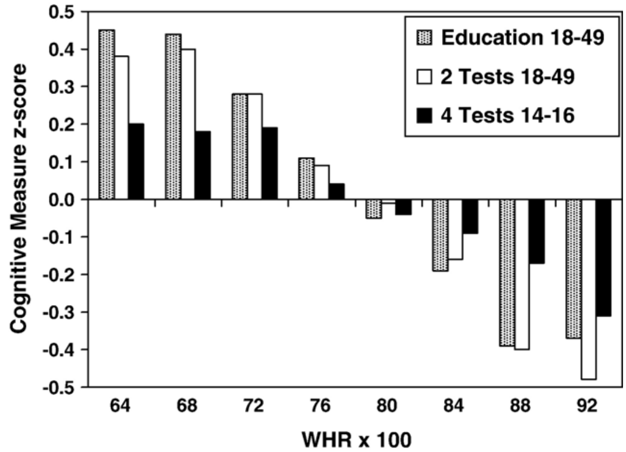

Fig. 2. WHR and cognitive measure *z*-scores for women aged 18–49 years (education and two tests) and 14–16 years (four tests).

Table 2
Relationship between an offspring's cognitive ability and a mother's WHR while controlling for other factors: standardized beta coefficients, Subsample 1a

	Standardized β coefficient	
	n=948	*n*=916
Mother's age	0.097 ***	0.112 ***
Mother's race/ethnicity	0.157 ***	0.140 ***
Mother's education	0.122 **	0.131 ***
Father's education	0.272 ***	0.237 ***
Family income	0.100 **	0.092 **
Mother's WHR		−0.062 *
Model r^2	.253 **	.264 **

* p<.05.
** p<.01.
*** p<.001.

The *z*-scoring of educational levels permits these two measures to be presented in parallel terms.

Generally, each analysis begins with simple descriptive statistics, including a bivariate regression showing the relationship between WHR and a particular cognitive variable. The overall relationships between WHR groups and cognitive variables are shown in Figs. 1–3 and are presented to illustrate the direction, magnitude, and monotonicity of the relationships. Because other factors affect cognitive ability, conclusions about the influence of WHR on cognitive performance can only be confidently derived from multivariate analyses. Thus, multiple linear regression was used to control for race/ethnicity, family income, and other such predictors (results in Tables 2–4). In Section 3.4, the mean cognitive performance of teen mothers with high and low WHRs was compared, using analysis of variance (ANOVA), on the assumption that restricting the sample to teen mothers provides good socioeconomic controls. SPSS was used for all statistical analyses.

3. Results

3.1. Relationship between WHR, BMI, and total body fat

For 752 nulligravidas aged 18–29 years (average age, 21.9±3.2 years), WHR explains 23% of the variance in total body fat estimated from bioelectrical impedance. Controlling for age and race/ethnicity, an increase of 0.01 in WHR increases total body fat by 0.83 kg. Similarly, WHR explains 28% of the variance in BMI, with an increase of 0.47 kg/m^2 for an increase of 0.01 in WHR. BMI explains 89% of the variance in estimated body fat; an increase of 1 kg/m^2 increases fat by 1.8 kg; when added to this regression, WHR makes no significant additional contribution.

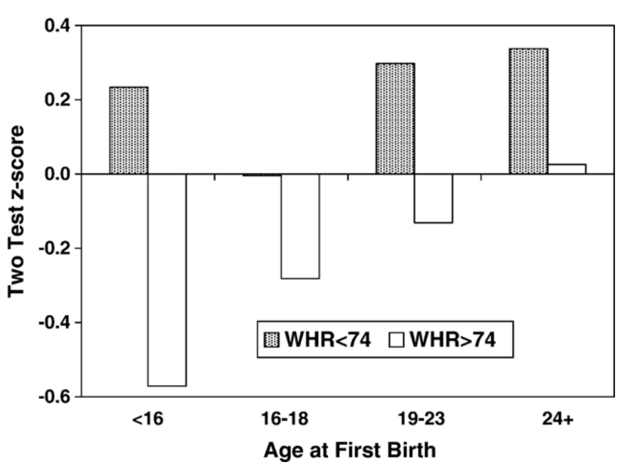

Fig. 3. Mean *z*-score for two cognitive tests in relation to age at first birth and current WHR in women aged 18–49 years.

Table 3
Relationship between cognitive ability and WHR in young and adult women while controlling for other factors

	Four tests	Education	Two tests
Sample	2b	3	3a
Age (years)	14–16	18–49	18–49
n	535	4698	2048
Standardized β coefficient			
Age	−0.024	0.138 **	−0.162 ***
Race/ethnicity	0.260 ***	0.130 ***	0.215 ***
Parity		−0.328 ***	−0.112 ***
Parental education	0.144 **		
Family income	0.230 ***	0.202 ***	0.191 ***
WHR	−0.120 *	−0.128 ***	−0.098 ***
Variance explained (r^2)			
Model	.277 ***	.249 ***	.261 ***
WHR additional	.014 *	.009 ***	.011 ***
WHR alone	.036 ***	.069 ***	.063 ***

* p<.01.
** p<.001.
*** p<.0001.

Table 4
Effects of teen birth and WHR on cognitive test performance in the mother: Sample 3a

Age (years)	18–49	18–49
Age at first birth (years)	Any	<19
n	1579	695
Cognitive measure	Two-test *z*-score	Two-test *z*-score
Standardized regression coefficients		
Age	−0.238 **	−0.260 **
Race/ethnicity	0.260 **	0.216 **
Family income	0.246 **	0.210 **
First birth at <19 years	−0.067 **	
WHR		−0.079 *

* $p<.05$.
** $p<.01$.

3.2. A mother's WHR predicts offspring's cognitive performance

As predicted, in Subsample 1, the mother's current WHR is negatively related to the child's mean test score on four cognitive tests (Fig. 1); WHR accounts for 2.7% of the variance in scores, with a decrease of 0.01 in the mother's current WHR increasing the child's mean cognitive score by 0.061 points ($p<.0001$). In Subsample 1a, using multiple regression to control for the mother's age, both parents' education, family income, and race/ethnicity, WHR is still negatively related to the mean cognitive score ($p<.05$; Table 2). With these control variables, a decrease of 0.01 in WHR increases the average score by 0.024 points ($p<.05$). BMI is not significant when added to this model or when substituted for WHR.

3.3. Women's WHR predicts their own cognitive ability

As predicted, adolescent and adult women with lower WHRs have higher cognitive abilities than those with higher WHRs. In girls aged 14–16 years (Subsample 2b), WHR accounts for 3.6% of the variance in the average of four cognitive tests. In adult women aged 18–49 years (Subsample 3a), WHR accounts for 7% of the variance in years of education and for 6% of the variance for two cognitive tests. The bivariate relationship of WHR to *z*-scores for each of these cognitive measures is illustrated in Fig. 2.

Table 3 displays the results of multiple regression, controlling for age, parity, family income, age at first birth, and race/ethnicity, and again uses standardized beta coefficients showing that WHR is significantly related to cognitive ability in young women aged 14–16 years (Subsample 3b) using four cognitive tests and in adult women using years of education or two cognitive tests. The age group 14–16 years is also controlled for the educational attainment of the householder parent. BMI is not significant when added to these models. Higher parity is independently associated with lower cognitive scores in adult women.

3.4. Mother–child competition for cognitive resources

Among adult women aged 18–49 years, women who had their first birth before the age of 19 years have a *z*-score on two cognitive tests that is 0.32 S.D. lower ($p<.0001$) than those with later first births. Controlling for age, family income, and race/ethnicity (Table 4), an early first birth still depresses a woman's cognitive performance by 0.21 S.D. ($p<.0001$). Among those with a first birth before the age of 19 years, increasing WHR decreases the mean *z*-score. For example, mothers who had their first birth before the age of 19 years and have a current WHR of ≥0.74 have a mean cognitive *z*-score of −0.27, while those with a WHR of ≥0.74 have a mean *z*-score of +0.14 [ANOVA, $F(1,743)= 20.8$, $p<.00001$]. Controlling for age, family income, and race/ethnicity, a decrease of 0.01 in WHR increases the *z*-score by 0.01 ($p<.05$). If BMI is substituted for WHR, it is not significant. In mothers with a current WHR of <0.74 ($n=219$), a first birth before the age of 19 years no longer has a significant effect on cognitive *z*-score. For the full 3a sample, the bivariate relationship of age at first birth, cognitive *z*-score, and WHR is illustrated in Fig. 3.

Mother–child competition for resources is also reflected in the cognitive development of the child. The effect of having a teen mother is shown in children in Subsample 2, where the age-adjusted average of four test scores for all children aged 6–16 years who were born when their mothers were less than the age of 19 years is 0.76 points (0.30 S.D.) lower than for children with older mothers ($p<.0001$; $n=2563$). Adjusting for race/ethnicity and family income, the difference is −0.37 points ($p<.01$; $n=2361$). The role of the mother's WHR in mediating this effect of teen pregnancy is shown in the matched mother–child sample (Subsample 1). Controlling for the mother's education, family income, and race/ethnicity, children born to mothers younger than 19 years have a decrease of 0.45 points in the average of four test scores ($p<.001$), similar to the difference in the larger sample. However, for children whose mothers have a current WHR of <0.76 ($n=384$), having had a teen mother is no longer related to test scores.

4. Discussion

4.1. WHR, BMI, and body fat

WHR is strongly positively related to body fat and BMI in young nulligravidas. BMI is very strongly related to body fat, and the relationship of WHR to BMI mediates the relationship of WHR with fat. Since women with low WHRs and BMIs generally have less body fat, they have less energy reserves to support the energy demands of pregnancy and to increase survival in times of famine, suggesting that female energy stores are not a major factor in male preferences for low WHRs. However the debate is resolved concerning the relative impact of BMI and WHR on female attractiveness, our present findings are clear: WHR predicts offspring cognitive ability, and BMI does not.

4.2. Offspring of mothers with lower WHRs have higher cognitive ability

As predicted, mothers with low WHRs have children with higher cognitive ability. Since we also found that women with low WHRs tend to have higher cognitive ability themselves, we would expect them to have smarter children. However, while controlling for family income and the mother's and father's education reduces the effect of WHR on the child's cognitive ability, there is still a significant residual effect, supporting the view that women with low WHRs provide both genes and materials (essential fatty acids) for neurodevelopment.

Controlling for the parents' cognitive ability may underestimate the effects of WHR. Women may have higher cognitive ability in part because their mothers and grandmothers had the inherited ability to concentrate and store LCPUFAs for their own use, as well as to provide more LCPUFAs to their daughters during gestation and lactation. Thus, these same women would inherit genes that augment the ability to synthesize, concentrate, and store LCPUFAs, which would be reflected in their lower WHRs. Thus, the relationship between the intelligence of parents and the intelligence daughters may be partly mediated by genes related to WHR and the ability to store essential fatty acids.

Moreover, social factors mediating differential opportunities for cognitive development (e.g., schooling, family income) were presumably trivial in the environment of evolutionary adaptedness (EEA). Under these more egalitarian conditions, WHR probably explained a larger proportion of the variance in cognitive abilities.

4.3. Women with lower WHR have higher cognitive ability

Women with lower WHRs have higher cognitive ability, as measured by performance on four cognitive tests in teenagers, and by years of education, and performance on two cognitive tests in premenopausal adult women. Controlling for age, family income, race/ethnicity, parity, and parental education for teens, this effect is still significant. As noted above, controlling for parental education may also underestimate the relationship of WHR to an individual's cognitive ability.

4.4. A lower WHR helps protect cognitive resources in teen mothers and their children

Teenage mothers have competing needs to complete their own cognitive development, store resources for future pregnancies, and provide for their growing fetus and infant; all three appear to be compromised. As this and other studies have shown, the cognitive development of their children is reduced, and their own cognitive development is impaired compared with those mothers with a later first birth. The negative relationship of parity and age at first pregnancy to cognitive test scores in adult women may reflect the continuing costs of competition between mothers and their children. In mothers who maintain lower WHRs, indicating more optimal fat stores, there is no decrement in the mother's cognitive function associated with teen pregnancy. Likewise, as other studies have shown, children born to teen mothers have significantly lower average test scores; but again, those whose mothers have lower current WHRs are protected from this decrement. Mothers who maintain lower WHRs appear to have sufficient resources available to support the cognitive development of their children even when they themselves are still growing.

4.5. Implications

For reasons that are still under debate (Miller, 2000), one or more selection pressures favored extensive brain expansion in the human lineage. It would be surprising if a tripling in brain size compared to our nearest primate relatives did not foster some changes in the processes supporting neurodevelopment. LCPUFAs, which comprise 20% of the mammalian brain and are dietarily scarce, are likely to have been developmentally limiting, and adaptations to acquire, store, and appropriately invest these resources are to be expected. Once such adaptations had emerged in females, they would have been likely targets of male choice. The data reviewed here suggest that, whatever else it might signal, WHR indicates critical resources for brain development. This view thus suggests a functional link between two highly derived human traits: a very large brain and sexually dimorphic fat distributions.

This perspective has obvious developmental and evolutionary implications. In particular, neurodevelopment may be compromised when omega-3 LCPUFAs are in short supply. Recent dietary changes in the modern West (Ailhaud et al., 2006) that reduce their availability may compromise cognitive ability on a populationwide level.

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References

Ailhaud, G., Massiera, F., Weill, P., Legrand, P., Alessandri, J. M., & Guesnet, P. (2006). Temporal changes in dietary fats: Role of $n-6$ polyunsaturated fatty acids in excessive adipose tissue development and relationship to obesity. *Progress in Lipid Research, 45*, 203–236.

Al, M. D., van Houwelingen, A. C., & Hornstra, G. (1997). Relation between birth order and the maternal and neonatal docosahexaenoic acid status. *European Journal of Clinical Nutrition, 51*, 548–553.

Andersson, M. B. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.

Bjorntorp, P. (1988). The association between obesity, adipose tissue distribution and disease. *Acta Medica Scandinavia,* (Suppl 723), 121–134.

Boot, A. M., Bouquet, J. J., de Ridder, M. A., Krenning, E. P., & de Muinck Keizer-Shrama, S. M. P. F. (1997). Determinants of body composition measured by dual-energy X-ray absorptiometry in Dutch children and adolescents. *American Journal of Clinical Nutrition, 66*, 232–238.

Brown, P. J., & Konner, M. (1987). An anthropological perspective on obesity. *Annals of the New York Academy of Sciences, 499*, 29–46.

Cant, J. G. H. (1981). Hypothesis for the evolution of human breasts and buttocks. *American Naturalist, 117*, 199–204.

Chumlea, W. C., Guo, S. S., Kuczmarski, R. J., Flegal, K. M., & Johnson, C. J. (2002). Body composition estimates from NHANES III bioelectrical impedance data. *International Journal of Obesity, 26*, 1596–1609.

Cohen, J. T., Bellinger, D. C., Connor, W. E., & Shaywitz, B. A. (2005). A quantitative analysis of prenatal intake of $n-3$ polyunsaturated fatty acids and cognitive development. *American Journal of Preventive Medicine, 29*, 366–374.

Decsi, T., Csabi, G., Torok, K., Erhardt, E., Minda, H., Burus, I., Molnar, S., & Molnar, D. (2000). Polyunsaturated fatty acids in plasma lipids of obese children with and without metabolic cardiovascular syndrome. *Lipids, 35*, 1179–1184.

Decsi, T., Molnar, D., & Koletzko, B. (1996). Long-chain polyunsaturated fatty acids in plasma lipids of obese children. *Lipids, 31*, 305–311.

Del Prado, M., Villapando, S., Lance, A., Alfonso, E., Demmelmar, H., & Koletzko, B. (2000). Contribution of dietary and newly formed arachidonic acid to milk secretion in women in low fat diets. *Advances in Experimental Medicine and Biology, 478*, 407–408.

Demmelmair, H., Baumheuer, M., Koletzko, B., Dokoupil, K., & Kratl, G. (1998). Metabolism of $U^{13}C$-labeled linoleic acid in lactating women. *Journal of Lipid Research, 39*, 1389–1396.

Dixson, B. J., Dixson, A. F., Li, B., & Anderson, M. J. (2007). Studies of human physique and sexual attractiveness: Sexual preferences of men and women in China. *American Journal of Human Biology, 19*, 88–95.

Downey, D. B. (2001). Number of siblings and intellectual development: The resource dilution explanation. *American Psychologist, 56*, 497–504.

Dufour, D. L., & Slather, M. L. (2002). Comparative and evolutionary dimensions of the energetics of human pregnancy and lactation. *American Journal of Human Biology, 14*, 584–602.

Eaton, S. B., Eaton, S. B., III, & Konner, M. J. (1997). Paleolithic nutrition revisited: A twelve-year retrospective on its nature and implications. *European Journal of Clinical Nutrition, 51*, 207–216.

Eijkemans, M. J. C., Imani, B. A., Mulders, A. G. M., Habbema, J. D. F., & Fauser, B. C. J. M. (2003). High singleton live birth rate following classical ovulation induction in normogonadotrophic anovulatory infertility. *Human Reproduction, 18*, 2357–2362.

Fidler, N., Sauerwald, T., Pohl, A., Demmelmair, H., & Koletzko, B. (2000). Docosahexaenoic acid transfer into human milk after dietary supplementation: A randomized clinical trial. *Journal of Lipid Research, 41*, 1376–1383.

Fredriks, A. M., van Buuren, S., Fekkes, M., Verloove-Vanhorick, S. P., & Wit, J. M. (2005). Are age references for waist circumference, hip circumference and waist–hip ratio in Dutch children useful in clinical practice? *European Journal of Pediatrics, 164*, 216–222.

Frisch, R. E. (1980). Pubertal adipose tissue: Is it necessary for normal sexual maturation? Evidence from the rat and human female. *Federation Proceedings, 39*, 2395–2400.

Furnham, A., & Baguma, P. (1994). Cross cultural differences in the perception of female body shapes. *International Journal of Eating Disorders, 15*, 81–89.

Furnham, A., McClelland, A., & Omer, L. (2003). A cross cultural comparison of ratings of perceived fecundity and sexual attractiveness as a function of body weight and waist to hip ratio. *Psychology, Health and Medicine, 8*, 219–230.

Furnham, A., Moutafi, J., & Baguma, B. (2002). A cross-cultural study on the role of weight and waist-to-hip ratio on female attractiveness. *Personality and Individual Differences, 32*, 729–745.

Fuhrman, B. J., Barba, M., Krogh, V., Micheli, A., Pala, V., Lauria, R., et al. (2006). Erythrocyte membrane phospholipid composition as a biomarker of dietary fat. *Annals of Nutrition and Metabolism, 50*, 95–102.

Furstenberg Jr., F. F., Brooks-Gunn, J., & Morgan, S. P. (1987). Adolescent mothers and their children in later life. *Family Planning Perspectives, 19*, 142–151.

Garaulet, M., Perez-Llamas, F., Perez-Ayala, M., Martinez, P., de Medina, F. S., Tebar, F. J., & Zamora, S. (2001). Site-specific differences in the fatty acid composition of abdominal adipose tissue in an obese population from a Mediterranean area. *American Journal of Clinical Nutrition, 74*, 585–591.

Gleicher, N., & Barad, D. (2006). An evolutionary concept of polycystic ovarian disease: Does evolution favour reproductive success over survival? *Reproductive Biomedicine Online, 12*, 587–589.

Goodwin, R. L. (2000). *Perceptions of female physical attractiveness in African-American and Caucasian populations: Testing evolutionary and sociocultural theories*. Dissertation, Washington State University.

Groop, L. (2000). Genetics of the metabolic syndrome. *British Journal of Nutrition, 83*(Suppl 1), S39–S48.

Hachey, D. L., Thomas, M. R., Emken, E. A., Garza, C., Brown-Booth, L., Adlof, R. O., et al. (1987). Human lactation: maternal transfer of dietary triglycerides labeled with stable isotopes. *Journal of Lipid Research, 28*, 1185–1192.

Hammer, L. D., Wilson, D. M., Killen, J. D., Hayward, C., Miner, B., Vasti, C., & Taylor, C. B. (1991). Impact of pubertal development on body fat distribution among white, Hispanic, and Asian female adolescents. *Journal of Pediatrics, 118*, 975–980.

Hibbeln, J. R., Davis, J. M., Steer, C., Emmett, P., Rogers, I., Williams, C., et al. (2007). Maternal seafood consumption in pregnancy and neurodevelopmental outcomes in childhood (ALSPAC study): an observational cohort study. *Lancet, 369*, 578–585.

Hollmann, M., Runnebaum, B., & Gerhard, I. (1997). Impact of waist–hip-ratio and body-mass-index on hormonal and metabolic parameters in young, obese women. *International Journal of Obesity, 21*, 476–483.

Imani, B., Eijkemans, M. J. G., te Velde, E. R., Habbema, J. D. F., & Fauser, B. C. J. M. (2002). A nomogram to predict the probability of live birth after clomiphene citrate induction of ovulation in normogonadotropic oligoamenorrheic infertility. *Fertility and Sterility, 77*, 91–97.

Jackson, L. A., & McGill, O. D. (1997). Body type preferences and body characteristics associated with attractive and unattractive bodies by African Americans and Anglo Americans. *Sex Roles, 35*, 295–307.

Jagust, W., Harvey, D., Mungas, D., & Haan, M. (2005). Central obesity and the aging brain. *Archives of Neurology 62*, 1545–1548.

Jasienska, G., Ziomkiewicz, A., Ellison, P. T., Lipson, S. F., & Thune, I. (2004). Large breasts and narrow waists indicate high reproductive potential in women. *Proceedings of the Royal Society of London Series B, 271*, 1213–1217.

Karlsson, M., Marild, S., Brandberg, J., Lonn, L., Friberg, P., & Strandvik, B. (2006). Serum phospholipid fatty acids, adipose tissue and metabolic markers in obese adolescents. *Obesity, 14*, 931–939.

Klein-Platat, C., Davis, J., Oujaa, M., Schleinger, J. L., & Simon, C. (2005). Plasma fatty acid composition is associated with the metabolic syndrome and low-grade inflammation in overweight adolescents. *American Journal of Clinical Nutrition, 82*, 1178–1184.

Kowner, R. (2002). Japanese body image: Structure and esteem scores in a cross-cultural perspective. *International Journal of Psychology, 37*, 149–159.

Lassek, W. D., & Gaulin, S. J. C. (2006). Changes in body fat distribution in relation to parity in American women: A covert form of maternal depletion. *American Journal of Physical Anthropology, 131*, 295–302.

Lassek, W. D., & Gaulin, S. J. C. (2007). Menarche is related to fat distribution. *American Journal of Physical Anthropology, 133*, 1147–1151.

Marlowe, F., Apicella, C., & Reed, D. (2005). Men's preferences for women's profile waist-to-hip ratio in two societies. *Evolution and Human Behavior, 26*, 458–460.

Marlowe, F., & Wetsman, A. (2001). Preferred waist-to-hip ratio and ecology. *Personality and Individual Differences, 30*, 481–489.

McFadyen, M., Farquharson, J., & Cockburn, F. (2001). Maternal and umbilical cord erythrocyte omega-3 and omega-6 fatty acids and haemorheology in singleton and twin pregnancies. *Archives of Diseases in Childhood, 88*, F134–F138.

Miller, G. (2000). *The mating mind*. New York: Doubleday.

Moran, C., Hernandez, E., Ruiz, J. E., Fonseca, M. E., Bermudez, J. A., & Zarate, A. (1999). Upper body obesity and hyperinsulinemia are associated with anovulation. *Gynecologic and Obstetric Investigation, 47*, 1–5.

Oatridge, A., Holdcroft, A., Saeed, N., Hajnal, J. V., Puri, B. K., Fusi, L., & Bydder, G. M. (2002). Change in brain size during and after pregnancy: study in healthy women and women with preeclampsia. *American Journal of Neuroradiology, 23*, 19–26.

Pall, M., Stephens, K., & Azziz, R. (2006). Family size in women with polycystic ovary syndrome. *Fertility and Sterility, 85*, 1837–1839.

Pasquali, R., Gambineri, A., & Pagotto, U. (2006). The impact of obesity on reproduction in women with polycystic ovary syndrome. *BJOG: An International Journal of Obstetrics & Gynaecology, 113*, 1148–1159.

Pawlowski, B., & Dunbar, R. I. M. (2005). Waist-to-hip ratio versus body mass index as predictors of fitness in women. *Human Nature, 16*, 164–177.

Phinney, S. D. (1996). Arachidonic maldistribution in obesity. *Lipids, Suppl. 31*, s271–s274.

Phinney, S. D., Stern, J. S., Burke, K. E., Tang, A. B., Miller, G., & Holman, R. (1994). Human subcutaneous adipose tissue shows site-specific differences in fatty acid composition. *American Journal of Clinical Nutrition, 60*, 725–729.

Pittet, P. G., Halliday, D., & Bateman, P. E. (1979). Site differences in the fatty acid composition of subcutaneous adipose tissue of obese women. *British Journal of Nutrition, 42*, 57–61.

Rebuffe-Scrive, M. (1987). Regional adipose tissue metabolism in women during and after reproductive life and in men. *Recent Advances in Obesity Research, 5*, 82–91.

Rebuffe-Scrive, M., Enk, L., Crona, N., Lonnroth, P., Abrahamsson, L., Smith, U., & Bjorntorp, P. (1985). Fat cell metabolism in different regions in women: Effect of menstrual cycle, pregnancy and lactation. *Journal of Clinical Investigation, 75*, 1973–1976.

Ronalds, G. A., De Stavola, B. L., & Leon, D. A. (2005). The cognitive cost of being a twin: Evidence from comparisons within families in the Aberdeen children of the 1950s cohort study. *British Medical Journal, 331*, 1306.

Seidell, J. C., Cigolini, M., Deslypere, J. P., Charzewska, J., & Ellsinger, B. M. (1991). Polyunsaturated fatty acids in adipose tissue in European men aged 38 years in relation to serum lipids, smoking habits, and fat distribution. *American Journal of Epidemiology, 134*, 583–589.

Shafer, L., & Overvad, K. (1990). Subcutaneous adipose-tissue fatty acids and vitamin E in humans: Relation to diet and sampling site. *American Journal of Clinical Nutrition, 52*, 486–490.

Siervo, M., Grey, P., Nyan, O. A., & Prentice, A. M. (2006). A pilot study on body image, attractiveness and body size in Gambians living in an urban community. *Eating and Weight Disorders, 11*, 100–109.

Singh, D. (1993). Adaptive significance of female physical attractiveness: Role of waist–hip ratio. *Journal of Personality and Social Psychology, 65*, 293–307.

Singh, D., & Randall, P. K. (2007). Beauty is in the eye of the plastic surgeon: Waist–hip ratio (WHR) and women's attractiveness. *Personality and Individual Differences, 43*, 329–340.

Sugiyama, L. S. (2004). Is beauty in the context-sensitive adaptations of the beholder? Shiwiar use of waist-to-hip ratio in assessments of female mate value. *Evolution and Human Behavior, 25*, 51–62.

Sugiyama, L. S. (2005). Physical attractiveness in adaptationist perspective. In D. M. Buss (Ed.), *Handbook of evolutionary psychology* (pp. 292–343). Hoboken, NJ: John Wiley.

Swami, V., Caprario, C., Tovee, M. J., & Furnham, A. (2006). Female physical attractiveness in Britain and Japan: A cross-cultural study. *European Journal of Personality, 20*, 69–81.

Swami, V., & Tovee, M. J. (2006). Does hunger influence judgments of female physical attractiveness? *British Journal of Psychology, 97*, 353–363.

Tichet, J., Vol, S., Balkau, B., Le Clesiau, H., & D'Hour, A. (1993). Android fat distribution by age and sex: The waist hip ratio. *Diabete et Metabolisme, 19*, 273–276.

Tovee, M. J., Mason, S. M., Emery, J. L., McCluskey, E. M., & Cohen-Tovee, E. M. (1997). Supermodels: stick insects or hourglasses? *Lancet, 350*, 1474–1475.

Tovee, M. J., Hancock, P. J. B., Mahmoodi, S., Singleton, B. R. R., & Cornelissen, P. L. (2002). Human female attractiveness: Waveform analysis of body shape. *Proceedings of the Royal Society of London Series B, 269*, 2205–2213.

Tovee, M. J., Maisey, D. S., Emery, J. L., & Cornelissen, P. L. (1999). Visual cues to female physical attractiveness. *Proceedings: Biological Sciences, 266*, 211–218.

van Hooff, M. H. A., Voorhorst, F. J., Kaptein, M. B. H., & Hirasing, R. A. (1999). Endocrine features of polycystic ovary syndrome in a random population sample of 14–16 year old adolescents. *Human Reproduction, 14*, 2223–2229.

van Hooff, M. H. A., Voorhorst, F. J., Kaptein, M. B. H., Hirasing, R. A., Koppenaal, C., & Schoemaker, J. (2000a). Insulin, androgen, and gonadotropin concentrations, body mass index, and waist to hip ratio in the first years after menarche in girls with regular menstrual cycles, irregular menstrual cycles, or oligomenorrhea. *Journal of Clinical Endocrinology and Metabolism, 85*, 1394–1400.

van Hooff, M. H. A., Voorhorst, F. J., Kaptein, M. B. H., Hirasing, R. A., Koppenaal, C., & Schoemaker, J. (2000b). Polycystic ovaries in adolescents and the relationship with menstrual cycle patterns, luteinizing hormone, androgens, and insulin. *Fertility and Sterility, 74*, 49–58.

van Noord-Zaadstra, B. M., Seidell, J. C., Vrieswijk, B., & Van Noord, P. A. H. (1991). The relationship between fat distribution and fertility: A prospective study of healthy Dutch women. *International Journal of Obesity, 15*(Suppl 3), 36.

Voracek, M., & Fisher, M. L. (2006). Success is all in the measures: Androgenousness, curvaceousness, and starring frequencies in adult media actresses. *Archives of Sexual Behavior, 35*, 297–304.

Waldstein, S. R., & Katzel, L. I. (2006). Interactive relations of central versus total obesity and blood pressure to cognitive function. *International Journal of Obesity, 30*, 201–207.

Wass, P., Waldenstrom, U., Rossner, S., & Hellberg, D. (1997). An android body fat distribution in females impairs pregnancy rate of in-vitro fertilization–embryo transfer. *Human Reproduction, 12*, 2057–2060.

Wetsman, A., & Marlowe, F. (1999). How universal are preferences for female waist-to-hip ratios? Evidence from the Hadza of Tanzania. *Evolution and Human Behavior, 20*, 219–228.

Wilson, J. M. B. (2005). The relative contributions of waist-to-hip ratio and body mass index to judgments of attractiveness. *Sexualities, Evolution and Gender, 7*, 245–267.

Yang, F., Lv, J. H., Lei, S. F., Chen, X. D., Liu, M. Y., Jian, W. X., et al. (2006). Receiver-operating characteristic analyses of body mass index, waist circumference and waist-to-hip ratio for obesity: Screening in young adults in central south of China. *Clinical Nutrition, 25*, 1030–1039.

Yu, D. W., & Shepard, G. H. (1998). Is beauty in the eye of the beholder? *Nature, 396*, 321–322.

Zaadstra, B. M., Seidell, J. C., Van Noord, P. A., te Velde, E. R., Habbema, J. D., Vrieswijk, B., et al. (1993). Fat and female fecundity: prospective study of effect of body fat distribution on conception rates. *British Medical Journal, 306*, 484–487.