Reports

Waist-to-Hip Ratio across Cultures: Trade-Offs between Androgen- and Estrogen-Dependent Traits

Elizabeth Cashdan

Department of Anthropology, University of Utah, 170 South 1400 East, Room 102, Salt Lake City, UT 84112-0060, U.S.A. (cashdan@anthro.utah.edu). 4 VIII 08

CA+ Online-Only Material: Supplements A–C

A gynoid pattern of fat distribution, with small waist and large hips (low waist-to-hip ratio, or WHR) holds significant fitness benefits for women: women with a low WHR of about 0.7 are more fecund, are less prone to chronic disease, and (in most cultures) are considered more attractive. Why, then, do nearly all women have a WHR higher than this putative optimum? Is the marked variation in this trait adaptive? This paper first documents the conundrum by showing that female WHR, especially in non-Western populations, is higher than the putative optimum even among samples that are young, lean, and dependent on traditional diets. The paper then proposes compensating benefits to a high WHR that can explain both its prevalence and variation in the trait. The evidence indicates that the hormonal profile associated with high WHR (high androgen and cortisol levels, low estrogens) favors success in resource competition, particularly under stressful and difficult circumstances, even though this carries fitness costs in fecundity and health. Adrenal androgens, in particular, may play an important role in enabling women to respond to stressful challenges.

The medical profession has long argued that a body shape with fat on the hips rather than the abdomen (low waist-to-hip ratio, or WHR) is ideal from the perspective of both health and fertility. These advantages have suggested to many evolutionary psychologists that a low WHR is an honest signal of good condition; hence, men everywhere have an evolved preference for this body shape when seeking a mate.

The benefits of greater fertility, health, and attractiveness would seem to be so compelling that one might expect all women to have a low WHR. But this is not the case. Most women, particularly in non-Western populations, have WHRs larger than would be expected by these criteria, and a few populations do not even find a low WHR especially attractive. From an evolutionary perspective, this is puzzling. If, as has been claimed, a WHR of 0.7 or less enhances both fertility and survivorship, and if the average for women is higher than this, why has selection not moved this trait to the optimal value? I address this conundrum here and consider reasons for the wide variation in female WHR.

 0011-3204/2008/4906-0006$10.00. DOI: 10.1086/593036

Average WHR Is Larger than the Putative Optimum

What Is the Optimal WHR?

A large WHR is a threat to health and survivorship, and it appears that the lower the WHR, the better. The risks increase monotonically as WHR increases, for both cardiovascular disease (Deurenberg-Yap et al. 1999; Zhang et al. 2004) and diabetes (Hartz et al. 1984). The health problems stem chiefly from excess truncal (particularly visceral) fat, which predisposes women to insulin resistance, diabetes, and cardiovascular disease (Wajchenberg 2000; Lee et al. 2008), breast cancer (Sonnenschein et al. 1999), and preeclampsia (Yamamoto et al. 2001).

Women with low WHR also have significantly higher fecundity (Zaadstra et al. 1993; Wass et al. 1997; Moran 1999; Jasieńska et al. 2004; Kirchengast and Huber 2004), and the effect is large. Jasieńska et al. (2004) estimated the most fecund quartile in their sample (low WHR with large breasts) to have estradiol levels indicative of a threefold increase in the probability of conception over the rest of the sample. Similarly large effects were apparent in a study of donor insemination, where a 0.1 increase in WHR (controlling for age and body weight) decreased the probability of conception per cycle by 30% (Zaadstra et al. 1993).

Because low WHR signals both fertility and good health and may have other advantages as well (Lassek and Gaulin 2008), many evolutionary psychologists have suggested that we have evolved a preference for women with this shape. This argument has considerable empirical support, with most studies finding the most attractive WHR to be 0.7 or even lower (see, e.g., Singh and Louis 1995; Henss 2000; Furnham et al. 2003; Streeter and McBurney 2003, and references therein).

Average Values of WHR

If women's WHR were determined by selection pressures on fecundity, mortality, and male preferences, therefore, we would expect them to center around 0.7 or below. But they do not, particularly in non-European populations.

Tables 1 and 2 contain data on 33 non-Western populations, with four European populations and Playboy centerfolds included for comparison. Because WHR increases with both age and weight, the data are grouped by approximate age and are divided into normal weight (table 1) and overweight/obese (table 2) populations. Table 3 provides a more fine-grained comparison of young adult samples. To save

Table 1. Female BMI and WHR across Populations: Normal Weight

Society	*n*	Age (years)	BMI	WHR
Older normal-weight samples (40s):				
UK Chinese	197	25–64	23.5	.84
Korea	3,416	46.5	23.4	.84
South China:				
Urban	1,400	45.3	21.9	.81
Rural	1,755	46.0	20.2	.80
Mauritius:				
Muslim	371	41.7	24.7	.82
Creole	744	45.3	24.9	.82
Hindu	1,353	42.5	23.8	.81
Chinese	201	46.9	23.3	.78
Younger normal-weight samples (30s):				
Aboriginal Australia (Arnhem Land)	204	36	23.2	.93
Shiawar (Amazonian forager/farmers)	24	34.3	24.7	.87
Hadza (East African foragers)	75	37.5	20.3	.83
Mongolia (nomads)	. . .	25–39	23.7	.82
Australian Vietnamese	165	36.4	21.3	.80
Singapore Chinese	1,211	37.8	22.1	.73
Youngest normal-weight samples (20s):				
Guatemala	547	18–25	22.0	.91
Shiawar (Amazonian forager/farmers)	12	23.5	24.0	.86
Jarawa (Andaman foragers)	16	28.2	19.8	.82
Iran	1,000	16.2	19.8	.80
Hadza (East African foragers)	10	22.0	20.6	.79
Orang Asli (Malay forager/farmers)	≈69	≈29	21.0	.79
Mongolia (nomads)	. . .	18–24	21.5	.73
Playboy centerfolds	240	19–35	18.1	.68

Note. See CA+ online supplement A for notes and sources.

space, explanatory notes, caveats, and data sources for the tables are given in CA+ online supplement A.

Tables 1–3 show that average female WHR for nearly all populations is above 0.8 and is high (but variable) in even the youngest age groups. The average WHR is 0.82 in the 18–24-year age group (table 3), 0.80 in the 18–29-year age group (table 3), and 0.81 in the 11 populations with mean age ≲29 years (tables 1 and 2).

Populations worldwide are becoming more obese; do these young women have a high WHR because of exposure to Western diets? Obesity is often measured by body mass index (BMI), a measure of weight scaled for height. The tables show that overweight women (those with a BMI ≥25) do have a higher WHR, but the average WHR numbers do not change much if we remove the young overweight populations from the calculations: the corresponding WHR numbers are 0.82 for the 18–24-year age group, 0.83 for the 18–29-year age group, and 0.81 for the seven lean populations with mean age ≲29 years. The WHR is also high (mean WHR = 0.84, mean age = 32 years) in the four populations that still depend heavily on foraging: Jarawa, Shiawar, Hadza, and Orang Asli (none of these populations is overweight).

The high WHR values in these data, therefore, cannot be explained away by appealing to age, economy, or modern diets. Even in Jasieńska et al.'s (2004) fecundity study, where average WHR was low (as is typical for young European women), the average was higher than the WHR associated with the greatest fecundity in the same sample. This paper will attempt to explain why actual WHR is higher than would seem to be optimal and will then consider why it increases with age and varies cross-culturally.

Is It a Consequence of Variation in Weight?

One explanation for variation in WHR is that it is an artifact of associated variation in fatness and that selection is operating on the latter, not the former. In traditional societies, where the challenge is getting enough to eat, men may be more concerned that their mates be plump (Wetsman and Marlowe 1986; Marlowe and Wetsman 2001; Sugiyama 2004), and they may even prefer women with a high WHR because it signals fatness (Tovée et al. 2001). To the extent that WHR is correlated with overall fatness, this argument also suggests that current WHR may be higher than optimal (in both sexes) because of the growing rates of obesity around the world.

The strength of this argument depends on the strength of the relationship between WHR and overall adiposity. One of the best data sets for such an analysis is the WHO MONICA

Table 2. Female BMI and WHR across Populations: Overweight

Society	*n*	Age (years)	BMI	WHR
Older overweight samples (40s):				
New Caledonia:				
Urban Melanesian	428	30–59	29.7	.97
Urban European	299	30–59	26.1	.90
Rural Melanesian	3,493	30–59	28.5	.90
Rural European	317	30–59	27.3	.83
Alaskan Eskimo	237	≥25	27.5	.93
Algonquin:				
Rural	70	38.3	29.1	.92
Urban	98	43.9	27.0	.85
Thailand	>900	42	25.4	.84
United Kingdom:				
South Asian	322	25–64	27.4	.86
European	309	25–64	26.1	.78
Hawaii (native)	134	20–59	31	.84
Jamaica	783	46.2	28.0	.80
Younger overweight samples (30s):				
Shuar (Amazonian farmers)	7	35.6	26.0	.98
Saudi Arabia	100	36	32.0	.90
Havasupai	50	34	34.0	.89
Aboriginal Australia (southeast)	108	34.1	28.8	.87
Youngest overweight samples (20s):				
Aboriginal Australia (central)	131	22.2	26.5	.83
Hawaii (native)	27	20–29	29	.81
New Zealand:				
Polynesian	40	21.7	31.2	.77
European	40	22.3	28.9	.75

Note. See CA+ online supplement A for notes and sources.

Table 3. Female BMI and WHR in Young Adult Samples

Society	n	Age (years) Mean	Age (years) Range	BMI	WHR
Age 18–29 years:					
Shiawar	12	23.5	18–29	24.0	.86
Hawaiian	27	. . .	20–29	29	.81
Hadza	13	24.2	18–29	20.6	.81
New Zealand:					
Polynesian	40	21.7	18–27	31.2	.77
European	40	22.3	18–27	28.9	.75
Age 18–24 years:					
Guatemalan	547	. . .	18–25	22.0	.91
Shiawar	6	21.2	18–24	24.0	.87
Aboriginal Australian	131	22.2	16–27	26.5	.83
Iranian	1,000	16.2	14–21	19.8	.80
Hadza	10	. . .	18–24	. . .	.79
Mongolian nomads	. . .	. . .	18–24	21.5	.73

Note. See CA+ online supplement A for characteristics of the populations, other notes, and sources.

study, which measured WHR and BMI in more than 32,000 men and women in 19 chiefly European populations, using a standard protocol. In this study, BMI explained only 18% of the variance in female WHR, with 70% unexplained by height, age, BMI, or population (Molarius et al. 1999).

The world-wide sample reviewed here has greater variation in BMI than does the MONICA study; about half of the groups are overweight or obese. The WHR is higher in the latter, and it is correlated with BMI overall ($r = .40$, $p = .01$, $n = 38$). However, WHR and BMI are not correlated when the sample is limited to the normal-weight populations.

Exposure to Western diets has increased obesity in many traditional as well as Western populations. It seems clear that the high WHR found in these overweight populations is, in part, a consequence of overall adiposity. The mean and variance in WHR in the normal-weight populations is also large, however, and requires a different explanation.

It is also worth considering that the relationship between BMI and WHR may itself be an adaptation, not an artifact. Many of the obese populations in table 2 have been characterized as having a "thrifty genotype" adapted to scarce or unpredictable food supplies but prone to obesity and diabetes in contact situations where food is abundant. Selection for a thrifty genotype might simultaneously select for a tendency to deposit fat preferentially on the abdomen, since abdominal (especially visceral) fat is more metabolically active than subcutaneous fat from other areas (Wajchenberg 2000). This will be discussed further below.

Compensating Advantages to a High WHR

Another explanation for a high WHR is that it has compensating advantages. Several possibilities have been suggested, including better adaptation to cold, higher offspring sex ratio in societies with son preference, and sexually antagonistic selection that favors male offspring at the expense of female offspring (see CA+ online suppl. B for further discussion). Here I suggest another trade-off: the hormonal profile associated with high WHR (high androgen and cortisol levels, low estrogens) may favor success in resource competition, particularly under stressful and difficult circumstances. High androgen levels in women are associated both with larger WHR and with greater assertiveness and competitive aggression in women (see below). Androgens also increase muscle mass and physical strength. Cortisol is also associated with larger WHR and enables the mind and body to respond effectively to stress. All of these effects could be adaptive in circumstances where women must work hard to support their children, compete directly for resources for them, and cope with resource scarcity. A truly optimal level of hormones, then, should weigh these considerable advantages against their well-known costs: lower fertility, health problems if overweight, and possibly lowered attractiveness to men. The optimal value is likely to vary in response to women's roles and environmental circumstances.

Women Need More than Fecundity

A low WHR will enhance a woman's fecundity and will probably (in most societies) help her to attract a desirable mate, but these are first steps only. Her fitness also depends on her ability to procure resources and help her children to be reproductively successful. Rarely can a woman depend solely on an investing man or even other allomothers to do this for her; she must also depend heavily on her own competitive efforts.

Data from the Standard Cross-Cultural Sample of 186 societies (Murdock and White 1969) support this claim while also underscoring the large variation that exists. Women's contribution to subsistence in this sample averages 34% (SD 15.3), but in five societies women contribute <10%, while in another five, they contribute 70% or more (data from White 1986). In 83% of societies, women have the sole or predominant say in determining how their economic contribution gets used or distributed, and in 23% of societies they also have at least equal control over the economic contributions of men (data from Whyte 1978, 1995). Women are also political actors who can contribute to the welfare of their children in a variety of ways, including arranging favorable marriages for them; in 45% of societies, their influence in this area is at least equal to that of men (data from Whyte 1978, 1995). Their direct role in politics is usually small, but in 57% of societies, women have at least informal influence in political affairs (data from Sanday 1985). For women in many societies, therefore, successful competition for material resources for themselves and their children is probably at least as important as is competition for male attention, and selection can be expected to respond to both.

Conditions are difficult and stressful for many women, food is often scarce, and work requires much physical effort. In order to perform well under such circumstances, women need physical strength, energy, and assertiveness. These are facilitated by the same hormones (cortisol and androgens) that raise the WHR.

Hormonal Effects on WHR and Behavior

Cortisol Effects

Cortisol helps the body respond to stress by shifting energy substrates from storage sites to the bloodstream, by increasing blood pressure and cardiac output, and by preparing the body for future stressful challenges (Sapolsky et al. 2000). As part of this response, cortisol increases WHR by increasing visceral fat. This change in fat distribution is seen most dramatically in people exposed to very high hormone levels (through Cushing's syndrome or exogenous corticosteroids) but is also seen in people exposed to high levels of stress. High-WHR women report less social support (Wing et al. 1991), report more chronic stress, and respond to a stressful situation with greater cortisol reactivity than do low-WHR women (Marin et al.1992; Epel et al. 2000). This stress response in women with high WHR may be maladaptive under normal circumstances, yet it could be adaptive where conditions are extreme or where stress is episodic rather than constant. Visceral fat cells are highly responsive to cortisol (Björntorp 1996) and have a stronger lipolytic response to catecholamines than subcutaneous fat, especially fat in the hip and thigh area (Wajchenberg 2000). This is consistent with the finding of a shorter half-life of glucose in abdominal than in femoral fat cells (Marin et al. 1987). The accumulation of visceral fat under stress, therefore, is likely to be adaptive in stressful, dangerous environments and in environments where food abundance is variable.

Androgen Effects

Like cortisol, androgens are associated with high WHR in women. Exogenous androgens increase visceral fat in women (Elbers et al. 1997), and women with high WHRs have more free testosterone (Evans et al. 1983; van Anders and Hampson 2005) and less sex hormone–binding globulin (SHBG; Santoro et al. 2005), the protein that binds to testosterone and keeps it biologically inactive.

The behavioral effects of androgens in women are similar to those described for men. Women with high androgen levels are more likely to describe themselves as action oriented, resourceful, controlling, and powerful (Baucom et al. 1985; Grant and France 2001) and to be more career oriented, with higher-status jobs (Purifoy and Koopmans 1979; Udry et al. 1995). Data on aggression are mixed, but some studies show high-androgen women to be more aggressive by self-report (Harris et al. 1996; van der Pahlen et al. 2002) and, in prison populations, by behavioral measures as well (Dabbs and Hargrove 1997). I found women high in androgens to be more prone to act on their competitive feelings, through verbal aggression and other means (Cashdan 2003), and more likely to overstate their rank in a status hierarchy (Cashdan 1995).

Experimental studies with exogenous androgens support the conclusions from correlational studies. A single administration of testosterone to healthy young women made them more responsive to angry faces (van Honk et al. 2001) and caused them to be more risk prone in a simulated gambling game (van Honk et al. 2004). When the adrenal androgen dehydroepiandrosterone (DHEA) was given to women low in androgen, their testosterone and androstenedione levels rose, and they reported having more stamina, alertness, initiative, and "[got] more done" (Johannsson et al. 2002). A low ratio of second- to fourth-finger length, now usually interpreted as an index of prenatal androgen exposure, is associated with assertiveness, competitiveness (Wilson 1983), and dominance (Manning and Fink 2008) in women, another indication that androgens have a causal role in these relationships. This suite of androgenic effects—stamina, initiative, risk proneness, assertiveness, dominance—should be especially useful when a woman must depend on her own resources to support herself and her children.

Is It Facultative?

If, as suggested, there is a hormonal trade-off between optimal fecundity and the toughness required to acquire and compete for material resources, we might expect the optimum to vary with circumstances. In societies where women are expected to provide most of the food, through hard physical work and in difficult environmental conditions, the balance should be tipped toward a hormonal profile consistent with a high WHR. In more benign conditions, where women are sedentary and get most of their resources from investing men, a hormonal profile consistent with a low WHR might be more adaptive. An evolved adaptation of this sort could be either obligate (if conditions remained the same for long enough) or facultative.

It is clearly not all facultative. Most heritability estimates for body shape are on the order of 40%–70%, with the higher values for central fat measures and lower ones for WHR (see, e.g., Schousboe et al. 2004 and references therein). However, the steroid hormones that shape WHR (estrogens, androgens, cortisol) are also highly sensitive to environmental conditions, which suggests that some of the variation in WHR is likely to be facultative.

Cortisol: Environmental Influences

As noted above, cortisol is secreted in direct response to stress. It helps the body cope with stress by suppressing less immediate requirements (growth, energy storage, reproduction) and mobilizing resources for immediate challenges. A cortisol response has been documented in women following a wide range of stressors, including surgery (Batrinos et al. 1999), athletic competition (Bateup et al. 2002; Kivlighan et al. 2005), cognitively demanding tasks (Bremner et al. 2003), and sustained exercise, especially in the heat (Brenner et al. 1998). In short, cortisol secretion responds to, and helps women cope with, the serious stressors of daily life.

Estrogen: Environmental Influences

Estrogen decreases WHR directly by increasing fat storage in the hip and thigh area and increasing lipolysis in abdominal fat (Rebuffé-Scrive 1986). Estrogen also decreases WHR indirectly by mitigating the effects of androgens through an increase in SHBG, which keeps more of the circulating androgen protein bound and unavailable to the tissues. Lower estrogen levels, therefore, shift body shape and behavior in an androgenic direction.

The facultative nature of this machinery lies in the responsiveness of estrogen to environmental constraints. Estrogen levels drop under conditions of negative energy balance, physical activity, and stress (Jasieńska and Ellison 1998; Ellison 2001; Jasieńska et al. 2006). These are circumstances that would favor deferring fertility (if the conditions were transient) in favor of enhanced ability to work, compete, and mobilize energetic resources for immediate challenges. The direct effects of estrogen regulate the former; the indirect effects (on androgens via SHBG) facilitate the latter.

Adrenal Androgens: Environmental Influences

Androgens in women also respond to stress. Much of a woman's circulating androgens arise directly or indirectly from adrenal androgens, and these, like cortisol, respond to stress-induced secretions of ACTH (Parker 1991; McKenna et al. 1997). Androgens in women have been shown to rise in response to a variety of stressors, including surgery (Batrinos et al. 1999), cognitive tasks (Boudarene et al. 2002), and endurance exercise such as running and cycling (Webb et al. 1984; Keizeret al. 1987; Copeland et al. 2002). Testosterone levels in women exposed to chronic marital stress are higher than in women in stable marriages (Powell et al. 2002), which suggests that adrenal androgens can also be increased by psychosocial stress. There is, however, little evidence to support the existence in women of a testosterone response to competition per se, as is found in males of several species, including humans (see CA+ online suppl. C for discussion).

The evidence, taken together, suggests that adrenal androgens respond facultatively to a variety of psychosocial, cognitive, and physical challenges and that this response enhances a woman's strength, assertiveness, and competitive aggression. The same hormonal stress response (through increased cortisol and, in women, testosterone) is involved in the association between stress and abdominal fat (Björntorp 2001).

Explaining Variation in WHR

Effects of Age and Parity

A woman's WHR is lowest in her early 20s, after which it typically increases throughout her life span. Figure 1 shows the age change in a probability sample of Korean women. The population is lean, but it nonetheless shows a marked increase in WHR, from a low of about 0.79 to a high of nearly 0.9, before decreasing at the oldest ages. An increase in WHR with age has also been found in the Hadza (Marlowe et al. 2005) and Mongolian nomads (Beall and Goldstein 1992).

At least some of this change is associated with age changes in hormone levels: menopause is associated both with decreased hip circumference (Björkelund 1996) and increased intra-abdominal fat (Tchernof et al. 2000; Toth et al. 2000). The metabolic differences between gluteofemoral fat cells and abdominal fat cells, which are responsible for the gynoid pattern of fat distribution in younger women, disappear after menopause (Rebuffé-Scrive et al. 1986). Declining levels of progesterone prior to menopause may also play a role, since this hormone facilitates accumulation of fat in the hip and thigh area (Björntorp 1987).

These hormonal changes, and the change in WHR, mirror the shift from reproduction to child care in a woman's life. At an ultimate level, therefore, the shift from a gynoid to an android shape may reflect this shift in priorities.

Parity has an independent effect on WHR (Rodrigues and Da Costa 2001; Lassek and Gaulin 2006) and may reflect the same trade-off. The fat that adolescent females deposit on the hips and thighs is less metabolically active than is central fat and is resistant to weight loss except during late pregnancy and lactation (Rebuffé-Scrive et al.1985). Lassek and Gaulin (2006) argue that because this fat is especially rich in long-chain polyunsaturated fatty acids important in infant brain growth, it is a scarce maternal resource that becomes increasingly depleted with each pregnancy. Their data show that with each live birth, hip and thigh circumference decreases by 0.5 cm, while waist circumference increases by the same amount.

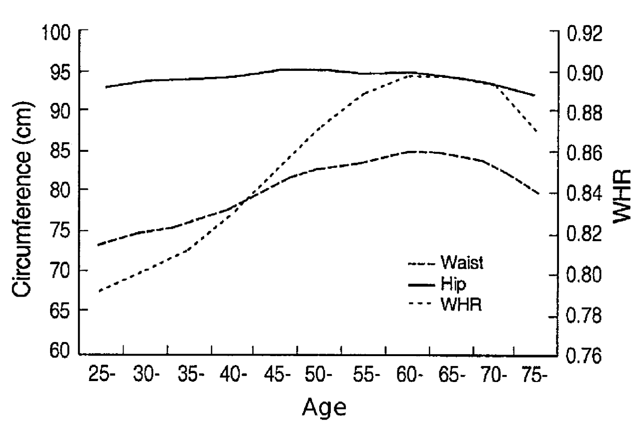

Figure 1. Age change in waist and hip circumference among Korean women. Reproduced from Kim et al. (2004).

It is interesting that fat gained during adolescence is directed toward the hips and thighs, whereas fat gained between births is instead preferentially allocated to the waist. This suggests not only the increasing depletion of a limiting resource but the reallocation of fat reserves from those needed for new births toward more readily metabolizable depots important in maintaining a woman's own energy balance.

The effect of age on WHR typically is taken for granted; when age appears in studies of WHR, it is usually so the author can control for its effects when studying another variable of interest. The suggestion made here is that the increase in WHR with age calls for explanation and that it may reflect the same trade-offs between fertility and competitive ability discussed earlier, but in the context of intertemporal life-history choices.

Population Differences

If variation in female WHR is adaptive for the reasons given here, we would expect higher WHR among women who must depend on their own hard work to provision children, particularly in difficult environments, and lower WHR where women gain resources by attracting investing men. Male preferences might shift accordingly. Available evidence is limited but consistent with this expectation.

Among Shiawar forager/horticulturalists (Sugiyama 2004) and Hadza foragers (Wetsman and Marlowe 1986; Marlowe and Wetsman 2001), men's preferences are determined less by WHR than by a concern that the woman not be thin. Traditional Matsigenka horticulturalists (Yu and Shepard 1998) and South African Zulu men (Tovée et al. 2006) prefer not only large women but a high WHR. These are societies where getting enough food is a challenge, and it is a woman's job to meet it. In Western societies, women under resource stress (unemployed or facing problems at work) have larger WHR, independent of BMI (Rosmond and Bjőrntorp 1999). Men apparently find this shape more attractive during difficult times: in an analysis of secular changes (1960–2000) in Playboy models, Pettijohn and Jungeborg (2004) found that during periods of economic and social hard times, the waist circumference and WHR of the models increased.

The importance men place on low WHR appears to vary with sex roles, with men in less sexually egalitarian societies, such as Greece (Swami et al. 2006*a*), Japan (Swami 2006*b*), and Portugal (Furnham and Nordling 1998), placing a greater value on low WHR than do men in Britain or Denmark, where women are economically and socially more independent. Although there are different ways of interpreting these results, they are consistent with the argument that higher WHR is adaptive in societies where women must get resources through their direct productive work rather than through investing males and that male preferences may reflect this adaptive shift. Women's mate preferences are related to their own WHR in an analogous way: high-WHR women are less concerned that their mates have resources and more concerned that they be attractive (Pawlowski and Jasieńska 2008), which is what we would expect if high-WHR women do not expect (or need) as much male investment.

Conclusions

This paper has documented and suggested an explanation for three observations: (*a*) most women have a larger WHR than would seem to be optimal, (*b*) there is a lot of variation in the trait, which may reflect environmental conditions, and (*c*) WHR in women rises with age and parity. Taken together, the data suggest that high cortisol and androgen/estrogen ratios in women enable them to respond adaptively to environmental and situational challenges, even though this hormonal profile, with its associated high WHR, also has fitness costs. Similar trade-offs between dominance and fertility have been reported for female baboons (Packer et al. 1995; but see Altmann et al. 1995) and male military officers (Mueller and Mazur 1998).

Waist-to-hip ratio may indeed be a useful signal to men, then, but whether men prefer a WHR associated with lower or higher androgen/estrogen ratios (or value them equally) should depend on the degree to which they want their mates to be strong, tough, economically successful, and politically competitive. And from a woman's perspective, men's preferences are not the only thing that matters.

Acknowledgments

This paper benefited from discussions with many people, including Peter Gray, Frank Marlowe, Alan Rogers, Emily Stone, Mercedes Ward, Dan Williams, and participants at the 2004 Hanse Institute for Advanced Study conference "Sex, Brain, and Human Aggression." I am grateful to Larry Sugiyama for compiling unpublished data on the Shiawar and permitting me to use it in this paper.

References Cited

Altmann, J., R. Sapolsky, and P. Licht. 1995. Baboon fertility and social status. *Nature* 377:688–89.

Bateup, H. S., A. Booth, E. A. Shirtcliff, and D. A. Granger. 2002. Testosterone, cortisol, and women's competition. *Evolution and Human Behavior* 23:181–92.

Batrinos, M. L., C. Panitsa-Faflia, C. Koutsoumanis, T. Vourlioti, and M. Koutsilieris. 1999. Surgical stress induces a marked and sustained increase of adrenal androgen secretion in postmenopausal women. *In Vivo* 13:147–50.

Baucom, D. H., P. K. Besch, and S. Callahan. 1985. Relation between testosterone concentration, sex role identity, and personality among females. *Journal of Personality and Social Psychology* 48:1218–26.

Beall, C. M., and M. C. Goldstein. 1992. High prevalence of excess fat and central patterning among Mongolian pastoral nomads. *American Journal of Human Biology* 4:747–56.

Björkelund C., L. Lissner, S. Andersson, L. Lapidus, and C. Bengtsson. 1996. Reproductive history in relation to relative weight and fat distribution. *International Journal of Obesity and Related Metabolic Disorders* 20:213–19.

Björntorp, P. 1996. The regulation of adipose tissue distribution in humans. *International Journal of Obesity and Related Metabolic Disorders* 20:291–302.

———. 1987. Fat cell distribution and metabolism. *Annals of the New York Academy of Sciences* 499:66–72.

———. 2001. Do stress reactions cause abdominal obesity and comorbidities? *Obesity Reviews* 2:73–86.

Boudarene, M., J. J. Legros, and M. Timsit-Berthier. 2002. Study of the stress response: Role of anxiety, cortisol and DHEAs. *Encephale* 28:139–46.

Bremner, J. D., M. E. Vythilingam, E. Vermetten, J. Adil, S. Khan, A. Nazeer, N. Afzal, T. McGlashan, B. Elzinga, G. M. Anderson, et al. 2003. Cortisol response to a cognitive stress challenge in posttraumatic stress disorder (PTSD) related to childhood abuse. *Psychoneuroendocrinology* 28: 733–50.

Brenner, I., P. N. Shek, J. Zamecnik, and R. J. Shephard. 1998. Stress hormones and the immunological responses to heat and exercise. *International Journal of Sports Medicine* 19: 130–43.

Cashdan, E. 1995. Hormones, sex, and status in women. *Hormones and Behavior* 29:354–66.

———. 2003. Hormones and competitive aggression in women. *Aggressive Behavior* 29:107–15.

Copeland, J. L., L. A. Consitt, and M. S. Tremblay. 2002. Hormonal responses to endurance and resistance exercise in females aged 19–69 years. *Journal of Gerontology: Biological Sciences* 57A:B158–65.

Dabbs, J. M., Jr., and M. F. Hargrove. 1997. Age, testosterone, and behavior among female prison inmates. *Psychosomatic Medicine* 59:477–80.

Deurenberg-Yap, M., T. B. Yian, C. S. Kai, P. Deurenberg, and W. A. Van Staveren. 1999. Manifestation of cardiovascular risk factors at low levels of body mass index and waist-to-hip ratio in Singaporean Chinese. *Asia Pacific Journal of Clinical Nutrition* 8:177–83.

Elbers, J. M. H., H. Asscheman, J. C. Seidell, J. A. J. Megens, and L. J. G. Gooren. 1997. Long-term testosterone administration increases visceral fat in female to male transsexuals. *Journal of Clinical Endocrinology and Metabolism* 82: 2044–47.

Ellison, P. T. 2001. *On Fertile Ground.* Cambridge, MA: Harvard University Press.

Epel, E. S., B. McEwen, T. Seeman, K. Matthews, G. Castellazzo, K. D. Brownell, J. Bell, and J. R. Ickovics. 2000. Stress and body shape: Stress-induced cortisol secretion is consistently greater among women with central fat. *Psychosomatic Medicine* 62:623–32.

Evans, D. J., R. G. Hoffmann, R. K. Kalkhoff, and A. H. Kissebah. 1983. Relationship of androgenic activity to body fat topography, fat cell morphology, and metabolic aberrations in premenopausal women. *Journal of Clinical Endocrinology and Metabolism* 57:304–10.

Furnham, A., A. McClelland, and L. Omer. 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* 8:219–30.

Furnham, A., and R. Nordling. 1998. Cross-cultural differences in preferences for specific male and female body shapes. *Personality and Individual Differences* 25:635–48.

Grant, V. J., and J. T. France. 2001. Dominance and testosterone in women. *Biological Psychology* 58:41–47.

Harris, J. A., J. P. Rushton, E. Hampson, and D. N. Jackson. 1996. Salivary testosterone and self-report aggressive and pro-social personality characteristics in men and women. *Aggressive Behavior* 22:321–31.

Hartz, A. J., D. C. Rupley, and A. A. Rimm. 1984. The association of girth measurements with disease in 32,856 women. *American Journal of Epidemiology* 119:71–80.

Henss, R. 2000. Waist-to-hip ratio and female attractiveness: Evidence from photographic stimuli and methodological considerations. *Personality and Individual Differences* 28: 501–13.

Jasieńska, G., and P. T. Ellison. 1998. Physical work causes suppression of ovarian function in women. *Proceedings of the Royal Society of London: Biological Sciences* 265:1847–51.

Jasieńska, G., A. Ziomkiewicz, P. T. Ellison, and S. F. Lipson. 2004. Large breasts and narrow waists indicate high reproductive potential in women. *Proceedings of the Royal Society of London: Biological Sciences* 271:1213–17.

Jasieńska, G., A. Ziomkiewicz, I. Thune, S. F. Lipson, and P. T. Ellison. 2006. Habitual physical activity and estradiol levels in women of reproductive age. *European Journal of Cancer Prevention* 15:439–45.

Johannsson, G., P. Burman, L. Wiré, B. E. Engström, A. G. Nilsson, M. Ottosson, B. Jonsson, B. Bengtsson, and F. A. Karlsson. 2002. Low dose dehydroepiandrosterone affects behavior in hypopituitary androgen-deficient women: A placebo-controlled trial. *Journal of Clinical Endocrinology and Metabolism* 87:2046–52.

Keizer, H. A., H. Kuipers, J. De Haan, E. Beckers, and L. Habets. 1987. Multiple hormonal responses to physical exercise in eumenorrheic trained and untrained women. *International Journal of Sports Medicine* 8:139–50.

Kim, M. H., M. K. Kim, B. Y. Choi, and Y. J. Shin. 2004. Prevalence of the metabolic syndrome and its association with cardiovascular diseases in Korea. *Journal of Korean Medical Science* 19:195–201.

Kirchengast, S., and J. Huber. 2004. Body composition characteristics and fat distribution patterns in young infertile women. *Fertility and Sterility* 81:539–44.

Kivlighan, K. T., D. A. Granger, and A. Booth. 2005. Gender differences in testosterone and cortisol response to competition. *Psychoneuroendocrinology* 30:58–71.

Lassek, W. D., and S. J. C. Gaulin. 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.

———. 2008. Waist-hip ratio and cognitive ability: Is gluteofemoral fat a privileged store of neurodevelopmental resources? *Evolution and Human Behavior* 29:26–34.

Lee, C. M. Y., R. Huxley, R. Wildman, and M. Woodward. 2008. Indices of abdominal obesity are better discriminators of cardiovascular risk factors than BMI: A meta-analysis. *Journal of Clinical Epidemiology* 61:646–53.

Manning, J. T., and B. Fink. 2008. Digit ratio (2D : 4D), dominance, reproductive success, asymmetry, and sociosexuality in the BBC Internet study. *American Journal of Human Biology* 20:451–61.

Marin, P., N. Darin, T. Amemiya, B. Andersson, S. Jern, and P. Björntorp. 1992. Cortisol secretion in relation to body fat distribution in obese premenopausal women. *Metabolism* 41:882–86.

Marin, P., M. Rebuffé-Scrive, and P. Björntorp. 1987. Glucose uptake in human adipose tissue. *Metabolism* 36:1154–60.

Marlowe, F., C. Apicella, and D. Reed. 2005. Men's preferences for women's profile waist-to-hip ratio in two societies. *Evolution and Human Behavior* 26:458–68.

Marlowe, F., and A. Wetsman. 2001. Preferred waist-to-hip ratio and ecology. *Personality and Individual Differences* 30: 481–89.

McKenna, T. J., U. Fearon, D. Clarke and S. K. Cunningham. 1997. A critical review of the origin and control of adrenal androgens. *Bailliere's Clinical Obstetrics and Gynaecology* 11: 229–48.

Molarius, A., J. C. Seidell, S. Sans, J. Tuomilehto, and K. Kuulasmaa. 1999. Waist and hip circumferences, and waist-hip ratio in 19 populations of the WHO MONICA Project. *International Journal of Obesity and Related Metabolic Disorders* 23:116–25.

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

Mueller, U., and A. Mazur. 1998. Reproductive constraints on dominance competition in male *Homo Sapiens*. *Evolution and Human Behavior* 19:387–96.

Murdock, G. P., and D. R. White. 1969. Standard cross-cultural sample. *Ethnology* 8:329–69.

Packer, C., D. A. Collins, A. Sindimwo, and J. Goodall. 1995. Reproductive constraints on aggressive competition in female baboons. *Nature* 373:60–63.

Parker, L. N. 1991. Control of adrenal androgen secretion. *Endocrinology and Metabolism Clinics of North America* 20: 401–21.

Pawlowski, B., and G. Jasieńska. 2008. Women's body morphology and preferences for sexual partners' characteristics. *Evolution and Human Behavior* 29:19–25.

Pettijohn, T. F., and B. J. Jungeberg. 2004. Playboy playmate curves: Changes in facial and body feature preferences across social and economic conditions. *Personality and Social Psychology Bulletin* 30:1186–97.

Powell, L. H., W. R. Lovallo, K. A. Matthews, P. Meyer, A. K. Midgley, A. Baum, A. A. Stone, L. Underwood, J. J. McCann, K. J. Herr, et al. 2002. Physiological markers of chronic stress in premenopausal, middle-aged women. *Psychosomatic Medicine* 64:502–9.

Purifoy, F., and L. Koopmans. 1979. Androstenedione, testosterone, and free testosterone concentration in women of various occupations. *Social Biology* 26:179–88.

Rebuffé-Scrive, M., J. Eldh, L. O. Hafström, and P. Björntorp. 1986. Metabolism of mammary, abdominal, and femoral adipocytes in women before and after menopause. *Metabolism* 35:792–97.

Rebuffé-Scrive, M., E. Lennart, N. Crona, P. Lönnroth, L. Abrahamsson, U. Smith, and P. Björntorp. 1985. Fat cell metabolism in different regions in women. *Journal of Clinical Investigation* 75:1973–76.

Rodrigues, M. L. C. F., and T. H. M. Da Costa. 2001. Association of the maternal experience and changes in adiposity measured by BMI, waist : hip ratio and percentage body fat in urban Brazilian women. *British Journal of Nutrition* 85: 107–14.

Rosmond, R., and P. Björntorp. 1999. Psychosocial and socioeconomic factors in women and their relationship to obesity and regional body fat distribution. *International Journal of Obesity and Related Metabolic Disorders* 23:138–45.

Sanday, P. 1985. Female power and male dominance. *World Cultures* 1(4).

Santoro, N., J. Torrens, S. Crawford, J. E. Allsworth, J. S. Finkelstein, E. B. Gold, S. Korenman, W. L. Lasley J. L. Luborsky, D. McConnell, et al. 2005. Correlates of circulating androgens in mid-life women: The study of women's health across the nation. *Journal of Clinical Endocrinology and Metabolism* 90:4836–45.

Sapolsky, R. M., L. M. Romero, and A. U. Munck. 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews* 21:55–89.

Schousboe, K., P. M. Visscher, B. Erbas, K. O. Kyvik, J. L. Hopper, J. E. Hennriksen, B. L. Heitmann, and T. I. A. Sorensen. 2004. Twin study of genetic and environmental influences on adult body size, shape, and composition. *International Journal of Obesity* 28:39–48.

Singh, D., and S. Luis. 1995. Ethnic and gender consensus for the effect of waist-to-hip ratio on judgment of women's attractiveness. *Human Nature* 6:51–65.

Sonnenschein, E., P. Toniolo, M. B. Terry, P. F. Bruning, I. Kato, K. L. Koenig, and R. E. Shore. 1999. Body fat distribution and obesity in pre- and postmenopausal breast cancer. *International Journal of Epidemiology* 28:1026–31.

Streeter, S. A., and D. H. McBurney. 2003. Waist-hip ratio and attractiveness: New evidence and a critique of a "critical test." *Evolution and Human Behavior* 24:88–98.

Sugiyama, S. L. 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.

Swami, V., N. Antonakopoulos, M. J. Tovée, and A. Furnham. 2006*a*. A critical test of the waist-to-hip ratio hypothesis of women's physical attractiveness in Britain and Greece. *Sex Roles* 54:201–11.

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

Tchernof, A., E. T. Poehlman, and J. P. Després. 2000. Body fat distribution, the menopause transition, and hormone replacement therapy. *Diabetes and Metabolism* 26:12–20.

Toth, M. J., A. Tchernof, C. K. Sites, and E. T. Poehlman. 2000. Menopause-related changes in body fat distribution. *Annals of the New York Academy of Sciences* 904:502–6.

Tovée, M. J., J. E. Brown, and D. Jacobs. 2001. Maternal waist-to-hip ratio does not predict child gender. *Proceedings of the Royal Society of London: Biological Sciences* 268: 10070–11010.

Tovée, M. J., V. Swami, A. Furnham, and R. Mangalparsad. 2006. Changing perceptions of attractiveness as observers are exposed to a different culture. *Evolution and Human Behavior* 27:443–56.

Udry, J. R., N. M. Morris, and J. Kovenock. 1995. Androgen effects on women's gendered behaviour. *Journal of Biosocial Science* 27:359–68.

Van Anders, S. M., and E. Hampson. 2005. Waist-to-hip ratio is positively associated with bioavailable testosterone but negatively associated with sexual desire in healthy premenopausal women. *Psychosomatic Medicine* 67:246–50.

Van Honk, J., D. J. L. G. Schutter, E. J. Hermans, P. Putman, A. Tuiten, and H. Koppeschaar. 2004. Testosterone shifts the balance between sensitivity for punishment and reward in healthy young women. *Psychoneuroendocrinology* 29: 937–43.

Van Honk, J., A. Tuiten, E. Hermans, P. Putman, H. Koppeschaar, J. Thijssen, R. Verbaten, and L. Van Doornen. 2001. A single administration of testosterone induces cardiac accelerative responses to angry faces in healthy young women. *Behavioral Neuroscience* 115:238–42.

Von der Pahlen, B., R. Lindman, T. Sarkola, H. Mäkisalo, and C. J. P. Eriksson. 2002. An exploratory study on self-evaluated aggression and androgens in women. *Aggressive Behavior* 28:273–80.

Wajchenberg, B. L. 2000. Subcutaneous and visceral adipose tissue: Their relation to the metabolic syndrome. *Endocrine Reviews* 21:697–738.

Wass, P., U. Waldenstrom, S. Rossner, and D. Hellbert. 1997. An android body fat distribution in females impairs the pregnancy rate of in-vitro fertilization-embryo transfer. *Human Reproduction* 12:2057–60.

Webb, M. L., J. P. Wallace, C. Hamill, J. L. Hodgson, and M. M. Mashaly. 1984. Serum testosterone concentration during two hours of moderate intensity treadmill running in trained men and women. *Endocrine Research* 10:27–38.

Wetsman, A., and F. Marlowe. 1986. How universal are preferences for female waist-to-hip ratios? Evidence from the Hadza of Tanzania. *Evolution and Human Behavior* 20: 219–28.

White, D. R. 1986. Female subsistence contribution: Measures and reliabilities. *World Cultures* 2(3).

Whyte, M. K. 1978. Cross-cultural codes dealing with the relative status of women. *Ethnology* 17:211–37.

———. 1995. Status of women in preindustrial societies. *World Cultures* 1(4).

Wilson, Glenn D. 1983. Finger-length as an index of assertiveness in women. *Personality and Individual Differences* 4:111–12.

Wing, R. R., K. A. Matthews, L. H. Kuller, E. N. Meilahn, and P. Planting. 1991. Waist to hip ratio in middle-aged women: Associations with behavioral and psychosocial factors and with changes in cardiovascular risk factors. *Arteriosclerosis and Thrombosis* 11:1250–57.

Yamamoto, S., T. Douchi, N. Yoshimitsu, M. Nakae, and Y. Nagata. 2001. Waist to hip circumference ratio as a significant predictor of preeclampsia, irrespective of overall adiposity. *Journal of Obstetric and Gynaecological Research* 27:27–31.

Yu, D. W., and G. H. Shepard. 1998. Is beauty in the eye of the beholder? *Nature* 396:321–22.

Zaadstra, B. M., J. C. Seidell, P. A. H. Van Noord, E. R. Te Velde, J. D. F. Habbema, B. Vrieswijk, and J. Karbaat. 1993. Fat and female fecundity: Prospective study of effect of body fat distribution on conception rates. *British Medical Journal* 306:484–87.

Zhang, X., X. O. Shu, Y.-T. Gao, G. Yang, C. E. Matthews, Q. Li, H. Li, F. Jim, and W. Zheng. 2004. Anthropometric predictors of coronary heart disease in Chinese women. *International Journal of Obesity* 28:734–40.