

Male Preferences for Female Waist-to-hip Ratio and Body Mass Index in the Highlands of Papua New Guinea

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ABSTRACT One hundred men, living in three villages in a remote region of the Eastern Highlands of Papua New Guinea were asked to judge the attractiveness of photographs of women who had undergone micrograft surgery to reduce their waist-to-hip ratios (WHRs). Micrograft surgery involves harvesting adipose tissue from the waist and reshaping the buttocks to produce a low WHR and an “hourglass” female figure. Men consistently chose postoperative photographs as being more attractive than preop-

erative photographs of the same women. Some women gained, and some lost weight, postoperatively, with resultant changes in body mass index (BMI). However, changes in BMI were not related to men’s judgments of attractiveness. These results show that the hourglass female figure is rated as attractive by men living in a remote, indigenous community, and that when controlling for BMI, WHR plays a crucial role in their attractiveness judgments. *Am J Phys Anthropol* 000:000–000, 2010. ©2009 Wiley-Liss, Inc.

While men are somewhat larger than women in body size, human beings show greater sexual dimorphism in muscularity and body fat (Carter and Heath, 1990). Women typically have a higher percentage of body fat than men (Clarys et al., 1984). This sex difference emerges at puberty, with increased levels of body fat being laid down in the hips, thighs, buttocks (the gluteal/femoral region), and breasts (Merzenich et al., 1993; Boot et al., 1997). The distribution of female body fat can be measured using the waist-to-hip ratio (WHR), which is calculated by dividing the circumference of the waist by the circumference of the hips and buttocks. A variety of factors may have determined the distribution of female body fat. Natural selection, in relation to biomechanical and thermoregulatory constraints, may have favored greater deposition of fat in certain areas of body (Cant, 1981; Pawlowski, 2001; Dixson, 2009). The evolution of upright gait and bipedalism as the principle mode of locomotion, coupled with the fact that women must be mobile during pregnancy, may have driven a low Center of Body mass in women, which correlates with low WHR (Pawlowski and Grabarczyk, 2003).

A low WHR of ~0.7 has been linked to the timing of menarche (Lassek and Gaulin, 2007), maintaining regular menstrual cycles (Van Hooff et al., 2000) and ovulatory cycles (Moran et al., 1999). In a sample of 119 Polish women, women with lower WHRs and larger breast volumes have been shown to have higher circulating levels of 17- β -estradiol and progesterone (Jasienska et al., 2004), which are predictors of the probability of conception (Lipson and Ellison, 1996). In studies conducted in fertility clinics, women with lower WHRs had higher success rates in artificial insemination (Zaadstra et al., 1993) and in *in vitro* fertilization programs (Wass et al., 1997). Women’s WHRs increase as they age, possibly due to reduction in estrogen production (Kirschner and Samojlik, 1991). The “hourglass” female body constitution may therefore signal health and reproductive status.

It has been suggested that human morphology that conveys biological information relating to health and

fertility was important in mate selection in ancestral environments (Barber, 1995; Symons, 1995; Thornhill and Gangestad, 1996). Although these claims cannot be directly tested in modern day human societies, it has been proposed that selection has shaped human psychological faculties to attend to morphological features that honestly signal health and reproductive status (Buss, 2003; Grammer et al., 2003).

Sexual selection via male partner preference may have driven the evolution of low WHR in women (Singh, 2006). Men rate stimulus images with low WHRs of 0.6 as most attractive for both short- and long-term relationships in North America (Dixson et al., *in press*) and China (Dixson et al., 2007a). Images of women with low WHRs of 0.6–0.7 are also attractive to men from Germany (Henss, 2000), England (Furnham et al., 1997), Poland (Rozmus-Wrzesinska and Pawlowski, 2005), and in New Zealand, where a female WHR of 0.7 was rated as most attractive by men when considering both short- and long-term relationships (Dixson et al., *in press*).

Adaptive claims for sexual preferences for traits such as female WHR are difficult to validate in the absence of such cross-cultural support. However, several studies in less industrialized cultures have questioned whether a low female WHR of 0.7 is universally attractive to men. For example, among the Shiwiar of the Ecuadorian Upper Amazon, men selected images of women with a high body weight as most attractive (Sugiyama, 2004). However, when controlling for body weight images with lower WHRs of 0.7 and 0.8 were selected as most attrac-

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tive (Sugiyama, 2004). Among the Matsigenka of Peru, a WHR of 0.9 was most attractive (Yu and Shepard, 1998). In Bakossiland, a community of subsistence farmers in rural Southwest Cameroon, a WHR of 0.8 was most attractive for both short- and long-term relationships (Dixson et al., 2007b). Initial studies among the Hadza hunter-gatherers of Tanzania found that a WHR of 0.9 was more attractive to Hadza men (Wetsman and Marlowe, 1999). However, in a follow-up study using images in profile view in which the buttocks were visible, Hadza men preferred a WHR of 0.6 (Marlowe et al., 2005). Therefore, the angle of the body pose may contribute to the differing male preferences across these cultures for female images varying in WHR.

Disconcordance in male preferences for images varying in WHR could also be due to the use of stimulus line drawings that confound the effects of WHR on female body mass index (BMI) (Tovée and Cornelissen, 2001). BMI is calculated as weight in kilograms divided by (height in meters \times height in meters). Women with a BMI of 20 are more attractive to men in the UK (Tovée et al., 1999). In a recent series of cross-cultural studies, differences in women's BMI were found to exert a greater influence than WHR on male ratings of female attractiveness in Japan (Swami et al., 2006), Malaysia (Swami and Tovée, 2005), and Zululand in South Africa (Tovée et al., 2006). These authors reject the WHR hypothesis based on the findings in these studies. However, there are some shortcomings in the study design that may have affected results. For example, in these studies men rated 50 images of women varying in BMI from 15 (emaciated) to over 30 (clinically obese). The ecological validity of these images is questionable, as men were asked to rate images that show women with a range of WHRs and BMIs that may not be typical of their daily experiences. It is, perhaps, not surprising that WHR becomes less important, if not irrelevant, when men are presented with images depicting emaciated and obese women. Therefore, as in research that uses line drawings, results in these studies may also have been affected by the nature of the stimuli employed to measure female attractiveness.

WHR and BMI are positively correlated and as such it is very difficult to test the individual contribution made by each of these traits to men's judgments of female attractiveness. A recently developed procedure called micrograft surgery provides such an opportunity, as in this procedure adipose tissue is harvested from the waist and used to re-shape the buttocks of female patients; this results in reduction of female WHR without altering BMI (Roberts et al., 2005; Singh and Randall, 2007). If female body fat distribution and body shape have been important in the evolution of male mate selection as a fundamental and perhaps ancient cue to health and fecundity, then postoperative images with lower WHRs should be more attractive than preoperative images of the same women. To test this hypothesis, 100 men from three remote villages in the Okapa district of the highlands of Papua New Guinea (PNG) completed a questionnaire in which they judged the attractiveness of photographs of women before and after micrograft surgery.

METHOD

Study site and participants

PNG is the eastern half of the island of New Guinea and has a population of 4.5 million people. The Okapa



Fig. 1. A map showing where the Okapa district is located on the Island of Papua New Guinea.

district is located in the Eastern Highlands Province of PNG (see Fig. 1). There are ~54,000 people living in the Okapa district. These people form five separate ethnic groups, as defined on linguistic grounds; Fore, Auyana, Kimi, Keagana, and Kanite. We conducted surveys among the Kanite, which is the language spoken by people who live north of the Wanevinti mountains. There are ~8,000 Kanite people living in the Okapa district. We interviewed a hundred Kanite men (mean age \pm s.d = 27.55 years \pm 8.365, range = 18–58 years) from three small villages; Kimiagomo, Yafanagomo, and Foseya. These villages are located in the Northern part of Okapa, the capital of the Okapa district. Participants completed questionnaires with the aid of one of the researchers (KS), who is from this region of PNG and is fluent in both English and Kanite. In this region, polygynous marriages can occur. Of the 100 men interviewed, 42% were unmarried, 48% were married to one wife, and 10% had two or more wives. Kimiagomo village has a population of 486; Yafanagomo village and Foseya village each have 200 residents. All three villages are extremely remote. These villages have no mains water supply, electricity, television, or land phone lines (although recently mobile phones can be used). There is a road from the provincial capital, Goroka to Kimiagomo village but it is rarely used as it can only be accessed by four-wheel drive vehicles. These villages are typical of the Highland regions of PNG, where all the residents are subsistence farmers who sustain their livelihood through tilling the land. Small plots of bush are slashed for gardening and planting coffee trees. The main income in these villages comes from selling coffee. The villages and the surrounding areas do not support large animals; therefore hunting is a rare activity.

Procedure

All the men were interviewed individually, either in their homes, at their farms, or in communal huts. Participants completed a questionnaire containing color photographs of 10 women who had undergone cosmetic micrograft surgery. Preoperative and postoperative photographs of the same patient were presented on a single page, but their positions (right or left) were randomized.

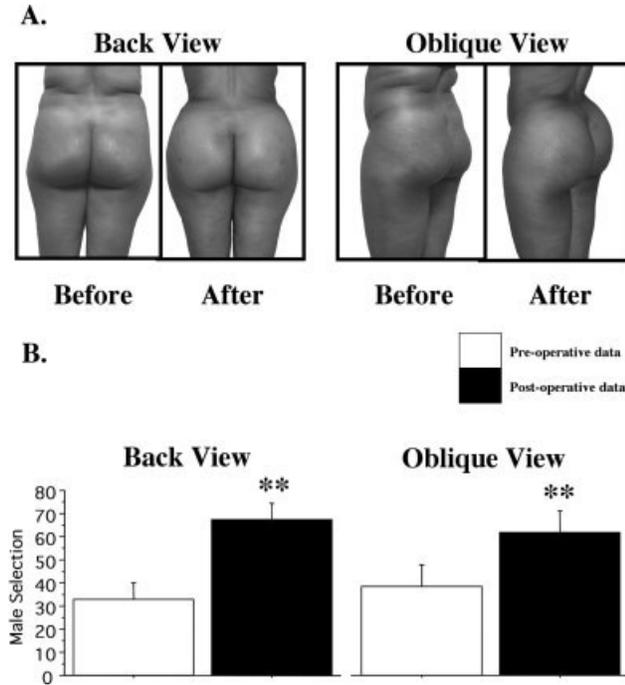


Fig. 2. (A) An example of a patient who has undergone micrograft surgery. Images show the same woman preoperatively and postoperatively, from back and oblique view. (B) Men's preferences for preoperative and postoperative female images in Papua New Guinea. Open histograms = preoperative data. Black histograms = postoperative data. Data are the mean number of subjects (+standard errors). ** $P < 0.01$.

Participants viewed each pair of images for 10 s and selected only the image they found most attractive. To examine possible effects of body pose on judgments of attractiveness, the photographs of patients before and after surgery were taken using back-posed and oblique views. Only the torso, including the waist, hips and buttocks, was shown in each photograph. Figure 2A shows examples of the images used in this study.

Preoperative and postoperative measurements were made of women's height and weight (in order to calculate BMI). WHRs were also measured in all subjects in a standardized way (Singh and Randall, 2007). All subjects were North American in origin and included five Caucasians and five African Americans or Hispanic Americans (As detailed in Table 1). Table 1 also shows the preoperative and postoperative WHR and BMI measurements of the women in this study. We selected five patients (Group A) whose BMIs had increased after surgery and five (Group B) who decreased in BMI after surgery. All women had significantly lower WHRs after surgery ($t = 7.364$, $df = 9$, $P < 0.001$), but group A had significantly higher postoperative BMI measures than group B ($t = 3.559$, $df = 4$, $P < 0.05$).

Statistical procedure

Wilcoxon Signed Rank tests were used to determine whether male preferences for preoperative or postoperative images were statistically significant. Mann-Whitney U tests were conducted to test whether selections for postoperative images were affected by increases (Group A) or decreases (Group B) in female BMI. Spearman

TABLE 1. Waist-to-hip ratio (WHR) and body mass index (BMI) measurements of micrograft patients before and after micrograft surgery

Patient No.	WHR		BMI		Patient ethnicity
	Pre-op	Post-op	Pre-op	Post-op	
Group A					
1	0.84	0.75	21.13	21.46	Caucasian
2	0.93	0.78	22.84	23.92	Caucasian
3	0.84	0.75	25.06	25.32	Hispanic
4	0.78	0.68	26.31	26.47	Caucasian
5	0.80	0.69	26.36	26.66	African American
Group B					
6	0.74	0.70	25.18	24.05	Caucasian
7	0.76	0.68	22.53	19.99	African American
8	0.78	0.74	23.71	21.44	Hispanic
9	0.77	0.71	25.74	23.51	Caucasian
10	0.80	0.75	21.95	20.82	African American
Mean	0.80	0.72	24.80	23.36	
SEM	0.01	0.01	0.60	0.748	

All patients have lower postoperative WHRs. Group A have higher postoperative BMI whereas in Group B, BMI decreased slightly.

Rank correlation coefficients were calculated in order to test for possible correlations between the magnitude of postoperative changes in female WHR and BMI and men's judgments of female attractiveness.

RESULTS

Figure 2B shows the number of men who selected either the preoperative or postoperative photographs of women. The postoperative images were chosen as significantly more attractive ($z = 3.461$, $P < .01$). There was also a significant effect of body pose on attractiveness judgments, so that more postoperative images were selected when images were presented in back views as opposed to oblique views ($z = 2.497$, $P < 0.01$).

We compared the preferences for the five women whose BMI increased postoperatively (Group A) to the five women who decreased in BMI postoperatively (Group B). Because of the significant differences between selection rates for back and oblique-posed images, these data were analyzed separately. A minimum U -value of 23 is required for significance at the 5% level. However, U -values were well below those required for significance for images in both back ($U = 11$) and oblique ($U = 11.5$) views. Thus, the changes in BMI after micrograft surgery did not affect selection rates for postoperative images.

The degree on men's preferences for postoperative images was not correlated with the magnitude of postoperative changes in female WHR (Back view: $z = 0.664$, $P = 0.507$; Oblique view: $z = 0.672$, $P = 0.531$) or BMI (Back view: $z = 0.945$, $P = 0.344$; Oblique view: $z = 1.145$, $P = 0.252$). To further examine possible fine-grained differences in the attractiveness of images, dependant upon the amount of postoperative changes in WHR and BMI, we compared a specific pair of images. Thus, patient 1 and patient 7 had very similar changes in WHR (0.09 and 0.08, respectively). However, patient 1 increased in BMI by 0.33 and patient 7 decreased in BMI by 2.54. Interestingly, men's choices of postoperative images of these women were very similar (patient 1 = 67/100 and patient 7 = 63/100). Chi-square tests revealed that selections for these images achieved the

same degree of statistical significance (patient 1: $\chi^2 = 5.78, P = < 0.05$; patient 7: $\chi^2 = 3.38, P = < 0.05$).

It is possible that the ethnicity of the subjects in the photographs might have influenced male selections. Five women were Caucasian and five were of African American or Hispanic descent. We compared men's selections of postoperative images of the five Caucasian women to their choices of the five women of African American or Hispanic descent. A minimum U -value of 23 would be required for significance at the 5% level. However, U -values were well below those required for significance, for images in both back ($U = 8.5$) and oblique ($U = 8.5$) views. Therefore, differences in ethnicity between the subjects in the photographs are unlikely to account for selection rates for postoperative images.

DISCUSSION

The current study tested whether body shape (WHR) affected male preferences for female physique when BMI was controlled for. Men from the highlands of PNG expressed a clear preference for a curvaceous hourglass-shaped female physique with low a WHR, irrespective of changes in BMI. Although these data do not provide definitive evidence, they are consistent with Singh's (1993) theory that male preferences for low female WHRs has evolved as an important "first pass filter" used in mate selection.

The role of WHR and BMI in determining female physical attractiveness has been heavily debated since Singh's (1993) publication. A large number of studies using line drawings have shown that a low WHR (0.7) is most attractive to men (For review see Singh, 2006). However, these studies have been criticized for presenting participants with unrealistic images and for confounding the effects of WHR and BMI, as the two traits are positively correlated (Tovée and Cornelissen, 2001).

A series of cross-cultural studies has been conducted in which photographs of women varying in BMI and WHR were rated for attractiveness (Swami and Tovée, 2005; Swami et al., 2006; Tovée et al., 2006). These studies have thrown the validity of the WHR hypothesis into contention, as the results were interpreted as showing that BMI is a greater predictor of female attractiveness than WHR. Tovée et al. (2006) have suggested that human mate preferences may be contextually specific to a given environment, with preferences for BMI changing when men move to new ecological settings. This was posited to be the case for Zulu men in South Africa who stated a greater preference for women with high BMIs (over 30), whereas Zulu men living in the U.K. had very similar preferences to British Caucasians for women with BMIs in the range 20–22 (Tovée et al., 2006). These authors propose that human sexual preferences are plastic, that low WHR is not a trait that is universally preferred, and that male preferences for female BMI will account for cross-cultural variation due to context-specific psychological adaptations.

The data in the current study were collected in three small villages in the Highlands of PNG. This region existed in relative isolation until the 1950s, when doctors, anthropologists, and Australian government officials began establishing contact with local people (Anderson, 2008). The Okapa district has remained isolated from modern cultural influences such as the Internet, television, advertising, and Hollywood films. Indeed, the area remains extremely challenging to contact, as

one researcher recounts "Poor (to appalling and impassable in the wet season) road conditions hampered work. The roads have significantly deteriorated in recent years. It takes 36 h to cover 40 km in the wet season with heavy vehicle rescue equipment and a six-man team" (Collinge, 2008). It is important for researchers studying human mate choice and physical attractiveness to include the responses of people from more remote and culturally isolated communities like the Okapa district in PNG. A significantly larger proportion of men in the current study selected postoperative images with a lower WHR as most attractive, irrespective of body pose or postoperative changes in BMI. This questionnaire has recently been applied in several less remote and isolated cultures, with similar results reported from Cameroon, Indonesia, Samoa, and New Zealand (Singh et al., in press). Therefore, across a diverse range of cultures, which vary in socioeconomic status and exposure to Western media, it appears that WHR is a trait that defines female attractiveness when controlling for BMI.

Why do these data differ from those presented in other studies of female attractiveness that have found that BMI accounts for greater variance in male attractiveness ratings (e.g., Tovée et al., 1999, 2006)? It may be that BMI accounts for greater variance in these studies because of the extreme range of BMIs presented, ranging from under 15 (emaciated) to over 30 (clinically obese), while WHRs ranged from 0.68 to 0.98. In the current study, photographs of women fell within a narrower range of BMI, from 19.99 to 26.66, and a comparable range of WHRs (0.69–0.93). Thus, while the wider range of female BMI and WHR that Tovée et al. (1999) employed were not used in the current study, the consistent finding that postoperative images with low WHRs were preferred irrespective of changes in postoperative BMI, suggests that WHR is an important trait in male judgments of female attractiveness. The advantage in this study was the simplicity of the design. In many studies, Likert scales for rating attractiveness are used and confusion may arise between different cultures as to how to rate images. This is particularly the case in cultures where levels of literacy are low. In this study, men were asked to select one image from a pair of images. For an anthropologist who tries to collect data and replicate studies under field conditions, methods that may appear overly simple can have many practical advantages.

In the first study testing the role of BMI and WHR in male judgments of female attractiveness using images of women who had undergone micrograft surgery, Singh and Randall (2007) found that men and women from U.S.A. rated postoperative images as more attractive regardless of changes in BMI. However, Cornelissen et al. (2009) have criticized the use of these stimuli because they show only the torso and in order to visually process BMI one must have the full body in view. In response to this critique we suggest that although the full body is not in view, the effects of BMI are controlled for as men viewed pairs of images in which the height of the torso is identical. If a curvy physique with a low WHR were not attractive to men, they would have selected the preoperative images more frequently. It is clear from this study that men prefer images of women with lower WHRs and, while BMI is still an important cue in mate selection, it does not outweigh the importance of the low WHR in male preferences for female physique.

As ancestral human beings left Africa, migrated across Asia and Europe and eventually expanded into the far-

these regions of the planet, genetic and phenotypic diversity was lost due to genetic bottlenecks (Manica et al., 2007). Thus, small founder populations successfully negotiated reproduction in times of heavy nutritional scarcity and it is clear that human sexual preferences can adapt to very different conditions. In Finland, for example, healthy young women have WHRs ranging from 0.67 to 0.80 (Marti et al., 1991). However, women from subsistence farming and hunter-gatherer societies tend to have higher WHRs. For example, among the Hadza hunter-gatherers young women with normal body weight have WHRs of 0.79 and young Amazonian Shiwiar women, who are foragers and farmers, have WHRs of 0.86 (Cashdan, 2008). Higher WHRs may have been selected for in these populations because these women, as providers of food to their children, are under pressure to compete for limited food resources. Women with higher levels of testosterone tend to have higher WHRs (Van Anders and Hampson, 2005) and are more verbally and physically competitive than women with lower testosterone (Dabbs and Hargrove, 1997; Cashdan, 2003). Thus, in hunter-gatherer and subsistence farming communities, selection may have favored women who must provide for their offspring through competition for limited food resources and, as a by-product of their behavioral ecology, these women have higher WHRs (Cashdan, 2008). Interestingly, however, both Hadza and Shiwiar men select images with low WHRs (0.6–0.8) as most attractive (Sugiyama, 2004; Marlowe et al., 2005).

Fat reserves in the gluteal/femoral region become mobilized during pregnancy. During the early phases of pregnancy, women in well nourished societies can gain up to 3.5 kg of fat (Adair and Bisgrove, 1991), which is stored in the hips and thighs (Rebuffe-Scrive, 1987). Low WHR in women, prior to pregnancy, is a significant predictor of child neonatal weight, which can have major effects on the survival of the baby (Pawlowski and Dunbar, 2005). BMI in women is only significant in predicting a child's birth-weight if the mother weighs less than 54 kg (Pawlowski and Dunbar, 2005). Lassek and Gaulin (2006) showed in a sample of American women that, although repeated pregnancies resulted in body fat and weight gain, hip and thigh circumference decreased with parity. This phenomenon is termed *maternal depletion*. Among subsistence farmers and hunters, such as the highlanders of PNG, where food is scarce and subsistence farming is a grueling activity, maternal depletion can be quite severe (Harrison et al., 1975; Tracer, 1991; Garner et al., 1994). In the current study, after controlling for the effects of BMI, men selected photographs of women with low WHRs significantly more frequently than images of the same women with higher WHRs. Therefore, while having a healthy BMI is important for offspring survival, particularly in an ecological setting of low nutritional resources, this does not overshadow male preferences for women with low WHRs in the remote highlands of PNG.

LITERATURE CITED

- Adair LS, Bisgrove EZ. 1991. Maternal anthropometry during pregnancy, pregnancy weight gain, and pregnancy outcome. In: Himes J, editor. *Anthropometric assessment of nutritional status*. New York: John Wiley. p 233–257.
- Anderson WH. 2008. Early perceptions of an epidemic. *Philos Trans R Soc Lond B Biol Sci* 363:3675–3678.
- Barber N. 1995. The evolutionary psychology of physical attractiveness: sexual selection and human morphology. *Ethol Sociobiol* 16:395–424.
- Boot AM, Bouquet J, de Ridder MAJ, Krenning EP, Keizer-Shrama SM. 1997. Determinants of body composition measured by dual-energy x-ray absorptiometry in Dutch children and adolescents. *Am J Clin Nutr* 66:232–238.
- Buss DM. 2003. *The evolution of desire*, 2nd ed. New York: Basic Books.
- Cant JGH. 1981. Hypothesis for the evolution of human breasts and buttocks. *Am Nat* 117:199–204.
- Carter LEJ, Heath BH. 1990. *Somatotyping: development and applications*. Cambridge: Cambridge University Press.
- Cashdan E. 2003. Hormones and competitive aggression in women. *Aggress Behav* 29:107–115.
- Cashdan E. 2008. Waist-to-hip ratio across cultures: trade-offs between androgen- and estrogen-dependant traits. *Curr Anthropol* 49:1099–1107.
- Clarys JP, Martin AD, Drinkwater DT. 1984. Gross tissue weights in the human body by cadaver dissection. *Hum Biol* 56:459–473.
- Collinge J. 2008. Lessons of kuru research: background to recent studies with some personal reflections. *Philos Trans R Soc Lond B Biol Sci* 363:3689–3696.
- Cornelissen PL, Tovée MJ, Bateson M. 2009. Patterns of subcutaneous fat deposition and the relationship between body mass index and waist-hip-ratio: implications for models of physical attractiveness. *J Theor Biol* 256:343–350.
- Dabbs JM, Hargrove MF. 1997. Age, testosterone, and behavior among female prison inmates. *Psychosom Med* 59:477–480.
- Dixson AF. 2009. *Sexual selection and the origins of human mating systems*. Oxford: Oxford University Press.
- Dixson BJ, Dixson AF, Bishop P, Parish A. Human physique and sexual attractiveness in men and women: a New Zealand–U.S.A comparative study. *Arch Sex Behav*. DOI: 10.1007/s10508-008-9441-y.
- Dixson BJ, Dixson AF, Li B, Anderson MJ. 2007a. Studies of human physique and sexual attractiveness: sexual preferences of men and women in China. *Am J Hum Biol* 19:88–95.
- Dixson BJ, Dixson AF, Morgan B, Anderson MJ. 2007b. Human physique and sexual attractiveness: sexual preferences of men and women in Bakossiland, Cameroon. *Arch Sex Behav* 36:369–375.
- Furnham A, Tan T, McManus C. 1997. Waist-to-hip ratio and preferences for body shape: a replication and extension. *Pers Individ Dif* 22:539–549.
- Garner P, Smith T, Baea M, Lai D, Heywood DP. 1994. Maternal nutritional depletion in a rural area of Papua New Guinea. *Trop Geogr Med* 46:169–171.
- Grammer K, Fink B, Møller AP, Thornhill R. 2003. Darwinian aesthetics: sexual selection and the biology of beauty. *Biol Rev* 78:385–407.
- Harrison GA, Boyce AJ, Platt CM, Serjeantson S. 1975. Body composition during lactation in a New Guinea population. *Ann Hum Biol* 2:395–398.
- Henss R. 2000. Waist-to-hip ratio and female attractiveness. Evidence from photographic stimuli and methodological considerations. *Pers Individ Dif* 28:501–513.
- Jasińska G, Ziolkiewicz A, Ellison PT, Lipson SF, Thune I. 2004. Large breasts and narrow waists indicate high reproductive potential in women. *Proc R Soc Lond B Biol Sci* 271: 1213–1217.
- Kirschner MA, Samojlik E. 1991. Sex hormone metabolism in upper and lower body obesity. *Int J Obes* 15:101–108.
- Lassek WD, Gaulin SJC. 2006. Changes in body fat distribution in relation to parity in American women: a covert form of maternal depletion. *Am J Phys Anthropol* 131:295–302.
- Lassek WD, Gaulin SJC. 2007. Menarche is related to fat distribution. *Am J Phys Anthropol* 133:1147–1151.
- Lipson SF, Ellison PT. 1996. Comparison of salivary steroid profiles in naturally occurring conception and non-conception cycles. *Hum Reprod* 11:2090–2096.
- Manica A, Amos W, Balloux F, Hanihara T. 2007. The effects of ancient bottlenecks on human phenotypic variation. *Nature* 448:346–348.

- Marlowe F, Apicella CL, Reed D. 2005. Men's preferences for women's profile waist-to-hip ratio in two societies. *Evol Hum Behav* 25:371–378.
- Marti B, Tuomilehto J, Salomaa V, Kartovaara L, Korhonen HJ, Pietinen P. 1991. Body fat distribution in the Finnish population: environmental determinants and predictive power for cardiovascular risk factor levels. *J Epidemiol Community Health* 45:131–137.
- Merzenich H, Boeing H, Wahrendorf J. 1993. Dietary fat and sports activity as determinants for age of menarche. *Am J Epidemiol* 138:217–224.
- Moran C, Hernandez E, Ruiz IE, Fonseca ME, Bermudez JA, Zarate A. 1999. Upper body obesity and hyperinsulinemia are associated with anovulation. *Gynecol Obstet Invest* 47:1–5.
- Pawlowski B. 2001. The evolution of gluteal/femoral fat deposits and balance during pregnancy in bipedal Homo. *Curr Anthropol* 42:572–574.
- Pawlowski B, Dunbar RIM. 2005. Waist-to-hip ratio versus body mass index as predictors of fitness in women. *Hum Nat* 16:164–177.
- Pawlowski B, Grabarczyk M. 2003. Center of body mass and the evolution of female body shape. *Am J Hum Biol* 15:144–150.
- Rebuffe-Scrive M. 1987. Regional adipose tissue metabolism in women during and after reproductive life and in men. *Recent Adv Obes Res* 5:82–91.
- Roberts R, Weinfeld A, Nguyen K. 2005. "Universal" and ethnic ideals of beautiful buttocks and how to create them surgically. Paper presented at the annual meeting of the American Society for Aesthetic Plastic Surgery, New Orleans, LA, April 30, 2005.
- Rozmus-Wrzesinska M, Pawlowski B. 2005. Men's ratings of female attractiveness are influenced more by changes in female waist size compared with changes in hip size. *Biol Psychol* 68:299–308.
- Singh D. 1993. Adaptive significance of female attractiveness: role of waist-to-hip ratio. *J Pers Soc Psychol* 65:293–307.
- Singh D. 2006. The universal allure of the hour glass figure: an evolutionary theory of female sexual attractiveness. *Clin Plast Surg* 33:359–370.
- Singh D, Dixon BJ, Jessop TS, Morgan B, Dixon AF. Cross-cultural consensus for waist-to-hip ratio and women's attractiveness. *Evol Hum Behav*, in press.
- Singh D, Randall PK. 2007. Beauty is in the eye of the plastic surgeon: waist-to-hip ratio (WHR) and women's attractiveness. *Pers Individ Dif* 43:329–340.
- Sugiyama LS. 2004. Is beauty in the context-sensitive adaptations of the beholder? Shiwiari use of waist-to-hip ratio in assessments of female mate value. *Evol Hum Behav* 25:51–62.
- Swami V, Caprario C, Tovée MJ, Furnham A. 2006. Female physical attractiveness in Britain and Japan: a cross-cultural study. *Eur J Pers* 20:69–81.
- Swami V, Tovée MJ. 2005. Female physical attractiveness in Britain and Malaysia: a cross-cultural study. *Body Image* 2:115–128.
- Symons D. 1995. Beauty is in the adaptations of the beholder: the evolutionary psychology of human female sexual attractiveness. In: Abramson PR, Pinkerton SD, editors. *Sexual nature, sexual culture*. Chicago: University of Chicago Press. p 80–118.
- Thornhill R, Gangestad SW. 1996. The evolution of human sexuality. *Trends Ecol Evol* 11:98–102.
- Tovée MJ, Cornelissen PL. 2001. Female and male perceptions of female physical attractiveness in front-view and profile. *Br J Psychol* 92:391–402.
- Tovée MJ, Maisey DS, Emery JL, Cornelissen PL. 1999. Visual cues to female physical attractiveness. *Proc R Soc Lond B Biol Sci* 266:211–218.
- Tovée MJ, Swami V, Furnham A, Mangalparsad R. 2006. Changing perceptions of attractiveness as observers are exposed to a different culture. *Evol Hum Behav* 27:443–456.
- Tracer DP. 1991. Fertility-related changes in maternal body composition among the Au of Papua New Guinea. *Am J Phys Anthropol* 85:393–405.
- Van Anders SM, Hampson E. 2005. Waist-to-hip ratio is positively associated with bioavailable testosterone but negatively associated with sexual desire in healthy pre-menopausal women. *Psychosom Med* 67:246–250.
- Van Hooff MHA, Voorhorst FJ, Kaptein MB, Hirasig RA, Koppelaar C, Schoemaker J. 2000. 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. *J Clin Endocr Metab* 85:1394–1400.
- 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. *Hum Reprod* 12:2057–2060.
- Wetsman A, Marlowe F. 1999. How universal are preferences for female waist to-hip ratios? Evidence from the Hadza from Tanzania. *Evol Hum Behav* 20:219–228.
- Yu DW, Shepard GH. 1998. Is beauty in the eye of the beholder? *Nature* 396:321–322.
- Zaadstra BM, Seidell J, Van Noord PA, te Velde ER, Habbema JD, Vrieswijk B, Karbaat J. 1993. Fat and female fecundity: prospective study of body fat distribution in conception rates. *Br Med J* 306:484–487.