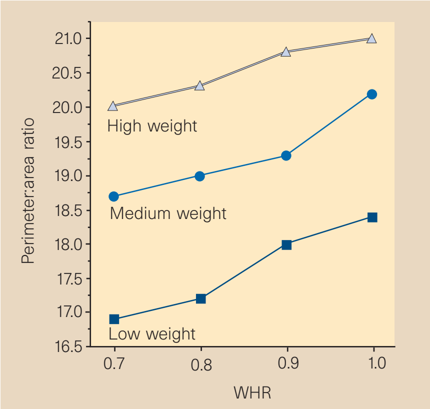

Figure 1 Correlation between perimeter-to-area ratio and WHR of figures produced by Singh[1] and used by Yu and Shepard[5]. In these line-drawn images, the BMI of the figures within each group of underweight, normal, and overweight women was assumed to be constant while their WHR was varied by narrowing the waist. However, this procedure alters not only the WHR, but also the apparent BMI: as the WHR rises, so does the apparent BMI. This correlation can be quantified by plotting the perimeter-to-area ratio of each of the line drawings used by Yu and Shepard against the WHR. The two measures are highly correlated ($r \geq 0.95$ for each of the three series).

because, when the figures are modified by altering the width of the torso around the waist, this alters not only the WHR but also the apparent BMI: as the value of the WHR rises, so does the apparent BMI[6,7].

This co-variation can be quantified. Using photographs of real women (with known BMI values), we have measured the path length around the perimeter of each figure and divided it by the area within the perimeter (the perimeter-to-area ratio). This ratio correlates well with the actual BMI of the woman (Pearson correlation coefficient is $r = 0.97$, $P < 0.0001$). We can then calculate the perimeter-to-area ratio for each of the drawings used by Yu and Shepard, and, by plotting these values against WHR, we can show that the two measures are clearly correlated ($r \geq 0.95$ for each of the three series) (Fig. 1).

This co-variation of BMI with WHR in the line-drawn figures means that if a subject chooses the least curvaceous shape, he is also choosing the highest BMI. BMI is a very strong cue to attractiveness[6,7], and this sample of Matsigenka people seem to prefer women with a high BMI (that is, the figures in the 'overweight' set). So it is quite possible that their reported preference for a less curvaceous shape merely represents a preference for a figure with a high BMI. Yu and Shepard's data set cannot differentiate between a preference for a higher BMI and/or a less curvaceous figure. Firm conclusions about the Matsigenka's preferences for female physical shape need to be based on a set of stimuli in which BMI and WHR vary independently, so that the relative importance of the two features can be determined.

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Yu and Shepard reply — We have proposed that cultural invariance in beauty preferences could be an artefact of exposure to a dominant culture, and also that evolutionary psychology should embrace variation because adaptive evolution is as likely to produce variable outcomes as fixed ones[1]. Accordingly, Manning *et al.* suggest that a culturally variable male preference for women with high WHR might reflect a culturally variable preference for producing more sons with higher testosterone levels. But this intriguing explanation probably does not apply to the Matsigenka people.

The Matsigenka marriage system is matrilocal, meaning that a man leaves his natal home to marry into the woman's family. As a result, families lose their economic investment in their sons, not daughters, and so sons are more costly than daughters. Also, elder sons traditionally marry polygamously, meaning that the expected reproductive success of younger sons is lower than that of any daughter, and thus, if anything, there should be a preference for female offspring. As it turns out, sex ratios seem to be female-biased. A genealogical survey of an even more culturally isolated group of Matsigenka, the Sotileja population, recorded a birth ratio of 73 females to 62 males, although this female bias was later reduced by higher female mortality[2].

Nor does the model of Manning *et al.* explain why westernized indigenous populations in South America should prefer hourglass-shaped females. First, what traditional society does not value strength (or sons)? Second, Peru's male-dominated economy should increase, not decrease, the value of males in westernized populations, and, by extension, the value of high-WHR females. Finally, how could such preferences change evolutionarily in a single generation?

Tovée and Cornelissen suggest that WHR is a proxy measurement for BMI. In Yomybato village, under all three decision criteria, figures were ranked O9, O7, N9, N7, U9, U7 (sorted by median then mean ranks; notation: O, N, U are overweight, normal and underweight, respectively, and numbers refer to high (9) and low (7) WHRs), which is consistent with the hypothesis that figures were ordered by BMI alone. However, Shipetiari males ranked the figures O7, O9, N7, N9, U7, U9 under the attractiveness and spouse criteria, which might not be consistent with the BMI hypothesis, because the ranks do not vary smoothly with BMI. Moreover, Alto Madre and United States males gener-ally grouped figures first by WHR (7, 9) and then by weight, which is inconsistent with the BMI hypothesis. Also, although both the latter populations generally ranked N7 first, O7 was the second choice of Alto Madre males, and U7 was that of United States males. On the other hand, by using a different set of (headless) figures, Tovée *et al.* found that British university students, in contrast, strongly disliked females with low or high values of BMI but were agnostic with regard to WHR[3]. Finally, a recent study has revealed that the culturally isolated hunter-gatherer Hadza men in Tanzania are also indifferent to WHR but prefer pictures of high-BMI women (A. Wetsman and F. Marlowe, personal communication).

What can we make of these cross-cultural differences? First, not only might WHR preferences be affected by westernization, but the very concept of using WHR at all to assess attractiveness might be culturally variable and, in Peru, an effect of westernization. Second, these results show that BMI preferences vary markedly across cultures (as well as through time[4]). If we were to rely on the weak cultural invariance test of adaptation, BMI and WHR preferences would not be considered as adaptations.

We obviously need a more sophisticated evolutionary analysis to explain variation in preferred body shapes and sizes, which does not ignore the effects of environment on ontogeny. For now, the nature of female beauty must remain mysterious, as perhaps it should.

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erratum

Colour was inappropriately added by *Nature* to Fig. 1 of Yu and Shepard's original paper[5], which should have appeared in black and white. We apologize for any confusion that may have arisen as a result.

Is beauty in the eye of the beholder?

Why are some humans considered more beautiful than others? Theory suggests that sexually reproducing organisms should choose mates displaying characters indicative of high genotypic or phenotypic quality[1]. Attraction to beautiful individuals may therefore be an adaptation for choosing high-quality mates[2–6]. Culturally invariant standards of beauty in humans have been taken as evidence favouring such an adaptationist explanation of attraction[3–7]; however, if standards of beauty are instead no more than artefacts of culture, they should vary across cultures[3–6]. Here we show that male preference for women with a low waist-to-hip ratio (WHR) is not culturally universal, as had previously been assumed.

In the developed world, healthy females have higher levels of oestrogen than testosterone. This causes more fat to be deposited on the buttocks and hips than on the waist[8], and leads to a low WHR, resulting in a 'wasp-waisted' or gynoid figure (Fig. 1). Females with high WHRs ('apple-shaped' or tubular figures) suffer disproportionately from a variety of health disorders, including infertility and adult-onset diabetes[8]. Males from several cultures (and times) strongly prefer female figures with a low WHR[8–11], despite otherwise variable preferences for overall weight. The WHR is therefore an accurate indicator of health status and fertility, and male preference for low-WHR females is considered to be one of the best-supported examples of a sexually selected adaptation for assessing mate quality[2,3,8].

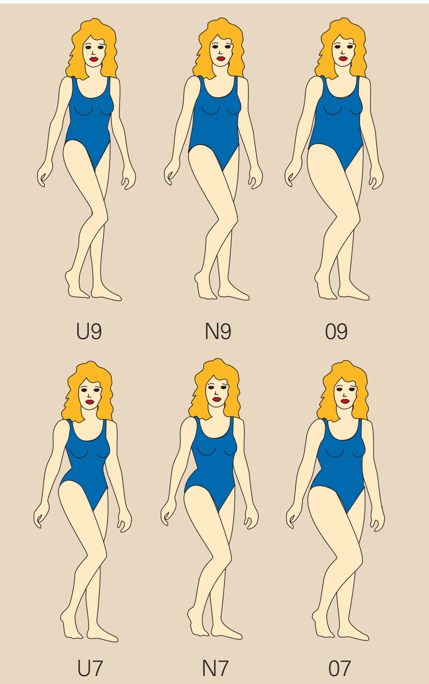

Figure 1 Female figures[8] depicting two WHR classes (high 0.9 and low 0.7, referred to as 9 and 7) and three weight classes ('overweight,' 'normal' and 'underweight', referred to as O, N and U, respectively). A man from Yomybato defined the classes as follows: O9, healthy; O7, had diarrhoea/was skinny in the waist; N9, pallid; N7, had fever, lost weight, especially in the waist; U7, had diarrhoea a few days ago, not skinny but pallid, almost better; U9, pale, almost dead. This figure was adapted with permission from the American Psychological Association (1993).

However, every culture tested so far has been exposed to the potentially confounding influence of western media. Many of the remotest places on Earth have access to television, cinema and advertising posters displaying exceptionally gynoid females draped over desirable products such as cars and beer. Here we test the hypothesis that a population free from such cultural influences would have a different standard of beauty to 'westernized' populations that have been exposed to them.

We assessed WHR preferences in a culturally isolated population of Matsigenka indigenous people from the 1.8-million-hectare Manu Park in southeast Peru. The Matsigenka practise swidden (slash and burn) agriculture, supplemented with fruit and game, using traditional tools. Access to the park's core is restricted to all but scientific and official visitors, and the 300 or so Matsigenka have lived all or most of their lives within the core, so they have not been westernized.

Long-term studies[12] in Yomybato village have familiarized residents with interviews, which were conducted in their native language. Although the people of Yomybato are by no means 'uncontacted', their degree of isolation is about as high as can be obtained today.

WHR preferences of males in Yomybato differed strikingly from those of the US control population (Fig. 2) and from previous results[8–11]. Female figures were ranked first by weight and then by WHR. 'Overweight' female O9 (Fig. 1) ranked highest under all three decision criteria: attractiveness, healthiness and preferred spouse. Within weight classes, high-WHR females always ranked significantly higher than low-WHR females (Fig. 2).

To gauge the effect of westernization on WHR preferences, we repeated the WHR test using two more westernized populations: a Matsigenka population living outside Manu Park (Shipetiari), and an even more westernized and ethnically mixed population of Amarakaeri, Huachipaeri and Piro (Alto Madre). Both populations live along the Alto Madre de Dios River, a major

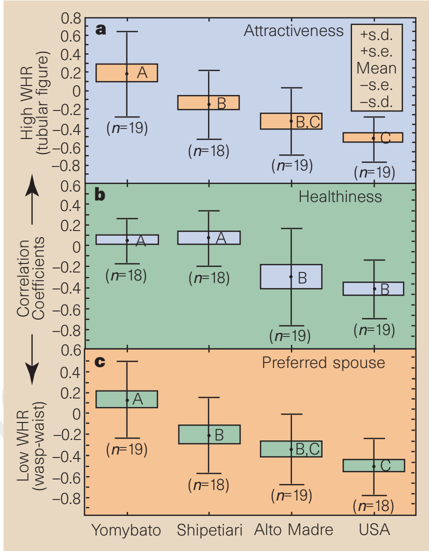

Figure 2 Contrast analyses of WHR preferences. Figures with low and high WHRs were assigned contrast values of +1 and -1, respectively, and, for each informant, correlated against the rank order of the six figures. Correlation coefficients were then pooled within population and decision criteria. Analysis of variance (ANOVA) was used with a post-hoc Tukey HSD for unequal sample sizes, except in the health criterion, in which unequal variances required the use of a Mann–Whitney *U* test and a sequential Bonferroni adjustment of pairwise population comparisons. Populations whose means differed significantly (by $P \leqslant 0.03$) after table-wide correction are indicated by different letters. In 1996 and 1997, males from several clan lineages were presented with all six figures placed in a circle in random order and asked to rank them from the most to the least beautiful. The process was repeated for healthiness and preferred spouse. Ages in the Yomybato group ranged from 13 to about 60 (median 24.5); Shipetiari, 14 to 50 (26); Alto Madre, 17 to 57 (27); and US, 18 to 60 (24). A fuller description of our results and methods is in preparation.

trading route. The Shipetiari and Yomybato populations are segregates of the same central population that was contacted 20 to 30 years ago.

As in Yomybato, males from Shipetiari grouped female figures by weight and then by WHR, preferred 'overweight' figures, and considered high-WHR females to be healthier (Fig. 2). However, Shipetiari males considered low-WHR females to be more attractive and more desirable as spouses (Fig. 2). Note that Shipetiari males did not consider the healthiest females to be the most attractive or the most desirable spouses, suggesting that WHR preferences may be changing.

Yomybato and Shipetiari women of child-bearing age have high WHRs even before first pregnancy, and post-childbearing women are thin and have a low WHR.

Alto Madre males did not differ significantly from males from the United States. They grouped female figures by WHR and then by weight: the N7 female (Fig. 1) was generally ranked highest, and low-WHR females were always ranked significantly higher than high-WHR females (Fig. 2). On the gradient of increasing westernization from Yomybato to Alto Madre, WHR and weight preferences become more like those of the US population and previous results[8–11] (Fig. 2). Our data urgently require replication, because opportunities are disappearing rapidly as more cultures are westernized.

Cultural invariance combined with an adaptive story has been used to support an adaptationist explanation of human beauty (and of other aspects of human psychology[13]). But our results suggest that, when culturally isolated populations are taken into account, some supposedly invariant standards may prove malleable. As a result, many 'cross-cultural' tests in evolutionary psychology may have only reflected the pervasiveness of western media.

A fuller evolutionary theory of human beauty must embrace variation, rather than focusing on 'universal' traits to the exclusion of cultural effects. Of course, physical features are involved in mate choice, and natural selection has probably shaped those preferences. However, in traditional societies, physical features may play a lesser role because mate choice is limited by kinship rules, and potential mates have access to direct information about mate quality, such as age and history of illness, so do not rely on information inferred from physical appearance. In contrast, in industrialized societies, daily exposure to strangers from an early age may increase the importance of using physical features to assess potential mates.

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A developmental model for thalidomide defects

Thalidomide was prescribed as a mild sedative until it was demonstrated in 1961 that it was responsible for inducing congenital malformations in children whose mothers took the drug during pregnancy. Perhaps the most striking aspect of this syndrome is phocomelia (a severe shortening of the limbs). The long bones are shorter than normal and more proximal elements are lost, such that in extreme cases the hand or fingers are attached directly to the shoulder, a condition described as resembling the flipper of a seal[1,2]. Here I show how these defects can be understood in the context of current models for limb patterning.

Although the pharmacological basis for thalidomide's effect remains controversial, the net result of thalidomide exposure is a decrease in growth of the limb-bud mesenchyme[3]. From the perspective of pattern formation, the challenge is to understand why the decrease in growth should lead to a specific loss of proximal limb elements. This effect could be viewed as paradoxical, as other perturbations that prevent limb-bud growth, such as removal of the specialized apical ectodermal ridge (AER) at the tip of the limb bud, lead to the opposite patterning defect: deletions of distal structures[4,5]. These truncations induced by AER removal are explained by the 'progress zone' model of proximodistal patterning[5], and consideration in this context can also explain the distinct proximodistal defect seen with thalidomide.

According to the progress-zone model, proximodistal structures are specified sequentially under the influence of a continuous signal, now believed to be a fibroblast growth factor (FGF)[6,7], produced by the AER. Initially, the entire limb mesenchyme has a proximal identity; left on its own, it would develop into proximal structures. However, the mesenchyme at the tip of the limb bud under the AER — the progress zone — is exposed to FGF and becomes re-specified to a slightly more distal fate. As limb development proceeds, the progress-zone cells divide and, as a result of this growth, not all of these cells remain within range of the FGF signal. Those too far from the AER maintain their already specified proximal fate, whereas those still in close proximity to the AER are once again re-specified to a still more distal fate (Fig. 1a). This model explains the distal truncations seen following surgical removal of the AER: without the source of the distalizing factor FGF, no further distal patterning occurs and only the proximal elements specified before the AER was removed are formed.

The phocomelia observed following thalidomide treatment can also be understood from this developmental perspective. Thalidomide treatment blocks mesenchymal proliferation in the limb bud[3]. I propose that this means that the progress zone does not increase in its number of cells, despite continued exposure to FGFs from the AER. As a result, no progress-zone cells end up outside the range of the FGFs, which would be required for them to remember proximally assigned fates. Instead, the entire progress zone is progressively distalized, ultimately programming the entire limb bud to form only the distalmost elements (Fig. 1b).

Consistent with this view, an effect like that of thalidomide can be produced by irradiating the limb mesenchyme, limiting proliferation in the progress zone without affecting the distalizing activity of the AER[8]. Based on these data, a similar mechanism was proposed as a general explanation for phocomelia[8]. Loss of intermediate limb elements, the most common type of limb malformation seen in offspring of women who used thalidomide, is therefore a predicted consequence of altering growth in the progress zone while leaving intact the production of FGFs by the AER.

Many of the pharmacological mechanisms proposed to explain thalidomide's

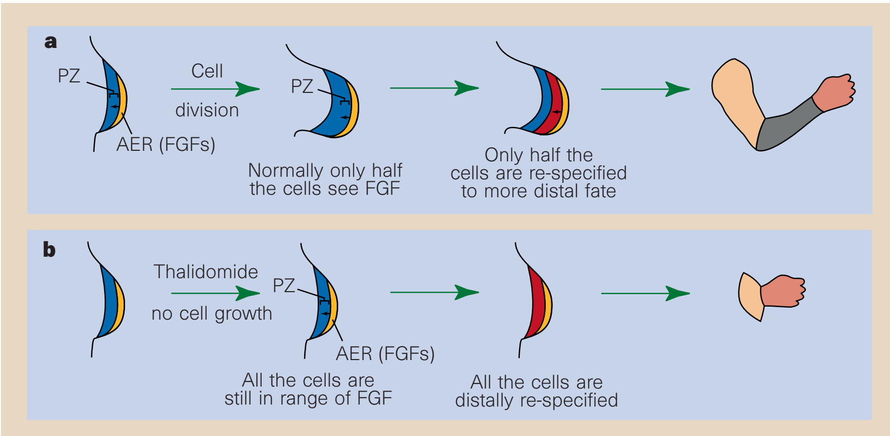

Figure 1 Progress-zone model for thalidomide teratology. **a,** Normal proximodistal pattern specification. **b,** Proximodistal patterning after exposure to thalidomide. PZ, progress zone.