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Original Article

Pathogen disgust sensitivity and resource scarcity are associated with mate preference for different waist-to-hip ratios, shoulder-to-hip ratios, and body mass index

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ABSTRACT

Environmental factors, such as pathogen prevalence and resource scarcity, are thought to influence mate preferences for traits related to health and resource provisioning potential. Specific body dimensions, such as women's waist-to-hip-ratio (WHR), men's shoulder-to-hip ratio (SHR), and body mass index (BMI) have also been theorised to be associated with health benefits, or ability to deal with resource scarcity. Here, we test across two studies using different study designs whether the effects of pathogen disgust sensitivity and socioeconomic status (SES; a negative proxy for resource scarcity) on mate preferences extend to men's WHR preferences, women's SHR preferences, and both sex's BMI preferences. Study 1 found that pathogen disgust significantly negatively influenced men's WHR preference in female bodies, while SES was significantly negatively associated with women's SHR and BMI preferences in male bodies. Study 2 found that pathogen disgust negatively predicted men's WHR preference, and positively predicted women's SHR preference, while SES negatively predicted men's WHR preference. Our findings support the notion that body shapes are used as cues to health and likelihood of resource provision, and may help explain inconsistencies in the literature regarding variation in body shapes preferences.

1. Introduction

Mate choice is one of the most important predictors of evolutionary fitness (i.e., an individual's contribution to the gene pool in the following generations). However, not all potential partners confer the same benefits and costs, and the importance of these benefits and costs varies depending on the circumstance. Therefore, it is evolutionarily beneficial to have a mechanism where individuals can perceive environmental factors and adjust their mate preferences towards partners that would be the most beneficial given the circumstances. Environmental factors, such as pathogen prevalence and resource scarcity, have been proposed to influence mate preferences for a variety of traits that are thought to be associated with health or resource provisioning potential, including physical attractiveness (Gangestad & Buss, 1993; Lee et al., 2013; Young, Sacco, & Hugenberg, 2011) sexual dimorphism (i.e., the masculinity of men and the femininity of women; DeBruine, Jones, Crawford, Welling, & Little, 2010; Jones, Fincher, Little, & DeBruine, 2013; Little, Cohen, Jones, & Belsky, 2007; Little, DeBruine, & Jones, 2011), and good parental traits (Lee & Zietsch, 2011; Lee et al., 2013).

Previous research (such as those cited above) has focused on preferences for broad, explicit traits, for example, self-reported preferences for 'physical attractiveness' (Gangestad & Buss, 1993), or specific facial cues (which are thought to convey cues of mate quality; DeBruine, Jones, Crawford, et al., 2010; Little et al., 2011), but recent work suggests that these effects may generalise to more specific cues, such as voices and body shapes (Jones et al., 2013). Much like with faces, the dimensions of an individual's body may be used as a cue to their suitability as a potential mate (Gaullup & Frederick, 2010). Jones et al. (2013) found that in women higher pathogen disgust was associated with preference for bodies rated as more masculine, though it is unclear what specific body indices affected masculinity ratings. Here, we investigate whether sensitivity to environmental factors, such as pathogen prevalence and resource scarcity, can influence preferences for specific body indices previously purported to be important in mate choice, namely women's waist-to-hip ratios (WHRs), men's shoulder-to-hip ratios (SHRs), and body mass index (BMI).

1.1. Waist-to-hip ratio

WHR is the circumference of the waist measured at its narrowest point, divided by the circumference of the hips measured at their widest point. WHR is highly sexually dimorphic, with women typically having a lower WHR than men. Traditionally, WHR has been used as a measure of female body shape as it represents the relative distribution of body fat on the body, which is indicative of hormonal levels in the body. A

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lower WHR indicates greater levels of circulating oestrogen, which stimulates fat deposits around the thighs and buttocks, while higher WHR is associated with higher levels of testosterone, which encourages fat deposits in the abdomen (DeRidder et al., 1990; Elbers, Asscheman, Seidell, Megens, & Gooren, 1997; Furnham, Tan, & McManus, 1997).

WHR has been found to influence ratings of attractiveness, with initial studies finding men preferred line-drawings of women with lower WHR (Singh, 1993; Singh & Young, 1995). Studies have since shown that this is a robust effect, with this preference also found in photographs (Henss, 2000; Tovee & Cornelissen, 2001), as well as videos of women's bodies (Smith, Cornelissen, & Tovee, 2007). Low WHRs are preferred even with minimal visual exposure (Schutzwohl, 2006), or no visual input at all (Karremans, Frankenhuis, & Arons, 2010), and have also been found using non self-report data, such as brain activity (Platek & Singh, 2010) and eye gaze patterns (Dural, Cetinkaya, & Guelbetekin, 2008). This preference remains even when controlling for correlates of WHR, such as BMI (Platek & Singh, 2010; Singh & Randall, 2007). Also in support of the notion that low WHR is more attractive, women with low WHR report having more interest from the opposite sex, and more sexual opportunities (Hughes & Gallup, 2003).

While most research in this area focuses on WHR, it remains controversial whether the ratio itself conveys any special information. Recent studies suggest that WHR actually explains less variation in attractiveness than mere waist circumference (Brooks, Shelly, Jordan, & Dixson, 2015). Other research suggests that other body measures better explain attractiveness than WHR (Brooks, Shelly, Fan, Zhai, & Chau, 2010), or that the influence of WHR is mainly accounted for by confounds with BMI (Tovee, Maisey, Emery, & Cornelissen, 1999), which we discuss in more detail below.

Men may use waist size or WHR as a cue to a number of evolutionarily beneficial traits. First, low WHR may be a cue of good health, since lower WHR predicts better health outcomes including lower risk of chronic diseases and premature death (Singh, 1993; Singh & Singh, 2006). Lower WHR may also be a cue of higher fertility, with low WHR women reporting less difficulty in conceiving (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004; Kaye, Folsom, Prineas, Potter, & Gapstur, 1990), more regular menstrual cycles (van Hooff et al., 2000), and more likelihood of success in artificial insemination and in vitro fertilisation (Wass, Waldenstrom, Rossner, & Hellberg, 1997; Zaadstra et al., 1993). Offspring of women with a lower WHR may also benefit indirectly, as low WHRs predict better infant health (Pawlowski & Dunbar, 2005), and better cognitive ability (Lassek & Gaulin, 2008). Due to any number of these potential benefits, it is likely to be advantageous for men to mate with a woman with a low WHR, and thus find lower WHRs more attractive.

Despite these potential benefits, preferences across history and cultures have varied considerably, contradicting the notion that men have evolved a consistent preference for an optimum WHR. While the majority of studies have been conducted with participants from modern Western societies, participants from non-Western backgrounds have shown a preference for higher WHR compared to Western participants (Sugiyama, 2004; Swami, Jones, Einon, & Furnham, 2009; Tovee, Swami, Furnham, & Mangalparsad, 2006; Wetsman & Marlowe, 1999; Yu & Shepard, 1998). Historical evidence also shows that WHR preferences change across time, with higher WHR more preferred in the past compared to contemporary preferences (Lamb, Jackson, Cassiday, & Priest, 1993; Swami, Gray, & Furnham, 2007). This may suggest that there are costs associated with choosing a partner with a low WHR, or that women with higher WHR may confer other benefits that are more advantageous in non-Western cultures.

Indeed, a potential explanation for this discrepancy could lie in a trade-off men face when choosing a partner. While women with narrow waists or a low WHR may confer indirect or direct health benefits, women with larger waists or a higher WHR may be better equipped to compete for resources and deal with food scarcity (Cashdan, 2008). Higher exposure to testosterone, which results in deposition of fat around the waist, is associated in women with traits beneficial in acquiring resources, such as being more aggressive (Dabbs & Hargrove, 1997; Harris, Rushton, Hampson, & Jackson, 1996) and being more likely to express competitive feelings (Cashdan, 2003), and, in Western cultures, may lead to being more career oriented (Udry, Morris, & Kovenock, 1995).

As a result, men could face a trade-off when choosing a mate between a low WHR indicative of genetic health, compared to one with a higher WHR who is better equipped for competing and acquiring resources. We could therefore predict that this trade-off is influenced by environmental factors in evolutionarily beneficial ways, such that when pathogen prevalence is salient men prefer a smaller WHR (as this is associated with increased health), and when resource scarcity is salient a larger WHR (associated with ability to acquire resources) is preferred.

1.2. Shoulder-to-hip ratio

SHR refers to the relative size of the shoulders compared to the hips. Similar to WHR, SHR is a cue of hormonal levels in the body, as the development of a higher SHR is dependent on exposure to high levels of testosterone, which stimulates both the development of upper body muscle (Bhasin, 2003), and structural growth in the shoulders (Kasperk et al., 1997). While not as widely studied as WHR, women have been found to show a preference for wedge shaped bodies (high SHR) as more attractive (Dijkstra & Buunk, 2001). Consistent with this notion, men with a high SHR report greater interest from women as well as more sexual opportunities (Hughes & Gallup, 2003).

Similar to low WHR women, high SHR men may convey many evolutionary benefits to women who prefer them. First, a higher SHR is a sexually dimorphic trait, and some evidence suggests that greater masculinity in men may be associated with health benefits (Gangestad, Merriman, & Thompson, 2010; Rhodes, Chan, Zebrowitz, & Simmons, 2003; Thornhill & Gangestad, 2006). Because of their putative association with good health, male masculinity may be more highly valued by women in environments of high pathogen prevalence. Consistent with this, individuals in countries with greater pathogen prevalence report greater preference for more masculine male faces (DeBruine, Jones, Crawford, et al., 2010; Penton-Voak, Jacobson, & Trivers, 2004). Also, women primed with pathogen-related cues had a greater preference for masculine traits and facial features (Lee & Zietsch, 2011; Little et al., 2011), and women with greater pathogen disgust sensitivity have also been shown to have greater preference for facial masculinity (DeBruine, Jones, Tybur, Lieberman, & Griskevicius, 2010; but see Lee et al., 2013). While more research has focused on preference for masculinity in faces, pathogen avoidance has also been shown to influence women's preference for voices and bodies perceived as masculine (Jones et al., 2013). Assuming there is a similar link between SHR and health, women could benefit directly by choosing a higher SHR partner, either through avoidance of pathogen transmission or having a partner who is less likely to succumb to disease, or indirectly through producing offspring that would inherit these health benefits (Frederick & Haselton, 2007; Tybur & Gangestad, 2011), though this latter point is contentious (Lee et al., 2014; Scott, Clark, Boothroyd, & Penton-Voak, 2013).

Despite the potential health benefits, some studies have found only a weak, or inconclusive preference for masculine traits (Komori, Kawamura, & Ishihara, 2009; Said & Todorov, 2011; Scott, Pound, Stephen, Clark, & Penton-Voak, 2010; Thornhill & Gangestad, 2006), while others find an overall preference for femininity (Boothroyd, Jones, Burt, & Perrett, 2007; Perrett et al., 1998). This would suggest that there is a cost in choosing a masculine male as a mate (Frederick & Haselton, 2007). Indeed, masculine men are less likely to be sexually faithful, tend to prefer short-term relationships (Boothroyd, Jones, Burt, DeBruine, & Perrett, 2008), and are rated as more dominant (Watkins, DeBruine, Little, Feinberg, & Jones, 2012). As a result, women may face a trade-off between choosing a masculine male with good health, versus a feminine male with good parental quality.

Indeed, previous research also stipulates that in environments where resources (e.g. food, shelter) are scarce, women prefer men with feminine features as these putatively associated with relationship commitment and parental qualities (Lee & Zietsch, 2011; Lee et al., 2013; Little et al., 2011; Watkins et al., 2012). Consistent with this, individual differences in socioeconomic status (a negative proxy for resource scarcity) are negatively associated with preferences more oriented towards feminine faces (Lee et al., 2013), and experimental studies have found that women primed with cues of resource scarcity prefer more feminine faces (Little et al., 2007; Watkins et al., 2012) or traits associated with parental quality (Lee & Zietsch, 2011). It could be the case that this trade-off between good health and good parental qualities generalises to preference for masculine/feminine body shape; however, in the case of SHR the opposite could also be predicted. SHR is positively correlated with upper body strength, and in ancestral times, men with greater SHR would be better equipped to provide adequate protection or be more competitive against other males for resources (Gaullup & Frederick, 2010; Lassek & Gaulin, 2009; Puts, 2010). These in turn would allow a better chance of survival for the choosing female and her offspring.

Therefore, based on previous theory and research, we could predict that when pathogen prevalence is salient, women would prefer a greater SHR (as it is potentially associated with health benefits); however, there is no clear expectation for how resource scarcity would influence women's SHR preferences, because high SHR could be indicative of both poorer parental quality and greater ability to compete for resources.

1.3. Body mass index

BMI refers to the weight of an individual scaled by height and has been used as an indicator of the fat stores on one's body. Possessing fat stores is highly adaptive — during ancestral times when food was not always plentiful, the ability to store energy in the form of body fat was highly adaptive in order to bridge periods when food was scarce (Gaullup & Frederick, 2010; Nelson & Morrison, 2005). Body fat stores also help in reducing the energetic demands of pregnancy and lactation production (Bronson & Manning, 1991; Dufour & Sauther, 2002; Ellison, 2003). However, despite these potential advantages, body fat appears to be disadvantageous for health, particularly in fighting infection and disease with high body weight associated with impaired immunocompetence response (Pawlowski, Nowak, Borkowska, & Drulis-Kawa, 2014; Rantala et al., 2013; Tanaka, Isoda, Ishihara, Kimura, & Yamakawa, 2001; Tanaka et al., 1993).

Contemporary Western societies (or WEIRD societies; Henrich, Heine, & Norenzayan, 2010) possess a preoccupation with maintaining a slender figure; individuals report slender bodies as ideal body shape for themselves and as preferred in partners (Swami et al., 2010). But in non-Western cultures preferences for low BMIs are not as strong, and high BMIs are sometimes preferred (Swami et al., 2010). The contemporary WEIRD aversion to body fat remains unexplained in the evolutionary psychology literature (Gaullup & Frederick, 2010). A potential explanation could come from variation in pathogen prevalence and resource scarcity between societies. Body fat may serve a less adaptive role in current Western societies compared to non-Western societies as resources are often plentiful and pathogen prevalence lower, decreasing the necessity for stored energy or the importance of choosing a partner with good health.

Supporting the notion that BMI preference may be facultatively calibrated according to the surrounding environment, Nelson and Morrison (2005) found that greater resource scarcity, manipulated via financial or caloric dissatistifaction, significantly increases men's body weight preferences in women. Also, preference for BMI appears to be malleable depending on cultural factors; Tovee et al. (2006) found that African Zulus adopt Western preferences for body fat (i.e., thinner bodies) after moving to the United Kingdom. One interpretation of these findings is that individuals may merely adopt the local cultural standards of beauty, but another non-exclusive alternative is that BMI preferences shift plastically in response to local environmental factors, such as pathogen prevalence and/or resource scarcity.

Based on this, we would predict that when health cues are salient, individuals would prefer a smaller BMI. However, when resource cues are salient, individuals would show a greater preference for larger BMIs.

1.4. Current research

The current research aims to investigate whether individual differences in sensitivity to pathogens or resource scarcity influence mate preference for different body shapes. We investigate this by testing the association of individual levels of pathogen disgust sensitivity and socioeconomic status (SES; a negative proxy for resource scarcity) with preference for different body shapes across two studies.

While most of the literature cited so far concerns societal differences in environmental threats, the current research focuses on individual differences in sensitivity to environmental cues of pathogens and resource availability. Previous research has found that individual and societal differences in health and resources are associated with mate preferences in consistent ways. Indeed, both health at a societal level and individual pathogen disgust sensitivity have been predicted and found to be associated with greater preference for facial masculinity in women (DeBruine, Jones, Crawford, et al., 2010; Jones et al., 2013). This is thought to be because in both cases individuals have increased salience of that threat, either through increased exposure (for societal differences) or through increased sensitivity (for individual differences).

In Study 1, we measure body preferences via attractiveness ratings, while Study 2 uses a forced-choice paradigm. Based on the purported trade-offs individuals may face when choosing a partner, we predict that men with greater pathogen disgust will favour bodies with narrower waists and thus lower WHRs (we will refer to WHR throughout), while those with greater resource scarcity will prefer higher WHRs. We also predict that women with greater pathogen disgust will prefer males with broader shoulders and thus higher SHRs, while previous theory and findings do not lead to unambiguous predictions of what effect (if any) resource scarcity will have on women's SHR preference. We also predict that BMI preference will be negatively influenced by sensitivity to pathogens, but positively influenced by resource scarcity, and that these effects will be independent of those on WHR and SHR preferences. These predictions and theoretical rationale are shown in Table 1.

2. Study 1

2.1. Method

2.1.1. Participants

Participants were 300 male and 287 female volunteers from an online surveying site (www.socialsci.com) who participated in return for redeemable store credit. The majority of participants resided in the United States (75% of men, 80% of women), while the remainder of the sample were from other Western countries (e.g., Canada, UK, Australia). Participation was conditional on being heterosexual and not currently in a long-term relationship. Responses from 8 males and 2 females were removed as they completed the survey in an unrealistic time (<5 min), suggesting a lack of attention to the survey items. An additional 40 males and 47 females were removed due to missing data on any of the key variables. The final samples included in analyses were to 252 males ($M = 23.69$, $SD = 6.38$) and 238 females ($M = 23.62$, $SD = 6.43$), which included a wide participant age range (18–59 years, though majority of participants were under 40 years).

2.1.2. Stimuli

Participants were asked to rate opposite-sex, computer generated bodies that were based on real body measurements (for more detail,

Table 1
Predictions for current research based on theory and prior research.

	Predictions:	Rationale based on theory and prior research:
Men's waist-to-hip ratio preferences.	1. Men with higher pathogen disgust sensitivity will prefer relatively lower waist-to-hip ratios. 2. Men with fewer resources (lower SES) will prefer relatively higher waist-to-hip ratios.	1. Women with lower waist-to-hip ratios are more immunocompetent. 2. Higher waist-to-hip ratios are indicative of greater resource provisioning potential in women.
Women's shoulder-to-hip ratio preferences.	3. Women with higher pathogen disgust sensitivity prefer relatively higher shoulder-to-hip ratios. 4. It is unclear whether women with increased resource scarcity (lower SES) will prefer relatively higher or lower shoulder-to-hip ratios.	3. Men with higher shoulder-to-hip ratios are more immunocompetent. 4. Men with higher shoulder-to-hip ratios are more able to compete for resources, but are also less reliable parents.
Body-mass index preferences.	5. Individuals with higher pathogen disgust sensitivity will prefer relatively lower BMIs. 6. Individuals with fewer resources (lower SES) will prefer relatively higher BMIs.	5. Lower BMI is associated with greater immunocompetence. 6. Higher body-mass indices are indicative of greater access to resources.

see Brooks et al., 2015). For each sex, there were 5 source bodies that differed naturally within the "normal" range of BMI (i.e. neither underweight nor obese). For the female bodies, we manipulated waist size of each source body by either subtracting or adding one or two inches. These, together with the original (unmanipulated) body, created 5 levels of waist size (and thus WHR) for each body. Similarly with male bodies, shoulder width was manipulated by either adding or subtracting one or two inches to the width of the shoulders, creating 5 levels of shoulder width (and thus SHR) for each body.

This created 25 bodies of each sex for each opposite sex participant to rate. For each female body, WHR was calculated by dividing the circumference around the hips from the circumference of the waist, while SHR was calculated for each male body by dividing the circumference around the hips from the width of the shoulders. BMI for each body was also calculated using area-perimeter ratios (APRs) from 2D images of the bodies. APR has previously been shown to be a good proxy for BMI from a 2D image (Tovee et al., 1999), and involves dividing the distance of the outline of the body from the area the body takes up. The perimeter and area were measured in pixels and pixels^2 respectively and were calculated using the GIMP software package. Bodies were presented in a pseudo-random order in which two bodies derived from the same source body were not presented consecutively. Participants rated each body on a 100-point sliding scale (0 = very unattractive, 100 = very attractive). For example of bodies, see Fig. 1.

2.1.3. Measures

The procedure used in this studied mirrored a previous study investigating the effect of sensitivity to pathogen and resource scarcity on mate preferences for facial attractiveness, sexual dimorphism, and intelligence (Lee et al., 2013). Following the presentation of bodies, participants were given the Three Domain Disgust Scale (Tybur, Lieberman, & Griskevicius, 2009), which is a 21-item questionnaire measuring participant's disgust sensitivity across three domains: moral, sexual, and pathogen disgust. Moral disgust refers to aversion towards social transgressions, such as "Intentionally lying during a business transaction". Sexual disgust measured aversion towards sexual deviance or unwanted sexual contact, such as "Hearing two strangers having sex". Pathogen disgust refers to aversion to exposure to pathogen contagions that could threaten one's health, such as "Accidently touching a person's bloody cut". Participants rated the degree to which they found these statements disgusting on a 7-point scale (0 = not disgusting at all; 6 = extremely disgusting).

Participants were also given a 1-item SES measure (Adler, Epel, Castellazzo, & Ickovics, 2000), which asked participants to rate their perceived standing compared to others on the three dimensions of SES: income, education, and occupation, on a 10 point scale (10 = best off, 1 = worst off). While only one item, this measure has previously been shown to correlate with more objective measures of SES (Adler et al., 2000). SES was used as a negative proxy for resource scarcity.

2.1.4. Analysis

Each participant rated 25 bodies, resulting in 6300 and 5950 observations for males and females respectively. These data are hierarchical in nature, as each of the 25 attractiveness ratings made by each participant (Level 1) is nested within the participant themselves (Level 2). As such, we analysed the data using Hierarchical Linear Modelling (HLM) in the R software package. By using HLM, we can assume that associations between attractiveness ratings and level 1 predictors (the WHR/SHR, and the BMI of each body) differ for each participant, and can control for this (for further description of the advantages of this technique, see Raudenbush & Bryk, 2002). We can also test our hypothesis by determining whether the level 2 predictors (pathogen disgust and SES) moderate these preferences. Separate analyses were conducted for men and women. The body dimensions SHR/WHR (depending on sex) and BMI were entered as Level 1 predictors, while participants' age, SES, and pathogen, moral and sexual disgust were entered at Level 2. Moral disgust and sexual disgust were included into the model in order to test whether any effect of disgust was uniquely attributable to pathogen disgust. Participant age was also included in the model as a control variable. We also ran a model that controlled for participants' ethnicity; however, this did not influence the pattern of significance and we therefore only report the original analyses here. To improve interpretability, all predictors were standardised before being entered into the model. See the Supplementary Material (available on the journal's website at www.ehbonline.org) for additional detail on the analyses conducted.

2.2. Results

The intra-class correlation (i.e., the proportion of the total variance on attractiveness ratings that is between-raters as opposed to within-raters) on attractiveness rating was .31 and .36 for males and females respectively. For full information on the random effects from the HLM analysis, see the Supplementary Materials (available on the journal's website at www.ehbonline.org).

The fixed effects from the HLM analysis are reported in Table 2. The intercept refers to the average slope between the Level 1 predictors and participants' ratings of attractiveness. Overall, men rating female bodies showed a preference for lower WHR, consistent with previous findings. Also consistent with previous studies, women overall preferred men with higher SHR. BMI preference differed as a function of sex. Overall, men preferred bodies with lower BMIs, but women showed greater preference for men with higher BMIs.

2.2.1. Association of pathogen disgust scores on WHR, SHR, and BMI preferences

The hypothesised association between pathogen disgust and men's WHR preference was supported, such that men with greater pathogen disgust showed a greater preference for bodies with lower WHRs. This is specific to pathogen disgust, as no relationship was found with moral or sexual disgust. However, the relationship between pathogen disgust and women's preference for bodies with greater SHR, while in the predicted direction, was not significant. Pathogen disgust also failed to have an association in BMI preference for both men and women. Interestingly, women's moral disgust significantly positively predicted preference for higher BMI.

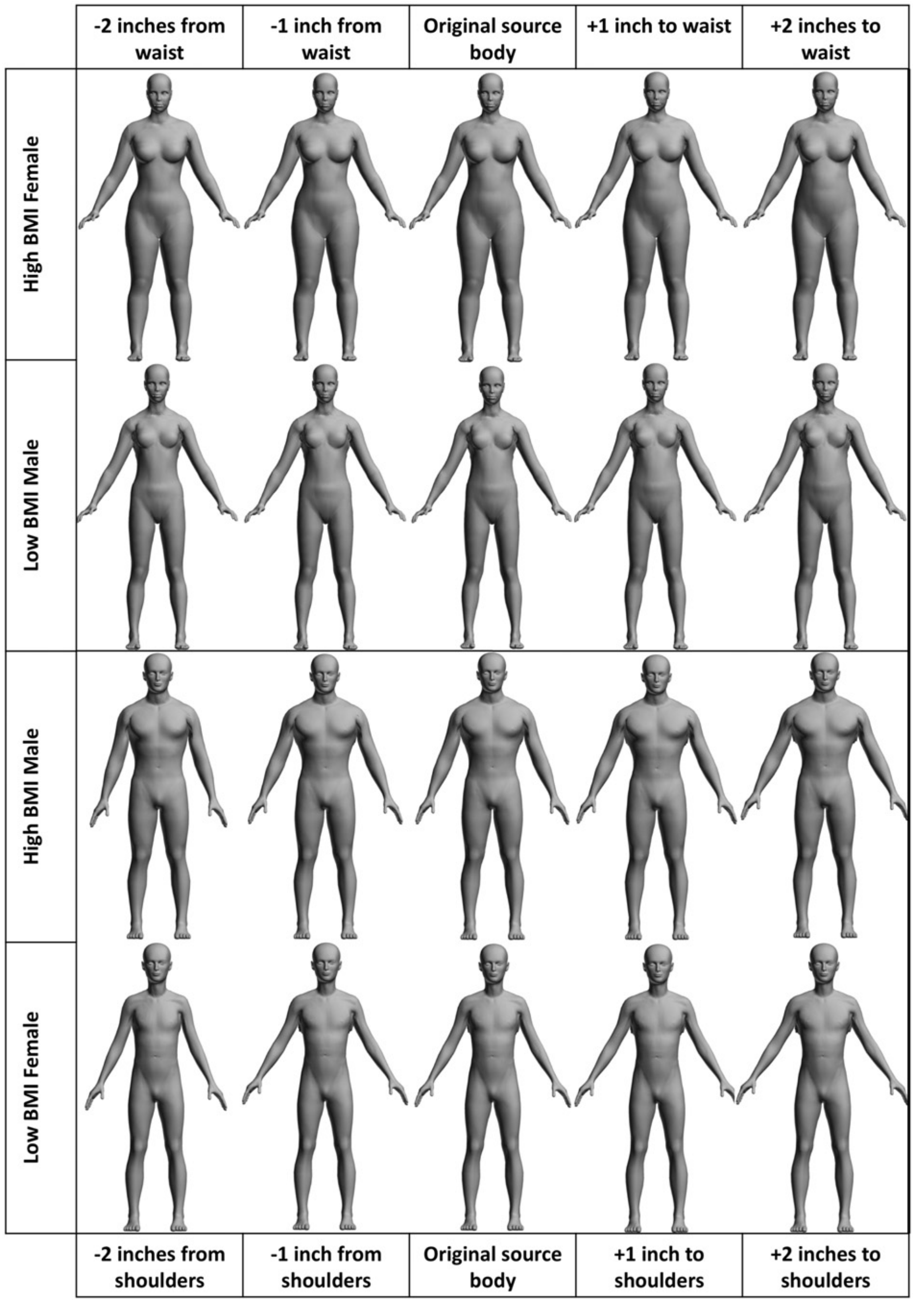

Fig. 1. Examples of bodies used in Studies 1 and 2. Note that there were a total of 5 source bodies that varied on BMI.

2.2.2. Association of SES with WHR, SHR, and BMI preferences

For men, SES did not significantly predict WHR or BMI preferences. However, women's SES was significantly associated with preference for higher SHR, such that women with greater resource scarcity (i.e., lower SES) preferred bodies with higher SHR. Further, women with greater resource scarcity preferred bodies with a higher BMI, consistent with our predictions.

3. Study 2

3.1. Method

3.1.1. Participants

Participants were 150 male and 150 female volunteers recruited from www.socialsci.com, who participated in return for redeemable store credit. Similar to Study 1, the majority of participants were from the US (80% of men, 83% of women) while the remainder were from other Western countries. Participation was conditional on being heterosexual and not currently in a long-term relationship. Data were handled identically to Study 1; that is participants who completed the survey in an unrealistic time (<5 min; 2 males) or were missing data on any variable were removed from analysis (10 males, 26 females). This reduced the sample to 138 males ($M = 23.07$ years, $SD = 9.27$ years) and 124 females ($M = 24.78$ years, $SD = 7.20$ years).

3.1.2. Stimuli

Study 2 used a forced-choice paradigm where participants were shown pairs of bodies side-by-side and asked to rate which body they found more attractive. Participants were shown the opposite-sex, computer generated bodies used in Study 1. Each trial consisted of one of the

Table 2
HLM (γ) fixed effects coefficients (and standard errors) and associated *t* statistics for age SES, pathogen disgust, moral disgust, and sexual disgust in the model predicting preference slopes for WHR, SHR, and BMI for Study 1.

	Males rating females		Female rating males	
	γ (S.E.)	*t* (df = 246)	γ (S.E.)	*t* (df = 232)
Intercept	49.01 (.89)	55.12***	50.46 (.96)	52.57***
Age	.26 (.93)	.28	−.97 (1.04)	−.93
SES	1.17 (.90)	1.30	.57 (.99)	.57
Pathogen Disgust	−.70 (.97)	−.72	−1.42 (1.05)	−1.36
Moral Disgust	3.86 (.94)	4.11***	.63 (1.04)	.60
Sexual Disgust	.65 (.96)	.68	1.31 (1.06)	1.24
WHR/SHR Preferences				
Intercept	−4.16 (.30)	−14.01***	2.81 (.30)	9.32***
Age	.01 (.31)	.03	.35 (.33)	1.07
SES	**.31 (.30)**	**1.04**	**−.63 (.31)**	**−2.03***
Pathogen Disgust	**−.80 (.32)**	**−2.48***	**.27 (.33)**	**.83**
Moral Disgust	.31 (.31)	1.00	.29 (.33)	.89
Sexual Disgust	.57 (.32)	1.78	−.26 (.33)	−.78
BMI Preferences				
Intercept	−10.32 (.50)	−20.77***	3.35 (.60)	5.60***
Age	.02 (.52)	.04	.66 (.65)	1.01
SES	**0.59 (.50)**	**1.18**	**−1.33 (.62)**	**−2.15***
Pathogen Disgust	**−.76 (.54)**	**−1.40**	**.49 (.65)**	**.74**
Moral Disgust	−.21 (.52)	−.41	1.66 (.65)	2.55*
Sexual Disgust	−.16 (.54)	−.29	.02 (.66)	.03

Associations relevant to the main hypotheses are in bold. Note that predictors have been standardised to increase interpretability.
* $p < .05$.
** $p < .01$.
*** $p < .001$.

Table 3
β coefficients and associated *t* statistics for age, SES, pathogen disgust, moral disgust, and sexual disgust in the regression model predicting preference for men's WHR preference, and women's SHR preference for Study 2.

	Males rating female bodies		Females rating male bodies	
	β	*t* (df = 137)	β	*t* (df = 123)
Age	−.08	−.97	.09	.95
SES	**−.19**	**−2.17***	**−.09**	**−.98**
Pathogen Disgust	**−.19**	**−2.07***	**.23**	**2.15***
Moral Disgust	.05	.54	−.14	−1.40
Sexual Disgust	.04	.47	−.10	−1.02

* $p < .05$.

five source bodies paired with the same body that had been manipulated on WHR for female bodies or SHR for male bodies. The manipulated bodies had either one inch added to or subtracted from the circumference of the waist for female bodies, or one inch added to or subtracted from the width of the shoulders for male bodies. This resulted in 10 trials where participants were asked to rate which body they found more attractive on an 8-point scale (1 = right body is much more attractive, 8 = left body is much more attractive). The order in which choices was presented, and whether the source body was presented on the left or right side was randomised. Participants' preference for higher WHR/SHR was calculated as the mean preference across all 10 trials.

3.1.3. Materials

As with Study 1, after completing the forced-choice task participants were given the Three Domain Disgust Scale (Tybur et al., 2009) and the 1-item SES measure (Adler et al., 2000).

3.2. Results

Participants' age, SES, and pathogen, moral and sexual disgust were entered as predictors into a regression with SHR/WHR preference as the outcome variable. Similar to Study 1, the pattern of significance remained unchanged when controlling for participants' ethnicity; therefore, only the original analyses are reported here. Men and women were analysed separately. The results from the regression are reported in Table 3.

3.2.1. Association of pathogen disgust scores with WHR and SHR preferences

For both men rating female bodies and women rating male bodies, we found an association with pathogen disgust and body preferences as predicted. Replicating key effects in Study 1, we found that men higher in pathogen disgust preferred lower WHR, while women higher in pathogen disgust preferred higher SHR. There was no effect of moral or sexual disgust on body shape preferences for either sex, suggesting that this effect was specific to pathogen disgust.

3.2.2. Association of SES scores with WHR and SHR preferences

Men's SES was significantly associated with WHR preference, such that men with greater resource scarcity (i.e., lower SES) preferred higher WHR. While women's SES influenced their SHR preferences in the same direction found in Study 1 (i.e., women with greater resource scarcity preferring higher SHR), this relationship was non-significant.

4. Discussion

In the current studies, we tested whether individual differences in pathogen avoidance or resource scarcity are associated with body shape preferences. Overall, we found that individual differences in pathogen disgust and SES were significantly associated with preferences for relatively narrow female waists (low WHR), broad shoulders relative to male waist circumference (high SHR), and lower body mass (BMI) in both sexes. This is in line with previous findings of environmental factors influencing preference for cues in other domains, such as facial cues, and also supports recent work suggesting that these effects extend to body cues (Jones et al., 2013).

4.1. Men's WHR preferences

Across both studies, we found the predicted association between men's pathogen disgust and their preference for lower WHR (or, simply, smaller waists) in female partners. Since lower WHR is associated with a number of health or fertility benefits (Jasienska et al., 2004; Kaye et al., 1990; Pawlowski & Dunbar, 2005; Singh, 1993; Singh & Singh, 2006; van Hooff et al., 2000; Wass et al., 1997; Zaadstra et al., 1993), this result may indicate that men use the distribution of body fat on a woman's body as a cue to health and men high in pathogen avoidance are placing greater importance on these benefits. We note that these effects cannot be explained by WHR covarying with BMI, as we do not find the same effect when BMI was manipulated in Study 1.

We also find some evidence that resource scarcity may influence men's WHR preference in the predicted direction in Study 2, such that a higher WHR is preferred in harsh environments. Assuming that this relationship exists, this may be because women with higher WHR are associated with higher levels of testosterone, which are thought to better equip these women to compete and acquire resources to deal with scarcity (Cashdan, 2008). This would be advantageous for men partnered with high WHR women, as well as for any mutual offspring during harsh times. However, the relationship between men's resource scarcity and WHR preference was non-significant in Study 1; therefore, we only provide partial support for this hypothesis.

Assuming such a relationship exists, our data could suggest that men face a trade-off between women with a low WHR indicative of good health (which may benefit men directly or indirectly), compared to women with a higher WHR who are better equipped for competing and acquiring resources. This facultative calibration of preferences according to environmental cues is similar to that found in other domains, such as preference for facial cues (Little et al., 2007; Little et al., 2011), or explicitly stated traits (Lee & Zietsch, 2011). These findings could also explain inconsistencies within the literature regarding historical and cultural variation on men's WHR preferences. Fluctuations in environmental conditions (e.g., pathogen prevalence, resource scarcity, or other factors not investigated here) shift the optimum WHR that is most evolutionarily beneficial, which contribute to findings of higher WHR being preferred in non-Western participants (Sugiyama, 2004; Swami et al., 2009; Wetsman & Marlowe, 1999; Yu & Shepard, 1998) or in the past (Lamb et al., 1993; Swami et al., 2007), presumably because these environments were more resource-scarce compared to modern WEIRD societies.

4.2. Women's SHR preferences

We also find evidence that environmental factors may influence women's SHR preference, but this effect is less clear. While both studies found that pathogen disgust and SES influenced SHR preference in the same directions, the pattern of significance was different between studies. In Study 1, SHR preference was significantly, negatively associated with SES, while the effect of pathogen disgust was non-significant. In Study 2, the reverse was true, where pathogen disgust significantly, positively influenced SHR preference, while the effect of SES was non-significant. Because of this, discussion below that environmental factors may influence women's SHR preferences is made tentatively.

If environmental factors do influence women's SHR preference, this may suggest that women use SHR as a cue to evolutionarily beneficial traits. First, results from Study 2 suggest that women may use high SHR as a cue to health; this is consistent with recent work that found an association between women's facial masculinity preference and pathogen avoidance (DeBruine, Jones, Crawford, et al., 2010; DeBruine, Jones, Tybur, et al., 2010; Jones et al., 2013; Little et al., 2011; Penton-Voak et al., 2004), and also recent work suggesting that this effect may also generalise to masculine body shape preferences (Jones et al., 2013). In combination with previous results, our data suggest that masculine facial and body information may act as back-up cues to health. Assuming that there is a link between SHR and health, women could benefit directly from choosing a partner with cues to good health, either indirectly (assuming such traits are heritable), or through direct avoidance of pathogen transmission, or by having a partner who is less likely to succumb to disease (Jones et al., 2013).

Existing theory and research were ambiguous with regard to the expected direction of association between resource scarcity and SHR preference. One possibility was that women may use SHR as a cue of ability to acquire or compete for resources, which could be beneficial for women for whom resource scarcity is salient (Gaullup & Frederick, 2010; Lassek & Gaulin, 2009; Puts, 2010). Our results are consistent with this idea, since women in more resource scarce circumstances (i.e. low SES) preferred higher SHR male bodies. However, our results directly oppose theory and prior research pointing in the other direction: masculine traits have been associated with poor parental attributes in men (Boothroyd et al., 2008; Watkins et al., 2012), and this has been used to successfully predict negative associations between resource scarcity and preference for facial masculinity (Lee et al., 2013; Little et al., 2007; Watkins et al., 2012). Given that high SHR is a masculine trait and is correlated with facial masculinity (Windhager, Schaefer, & Fink, 2011), the opposing findings raise questions regarding how body masculinity combines with other masculine traits to inform mate choice decisions.

4.3. BMI preferences

Study 1 found that pathogen disgust was not associated with BMI preferences in either men or women. This suggests that BMI may not be used as a cue to immunocompetence, despite previous work finding an association between high body weight and impaired immune functioning (Pawlowski et al., 2014; Rantala et al., 2013; Tanaka et al., 1993, 2001). However, we note that the stimuli used in both studies only included bodies that were within the normal range of BMI. If the purported association between BMI and immunocompetence is only apparent when considering bodies outside the normal range, then this could explain why we did not find an association between participants' pathogen disgust and their BMI preferences.

However, we found that SES significantly influenced women's BMI preference consistent with the prediction that higher BMI bodies would be preferred when resources are scarce, when fat stores are more valuable. This is consistent with previous work that has found that individual level resource scarcity influences body weight preferences (Nelson & Morrison, 2005), and may help explain Western societies' modern preoccupation with maintaining a slender figure presumably because resources are plentiful in these environments, and thus the potential health costs of fat storage may outweigh the benefits. However, as there was no significant influence of SES on men's BMI preference, we only provide partial support for this theory.

Alternatively, since BMI is affected by muscle mass as well as fat mass, the finding that women with lower SES prefer men with larger BMIs could reflect a greater preference for muscularity when resources are scarce. Since men have greater relative quantities and variability in fat free muscle mass compared to women (Hruschka, Rush, & Brewis, 2013; Wells, 2007), this may explain why this association is significant for women's preferences of men's bodies but not the reverse, and is consistent with the findings of women's preferences for SHR. Another alternative is that the negative association between SES and men's preferences may simply reflect the differences in average BMI across social class; that is, individuals from lower SES backgrounds may show a preference for higher BMI bodies because, at least in Western societies, higher BMI bodies are more prevalent in those with low SES. This is particularly true for women (Wang & Beydoun, 2007), which might explain why significant effects were found for men's preferences but not women's.

4.4. Limitations

While here we focused on individual differences, we assume that the salience of health and resource threats would have a similar effect on body preferences at an individual and environmental level (as has been found for preferences in other domains; see DeBruine, Jones, Crawford, et al., 2010; Jones et al., 2013). However, further research is needed to confirm this.

Also, while we use relative SES as a proxy for resource scarcity, this measure may not reflect scarcity in terms of decreased access to food or shelter. As the participants were all from Western countries (and had access to the Internet), it could be expected that all participants, regardless of SES, would have plenty of access to caloric resources, as opposed to scarcity experienced by individuals in poorer countries. This distinction between SES and actual scarcity could explain why the results for resource scarcity are inconsistent between studies compared to the associations with pathogen disgust.

Furthermore, we note that when manipulating WHR and SHR, we only altered waist circumference for WHR and shoulder width for SHR (as opposed to also altering hip circumference for both ratios); therefore, it could be the case that our findings reflect the importance of aspects of shape, including absolute waist girth or shoulder width, other than the ratios we use throughout his paper. Indeed, recent work on female body attractiveness suggests that waist width is a better predictor of female body attractiveness than WHR (Brooks et al., 2015), and reanalysis of our results (provided in the supplementary materials, available on the journal's website at www.ehbonline.org) using only waist circumference yielded similar results. However, reanalysis of our data on women's preferences for men suggests stronger associations between individual differences and preference for SHR than mere preference for shoulder width. Further work is needed to clarify more completely how individual differences alter preferences for other body shape attributes that have been found to be important in attractiveness judgements, such as bust, or limb length and girth (Brooks et al., 2010).

4.5. Conclusion

Our findings provide some support to the notion that body shape is used as a cue to health and/or likelihood of resource provision. We note that some associations must be interpreted cautiously; despite all associations being in predicted directions across both studies, the significance of some effects was not consistent over the two studies.

Supplementary materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2015.07.002.

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