Evolution and Human Behavior 36 (2015) 351–358

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Original Article

The multivariate evolution of female body shape in an artificial digital ecosystem☆

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ARTICLE INFO

Article history:
Initial receipt 27 August 2014
Final revision received 13 February 2015

Keywords:
Sexual selection
Body shape
Waist–hip ratio
Body mass index
Multivariate selection
Experimental evolution

ABSTRACT

Human bodies exemplify complex phenotypes, likely to be subject to complex evolutionary forces. Despite the importance of body shape to health, social interactions and self-esteem, our understanding of body evolution and integration remains simplistically focused on simple ratios like waist–hip ratio (WHR), and body mass index (BMI), or manipulations of one or a few traits. Evolutionary selection analyses give a multivariate perspective, but highly correlated body measures create multicollinearity problems. Here we develop an original approach mimicking Darwinian selection to study how clonal lines of bodies, allowed to vary in 24 attributes via a mutation-like process, evolve in a digital ecosystem over 8 generations. Ten of 24 traits changed by more than one |S.D.| over seven generations of selection. Analyses of selection within generations, change in population mean, and change within clonal family lines all implicate slenderness, particularly narrow waists and long legs as the most important dimension of body attractiveness. WHR did not offer any improvement on waist girth as a predictor of attractiveness. Within the most successful clonal lineages, selection favored greater shapeliness, including larger busts, in addition to slenderness. Our results reveal the complex, multivariate nature of attractiveness, and that the success of simple ratios like WHR and BMI in previous studies is probably incidental to the importance of waist girth and general slenderness. Our results also suggest that the integration of the entire body phenotype is at least as important as any one trait, and that more than one way exists to make an attractive body.

1. Introduction

The relationship between female body shape and attractiveness is one of the most vigorously contested subjects in the study of human behavioral evolution. Especially since Devendra Singh (Singh, 1993a) hypothesized that an hourglass physique with a low waist-to-hip ratio (WHR), represents a 'first pass filter' in women's mate value, unambiguously signaling youth, health and fertility to men. The hypothesis is intuitively satisfying because body composition and shape are sexually dimorphic (Wells, 2007), low WHRs are associated with menarche (Lassek & Gaulin, 2006, 2007), with normal menstrual and ovulatory cycling (Moran et al., 1999; van Hooff et al., 2000), with levels of steroid hormones associated with natural fertility (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004), with fecundity independently of overall body fat (Zaadstra et al., 1993), and because the hourglass physique usually wanes with age and toward menopause (Kirschner & Samojlik, 1991).

The significance of WHR as a target of mate choice, however, remains contested. Men prefer low WHRs (0.6–0.7) in England, Germany, Poland, China, the USA, New Zealand and Papua (Dixson, Dixson, Bishop, & Parish, 2010; Dixson, Dixson, Li, & Anderson, 2007; Furnham, Tan, & McManus, 1997; Henss, 2000; Rozmus-Wrzesinska & Pawlowski, 2005; Singh, 1993b; Sorokowski & Sorokowska, 2012). However, studies among several subsistence farming, horticultural and hunter–gatherer groups report that men prefer women with more masculine body shapes (i.e. WHRs >0.8; refs Dixson, Dixson, Morgan, & Anderson, 2007; Sugiyama, 2004; Wetsman & Marlowe, 1999; Yu & Shepard, 1998). While initial studies among Hadza hunter–gatherers using front-posed stimuli found that men preferred high WHRs (Wetsman & Marlowe, 1999), a subsequent replication using stimuli in profile view, so that the buttocks were visible, found that Hadza men preferred WHRs of 0.6 (Marlowe, Apicella, & Reed, 2005). These studies used stimuli that altered only the waist, which confounds WHR with body mass index (BMI = weight / height^2) (Toveé & Cornelissen, 2001) and with waist slenderness alone. While studies using female patients before and after cosmetic surgery found that feminine body shape was an important determinant of female attractiveness (Dixson, Sagata, Linklater, & Dixson, 2010; Singh, Dixson, Jessop, Morgan, & Dixson, 2010), stimuli displayed only the gluteal femoral region, so that height and weight were not assessed.

Cross-cultural research using natural stimuli reveals that BMI accounts for 2–3 times more variance than WHR in women's attractiveness (Swami, Caprario, Tovee, & Furnham, 2006; Swami, Neto, Tovee, & Furnham, 2007; Swami & Tovee, 2007). Other studies using full body stimuli find that abdominal depth (Rilling, Kaufman, Smith,

☆ This study was supported by an ARC Discovery Grant to RCB and BJD and an ARC Professorial Fellowship to RB.
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http://dx.doi.org/10.1016/j.evolhumbehav.2015.02.001
1090-5138/

Patel, & Worthman, 2009), the volume–height index (Fan, Liu, Wu, & Dai, 2004) and the perimeter–area ratio (Toveé, Maisey, Emery, & Cornelissen, 1999) are effective predictors of body attractiveness. Computer-modeling of gluteal femoral fat deposition reveals that the relationship between attractiveness and WHR reflects fat deposition during weight gain (Cornelissen, Toveé, & Bateson, 2009). Thus, WHR may provide only a proxy for attractiveness rather than conveying special biological information beyond size, weight and the amount of body fat.

While a large number of traits are implicated in female physical attractiveness, experimental studies often overlook their multivariate nature, manipulating one or a small number of traits or trait indices that correspond to shape and size. While this approach has the advantage of experimental power and simplicity, it lacks the capacity to detect how various traits integrate and interact to shape the attractiveness of the phenotype. Moreover, manipulating one trait might alter the attractiveness of the entire phenotype due to interactions between the manipulated trait/s and those left unaltered, rather than an independent effect of the manipulated trait (Brooks, Shelly, Fan, Zhai, & Chau, 2010; Donohoe, von Hippel, & Brooks, 2009; Rilling et al., 2009). This is a general problem in the study of correlated suites of traits, and original experimental tests of how various traits contribute to attractiveness can shed considerable new light on old, hotly contested questions.

Although many somatic indices can be measured, giving considerable detail to the dimensions by which bodies vary, many traits tend to be very tightly correlated with one another (Brooks et al., 2010). Selection analyses have been applied to attractiveness ratings of real or scanned images of bodies to some effect, revealing that low WHRs, arm length and breast size act in concert to determine female physical attractiveness (Brooks et al., 2010). However, the large number of correlated measurable traits means that multiple linear regressions run into serious issues of multicollinearity, even after a small number of traits have been added. This is especially true for body-scanning data, wherein hundreds of highly correlated measures are taken, resulting in difficulties in identifying the relative importance of some traits in determining attractiveness (Brooks et al., 2010; Fan, Dai, Liu, & Wu, 2005; Fan et al., 2004).

Evolutionary biologists have long appreciated the difficulties inherent to inferring selection on suites of correlated traits. Evolutionary selection analysis (Janzen, 1993; Lande & Arnold, 1983) can help resolve the true targets of selection among groups of correlated traits by means of linear and non-linear multiple regression analyses. These approaches have already been implemented to estimate selection on complex human phenotypes (e.g. Brooks et al., 2010; Hill et al., 2013). Unfortunately multicollinearity problems can still obscure a full understanding of selection when large numbers of tightly correlated traits are involved. This is the case for human bodies in which size and weight strongly influence most measures.

Together, selection analysis combined with experimental manipulation of several traits can contribute to a better understanding of how multivariate selection shapes complex suites of correlated traits. Our lab has previously developed this approach to study selection on tightly-coupled attributes of acoustic signals in small animals (Bentsen, Hunt, Jennions, & Brooks, 2006; Brooks et al., 2005; Gerhardt & Brooks, 2009), for a three-trait study of human torsos (Donohoe et al., 2009), and Mautz, Wong, Peters, and Jennions (2013) adopted this approach to estimate the effects of penis size, torso shape and height on men's attractiveness to women.

New digital techniques enable the experimental manipulation of body shape parameters in order to test their effects on physical attractiveness, including digital silhouettes and avatars (Koscinski, 2012, 2013b; Mautz et al., 2013). In the present study we extend this approach, constructing CGI images of bodies that we experimentally varied along 24 dimensions independently. We added a further innovation by 'breeding' from the most successful phenotypes (in this case the most attractive bodies), allowing those bodies, and the population, to evolve over multiple generations. By measuring selection on and change in the 24 traits, we infer their importance in determining the attractiveness of bodies.

2. Methods

2.1. Stimuli

We began with measures from 273 women living in the USA (from the SizeUSA data set, $[TC]^2$; www.tc2.com), from which we calculated means and standard deviations for the 24 traits used in this study (traits and descriptive statistics listed in Table 1). We then drew 20 of these women at random and compared their trait values in order to ensure no two females were too similar to each other (using pairwise summed Euclidian distances between bodies for all 24 traits). We found five pairs of women who were very similar to one another and replaced one from each of these pairs with another woman drawn at random, until we were satisfied we had 20 sufficiently different female bodies to act as our 20 "progenitor" females. The mean trait values for the 20 progenitor females were very similar to the overall mean for the sample of 273 measured females.

Across all generations of this experiment, bodies that descended from a given progenitor female are considered to be a part of the same clonal 'family'. From each progenitor female we made five F1 daughters by varying each of the 24 traits according to what we call our "mutation routine". For each trait we first generated a unique random number between 0 and 1 using Microsoft Excel's "rand()" function. We then converted this probability into a z-score (i.e. a place on a normal distribution with a mean of 0 and a standard deviation of 1) by applying Excel's "=normsinv" function to the probability. We then multiplied the z-score by the original standard deviation for that trait, divided it by five, and added the result to the parent's (in the case of F1 daughters, the progenitor female's) value for that trait. We repeated this procedure independently for each of the 24 traits (i.e. drawing a unique random number for each trait). The result is that each daughter's trait values changed by a small amount from those of her mother, with the changes independent of one another and each distributed with a mean of zero and a standard deviation of 0.2 times the original standard deviation. We applied the mutation routine independently to each of the 5 daughters of each progenitor female, giving six females from each 'family' for the first generation of selection that varied subtly, and in independent ways, from one another.

We used the trait values for the 20 progenitor females and their 100 F1 daughters to build three-dimensional computer-generated models of each in Avatar Engine, software custom built for us by $[TC]^2$ (www.tc2.com) based on their ImageTwin technology. Each body was rendered in a medium-grey color, without hair. To present a given body for assessment in the experiment, we rendered a front-on and a side-on version of that body (in Anim8or software, www.anim8or.com) and presented them with pixelated heads (to prevent faces or lack of hair from distracting raters) in a single graphic (see example in Fig. 1). Bodies were presented in front of a light gray Volkswagen Beetle car to provide a height scale that would be recognizable in most countries where people might be rating bodies on an internet website. We then uploaded the 120 images to our digital 'ecosystem' at bodylab.biz, where they were to be rated.

2.2. The first generation of selection

We recruited participants to www.bodylab.biz via social media promotion and by discussing our project with various news media. On entry to the study, each participant provided some biographic data and was shown a standard panel of six example bodies and provided information on the rating scale to be used. Each participant was then consecutively shown 30 stimulus bodies, drawn at random from that generation's pool of 120 bodies in the ecosystem, and asked to rate