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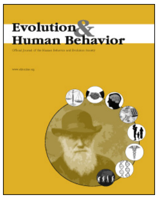

Original Article

Quantifying the strength and form of sexual selection on men's traits ☆

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ABSTRACT

Although recent research has increasingly focused on human sexual selection, fundamental questions remain concerning the relative influence of individual traits on success in competition for mates and the mechanisms, form, and direction of these sexual selective pressures. Here, we explore sexual selection on men's traits by ascertaining men's dominance and attractiveness from male and female acquaintances. On a large American university campus, 63 men from two social fraternities provided anthropometric measurements, facial photographs, voice recordings, and reported mating success (number of sexual partners). These men also assessed each other's dominance, and 72 women from two socially affiliated sororities assessed the men's attractiveness. We measured facial masculinity from inter-landmark distances and vocal masculinity from acoustic parameters. We additionally obtained facial and vocal attractiveness and dominance ratings from unfamiliar observers. Results indicate that dominance and the traits associated with it predict men's mating success, but attractiveness and the traits associated with it do not. These findings point to the salience of contest competition on men's mating success in this population.

1. Introduction

A rapidly growing literature suggests that sexual selection has shaped men's phenotypic traits (Puts, Jones, & DeBruine, 2012). Men's bodies (Pawlowski & Jasienska, 2005), faces (Penton-Voak & Perrett, 2000; Rhodes, Chan, Zebrowitz, & Simmons, 2003), and voices (Fitch & Giedd, 1999; Puts, Apicella, & Cárdenas, 2012) exhibit features that are highly sexually differentiated and develop at sexual maturity. These traits also appear to aid in competition for mates. In men, more masculine, muscular bodies (Dixson, Dixson, Bishop, & Parish, 2010; Frederick & Haselton, 2007; Hughes, Dispenza, & Gallup, 2004) and tall stature (Nettle, 2002; Pawlowski, Dunbar, & Lipowicz, 2000; Pawlowski & Jasienska, 2005) predict reported number of sexual partners and perceptions of attractiveness and dominance. Masculine faces also convey dominance (DeBruine et al., 2006; Perrett et al., 1998; Watkins, Jones, & DeBruine, 2010), and some studies (DeBruine et al., 2006; Johnston, Hagel, Franklin, Fink, & Grammer, 2001), but not others (DeBruine, Jones, Smith, & Little, 2010; Perrett et al., 1998; Rhodes, Hickford, & Jeffery, 2000), have found that women prefer masculine male faces, particularly during the fertile phase of the ovulatory cycle (Johnston et al., 2001; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999; Welling et al., 2007). Similarly, masculine voices have been found to predict men's number of reported sex partners (Hodges-Simeon, Gaulin, & Puts, 2011; Puts, 2005) and reproductive success (Apicella, Feinberg, & Marlowe, 2007). In addition, masculine acoustic features, such as deep timbre and low pitch influence perceptions of both dominance (Jones, Feinberg, DeBruine, Little, & Vukovic, 2010; Puts, Hodges, Cárdenas, & Gaulin, 2007; Watkins, Fraccaro, et al., 2010; Wolff & Puts, 2010) and attractiveness (Feinberg, Jones, Little, Burt, & Perrett, 2005; Hodges-Simeon, Gaulin, & Puts, 2010), the latter particularly during the fertile phase of the ovulatory cycle (Feinberg et al., 2006; Puts, 2005, 2006).

Such research has helped illuminate whether and how sexual selection has shaped men's phenotypes, yet a number of fundamental questions remain. First, prior studies have typically focused on either female choice or male contests without attempting to quantify the relative contributions of these mechanisms to the total sexual selective pressure on a particular trait (Hunt, Breuker, Sadowski, & Moore, 2009). Second, to our knowledge, no study reporting relationships between a male trait and mating success has investigated whether these relationships were mediated by attractiveness or dominance. Third, most studies of sexual selection in

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men have measured success under female choice or male contests from limited information, such as body size, strength, or ratings of faces or voices made by strangers in the laboratory (but see, e.g., Pillsworth, 2008; von Rueden, Gurven, & Kaplan, 2011). Attractiveness and dominance have thus frequently been assessed devoid of relevant information, such as personality and intelligence, and in isolation from the complex webs of social relationships in which we live. Fourth, facial, vocal, and bodily characteristics may be developmentally correlated (Feinberg, 2008; Fink, Neave, & Seydel, 2007), so when exploring relationships between each and success in mating competition, it is necessary to measure and statistically control for the others, as well as to explore their interactions (i.e., correlational selection). Fifth, nearly all prior research on these traits has assumed linear (directional) selection without exploring quadratic selection gradients (i.e., stabilizing or disruptive selection). Finally, previous studies have not explored whether female choice or male contests contribute more strongly to men's mating success, despite the centrality of this question in understanding human sexual selection (Puts, 2010). In sum, we still do not know the overall sexual selective pressures on individual traits, the relative strengths of sexual selection on different traits, the forms and mechanisms of this sexual selection, or even the relative importance of female choice and male contests in men's competition for mates.

In the present paper, we therefore investigated sexual selection on some of the strongest candidates for sexually selected traits in men: stature, body build, facial masculinity, and deep voices (Fig. 1). We measured these traits in a sample of men and obtained assessments of the men's success under intra- and intersexual selection from logically the most authoritative source: familiar male and female peers (Pillsworth, 2008; von Rueden et al., 2011). We also obtained assessments of the men's facial and vocal attractiveness and dominance from unfamiliar raters, as well as the men's self-reported mating success. We then 1) investigated the contributions of these traits to different mechanisms of sexual selection (mate choice and contests) and to mating success via their linear, quadratic, and correlational selection gradients, and 2) compared mechanisms of sexual selection to each other and to mating success using a sequential model-building approach (Draper & John, 1988) to identify whether the strength, direction, and form of sexual selection on male traits differ across these episodes, and if so, which traits contribute to these overall differences.

Although we are interested in how past selection produced present sexual dimorphisms, we take a behavioral ecological approach, which emphasizes contemporary selection. We take this approach because we expect that, in general, current function will provide insight into past function. However, attractiveness, dominance, and even mating success have likely been at least partly decoupled from reproductive success by features of modern industrial environments such as effective contraception and socially imposed monogamy (Perusse, 1993). We therefore examined components of reproductive success that are “upstream” of fertility. Assuming that these components affected ancestral men's reproductive output, and in parallel with nonhuman literature, which also frequently measures only proximate components of fitness, we refer to “selective surfaces”, “directional selection”, and the like.

2. Methods

2.1. Participants

We recruited members of two social fraternities ($N = 63$, mean age ± $SE = 19.9 \pm 0.15$) and two sororities ($N = 72$, mean age ± $SE = 19.4 \pm 0.11$) from a large university in the northeastern United States. Each fraternity was socially affiliated with one of the sororities, regularly attending joint social functions. Participating fraternity members (male *participants*) were paid US$15, and participating sorority members (female *participants*) were paid US$10. We also recruited male ($N = 36$, mean age ± $SE = 20.3 \pm 0.42$) and female ($N = 43$, mean age ± $SE = 19.0 \pm 0.14$) *raters* from the university's psychology department subject pool. Raters were unfamiliar with the male participants. All methods were approved by the university's Institutional Review Board.

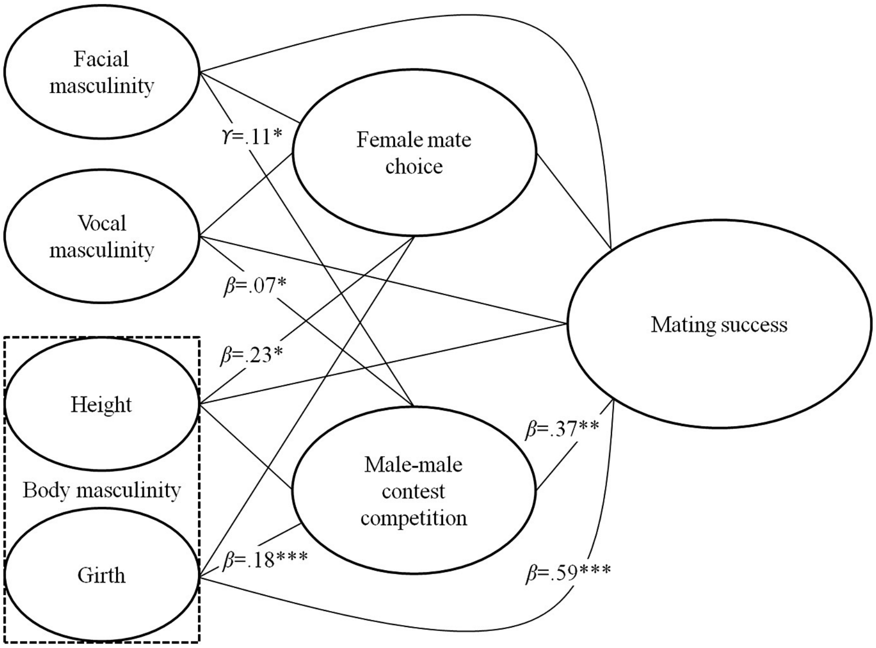

Fig. 1. Linear (β) and quadratic (γ) relationships (statistics shown for statistically significant relationships) between men's traits, success under female choice and male contests, and mating success. Linear, quadratic and interaction terms for variables in each level to the left (e.g., men's traits) were entered into multiple regression models to predict variables at higher levels to the right (e.g., success under female choice). Biceps, chest, and shoulder circumference, and weight were standardized and summed to produce the composite variable, Girth. $^{*}p < .05$, $^{**}p < .001$, $^{***}p < .0001$.

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2.2. Participant procedures

We collected data at male participants' residence (fraternity) houses using a series of stations. The first station acquired informed consent; other stations collected voice recordings, facial photographs, anthropometric measurements, and answers to online questionnaires. Male participants' voices were recorded in a quiet room using a Shure SM58 vocal cardioid microphone placed approximately 9.5 cm from the participant's mouth. Voices were recorded in mono with a sampling frequency of 44,100 Hz as male participants spoke the first six sentences of the Rainbow Passage (Fairbanks, 1960). For facial photographs, participants were instructed to remove all earrings, glasses, and facial jewelry, and to use a headband if hair covered any part of their faces. We asked participants to sit upright in a chair and maintain a relaxed, neutral facial expression with the mouth lightly closed. Participants posed approximately 2 m from the camera, and the flash was always used. Height and chest, shoulder, and flexed biceps circumference were taken with a measuring tape, and weight was obtained using an electronic scale (Table E1). For online questionnaires, participants were seated privately. Male participants answered demographic questions; the revised Sociosexual Orientation Inventory (SOI-R) (Penke & Asendorpf, 2008), which targets attitudes, desires, and behavior regarding uncommitted sex; and with how many women they had sexual intercourse in the past year (Table E1).

One week after initial data collection, we returned to the residences, at which time male participants were seated privately at computers and sequentially shown facial photographs of all other male participants from their fraternity. Participants were asked what percentage of men each pictured man could beat in a physical fight (0% to 100% in increments of 10%), and to estimate with how many women the pictured man had had sexual intercourse in the past year.

In order to control for any differences across photographs in ambient light, we chose a photograph with optimal lighting and matched all other photographs to its brightness using the Match Color function in Adobe Photoshop CS6. Interpupillary distance was also standardized across photographs. Order of rating tasks and presentation order of stimuli were randomized.

Female participants were brought individually into the lab, sequentially shown facial photographs on a computer of all male participants from their affiliated fraternity, and asked to rate on a 10-point Likert scale how attractive each was for a “short-term, purely sexual relationship, such as a one-night stand”, and demographic questions. Rating task order and stimulus presentation order were randomized as above. We utilized ratings of short-term, sexual attractiveness, rather than attractiveness for a long-term, committed relationship, because masculine traits more strongly affect short-term, sexual attractiveness (e.g., Frederick & Haselton, 2007; Puts, 2005), and because we expected sexual attractiveness to more strongly predict number of sexual partners. In other words, short-term, sexual attractiveness measures the type of intersexual selection that would more strongly link masculine traits with men's mating success.

2.3. Independent male and female rater procedures

Independent male and female raters viewed photographs of the male participants' faces and listened on Sennheiser HD 280 Pro headphones to recordings of male participants reading the first sentence of the Rainbow Passage. We standardized voice amplitude (mean ± SD = 71.5 ± 2.4 dB) using Praat version 5.3, and photographs were standardized as above. Face and voice stimuli were split randomly into two sets so that each independent rater rated half of the stimuli, but all stimuli were evaluated an equal number of times. Male raters evaluated faces and voices for fighting ability, while female raters evaluated faces and voices for attractiveness in a short-term, sexual relationship. The same questions and scales used for the male and female participants were used with the independent raters. Rating task order and stimulus presentation order were randomized as above.

2.4. Data treatment

We calculated a facial masculinity index (Table E1) by placing a series of 30 landmarks on each male participant's digital facial photograph, then calculating seven sexually differentiated inter-landmark distances and angles and standardizing and summing these measures. Eye width, lower face height/total face height, cheekbone prominence, and face width/lower face height were measured following Penton-Voak and Perrett (2001), and eye height, jaw angle, and nose width were measured following Burriss, Roberts, Welling, Puts, and Little (2011).

Vocal masculinity was computed by standardizing and summing two highly sexually differentiated acoustic parameters, fundamental frequency (F_0) and formant position (P_f), obtained from male participants' voice recordings measured in Praat, version 5.3 (Table E1). Lower F_0 and P_f correspond with deeper, more masculine pitch and timbre, respectively. Pitch floor and ceiling were 75 Hz and 300 Hz; otherwise, default settings were used. Formant frequencies F_1 through F_4 were measured at each glottal pulse and averaged across measurements, as in Puts et al. (2012). Formant measurements obtained by this method correlate highly (r varied between 0.93 and 0.98) with measurements obtained by measuring and averaging across individual vowels (Puts et al., 2012). We then computed P_f, defined as the average standardized formant value for the first four formants, as in (Puts et al., 2012). Means and SDs used to standardize formants were: $F_1 = 417.2 \pm 31.7$ Hz, $F_2 = 1476.9 \pm 47.0$ Hz, $F_3 = 2457.9 \pm 68.9$ Hz, $F_4 = 3426.8 \pm 91.2$ Hz.

Anthropometric measurements were entered into a principal components analysis with varimax rotation. Biceps, chest, and shoulder circumference, and weight loaded onto the first component, and height loaded onto the second component. We consequently standardized and summed biceps, chest, and shoulder circumference, and weight to produce the composite variable “girth”.

Each male participant's facial and vocal attractiveness and dominance were measured as the mean short-term attractiveness and fighting ability ratings, respectively, that he received from the independent raters who assessed his facial photo and voice recording (mean inter-class correlation coefficient (ICC) = 0.76, range: 0.60–0.91, Table E1). Each male participant's success under female choice was measured as the mean short-term attractiveness rating that he received from female participants (ICC = 0.90, 0.95 for the two fraternities, Table E1). Each male participant's success in male contests was measured as the mean rating of fighting ability that he received from the male participants who rated him (ICC = 0.91, 0.95 for the two fraternities, Table E1). To measure predisposition toward uncommitted sex, we summed the attitudinal and desire components of the SOI-R (Penke & Asendorpf, 2008). Lastly, we used self-reported number of sex partners in the past year (Faurie, Pontier, & Raymond, 2004; Hodges-Simeon et al., 2011) to measure mating success.

2.5. Statistical analysis

We first investigated the contributions of masculine traits to different mechanisms of sexual selection and to mating success via their linear, quadratic, and correlational selection gradients. After standardizing trait values (to zero mean and unit variance) and converting absolute fitness for each individual (mating success or success under each mechanism of sexual selection) to relative fitness (ω) by dividing by the mean fitness of the sample, we used multiple regression to estimate the standardized linear selection gradients (β) (Phillips & Arnold, 1989). We then estimated nonlinear forms of selection by running a separate regression that includes quadratic and cross-product terms to estimate the matrix of standardized nonlinear selection gradients (γ) (Phillips & Arnold, 1989).

Interpreting the size and strength of individual elements in γ can underestimate the true strength of nonlinear selection (Blows & Brooks, 2003). We therefore performed a canonical analysis of the γ matrix to find the major axes of the response surface (Phillips & Arnold, 1989). This results in an **M** matrix consisting of *i* eigenvectors ($\mathbf{m}_i$), each of which describes a major axis of the response surface (where *i* is the original number of traits being examined). The strength of linear selection along each eigenvector is given by $\boldsymbol{\theta}_i$, and the strength of nonlinear selection is given by its eigenvalue (λ_i). $\boldsymbol{\theta}_i$ and λ_i were estimated using the double linear regression method of Bisgaard and Ankenman (1996). As our response variables were not normally distributed, we tested the significance of our standardized selection gradients and linear and nonlinear selection operating on the eigenvectors of γ using randomization tests, as recommended by Mitchell-Olds and Shaw (1987). These procedures, including randomization tests, are provided in detail in Lewis, Wedell, and Hunt (2011).

We used thin-plate splines (Green & Silverman, 1994) to visualize the major axes of the response surface extracted from the canonical analysis of γ. We used the *Tps* function in *fields* package of R (version 2.13.0; freely available at http://www.r-project.org) to fit a spline surface using the lambda value that minimized the generalized cross-validation (GCV) score. We then plotted the surface using perspective view in R.

We compared mechanisms of sexual selection to each other and to mating success using a sequential model-building approach (Draper & John, 1988), a hierarchical model that first compares linear sexual selection, then quadratic and correlational sexual selection to identify whether the direction and form of sexual selection on male traits differ across these episodes, and if so, which individual trait contributes to the overall differences. Univariate interaction terms from the complete models were used to determine which individual traits contributed to any overall significant difference (see [Lewis et al., 2011] for a full description of this approach).

3. Results

3.1. Female choice

Female choice exerted directional (linear) selection favoring height (Fig. 1, Table 1A). There was also negative correlational selection between girth and facial and vocal masculinity (Table 1A): as girth increased, men with lower facial and vocal masculinity became more attractive. Female choice did not exert significant quadratic selection on male traits (Table 1A).

Table 1
The vector of standardized linear selection gradients (β) and the matrix of standardized quadratic and correlational selection gradients (γ) for facial masculinity (FaMasc), vocal masculinity (VoMasc), height and Girth operating through female choice, male contests and mating success.

		β	γ			
			FaMasc	VoMasc	Height	Girth
a. Fem. choice	FaMasc	0.08	0.20			
	VoMasc	−0.02	0.22	−0.01		
	Height	0.23*	−0.15	0.06	0.27	
	Girth	−0.09	−0.39**	−0.34*	0.07	−0.07
b. Male cont.	FaMasc	−0.03	0.11*			
	VoMasc	0.07*	0.05	−0.04		
	Height	−0.01	−0.04	0.04	0.01	
	Girth	0.18***	−0.19**	−0.02	−0.05	0.05
c. Mat. succ.	FaMasc	−0.13	0.16			
	VoMasc	−0.07	0.39*	0.02		
	Height	−0.18	−0.22	0.01	0.11	
	Girth	0.59***	0.05	−0.16	−0.32*	0.13

Randomization tests: ***$p < 0.0001$, **$p < 0.001$, *$p < 0.05$.

Canonical analysis of γ revealed two eigenvectors with significant nonlinear sexual selection ($\mathbf{m}_1$ and $\mathbf{m}_4$, Table 2A). The dominant eigenvector of nonlinear selection ($\mathbf{m}_1$) had a positive eigenvalue, indicative of disruptive selection, and was heavily weighted by a positive loading from girth and negative loadings from facial and vocal masculinity (Table 2A). This result parallels results of the regression analysis in that it signifies negative correlational selection between girth and facial and vocal masculinity. The second significant eigenvector of nonlinear selection ($\mathbf{m}_4$) had a negative eigenvalue, indicative of stabilizing selection, and was heavily weighted by a positive loading from girth (Table 2A). This combination of significant positive and negative eigenvalues suggests that the fitness surface for female choice is best described as a multivariate saddle (Fig. 2A). There was also significant linear selection on $\boldsymbol{m}_2$, which was heavily weighted by a positive loading from height (Table 2A).

3.2. Male contests

Male contests showed directional selection favoring increased girth and vocal masculinity (Fig. 1, Table 1B). There was also significant disruptive (positive quadratic) selection on facial masculinity (Fig. 1, Table 1B), as well as negative correlational selection between girth and facial masculinity (Table 1B).

Canonical analysis of γ revealed two eigenvectors with significant nonlinear sexual selection ($\mathbf{m}_1$ and $\mathbf{m}_4$, Table 2A). The dominant eigenvector of nonlinear selection ($\mathbf{m}_1$) had a positive eigenvalue and was heavily weighted by a positive loading from girth and a negative loading from facial masculinity (Table 2A). This eigenvector was also subject to significant positive linear selection (Table 2A). The second eigenvector of nonlinear selection ($\mathbf{m}_4$) had a negative eigenvector and was heavily weighted by positive loadings from girth and facial masculinity (Table 2A). This eigenvector also experienced significant positive linear selection favoring an increase in girth and facial masculinity. As shown for female choice, the combination of significant positive and negative eigenvalues suggests that the fitness surface for male contests is best described as a multivariate saddle (Fig. 2A). There was also significant negative linear selection on $\mathbf{m}_3$, which favors increased vocal masculinity (due to the negative contribution of this trait to this eigenvector).

Table 2
The **M** matrix of eigenvectors from the canonical analysis of γ in Table 1 for female choice, male contests and mating success.

		M				Selection	
		FaMasc	VoMasc	Height	Girth	$\boldsymbol{\theta}_i$	λ_i
a. Fem. choice	$\boldsymbol{m}_1$	−0.68	−0.47	0.07	0.56	−0.07	0.35**
	$\boldsymbol{m}_2$	−0.19	0.21	0.94	−0.17	0.21*	0.16
	$\boldsymbol{m}_3$	0.60	−0.74	0.30	0.07	0.12	−0.09
	$\boldsymbol{m}_4$	0.37	0.44	0.12	0.81	−0.02	−0.22**
b. Male cont.	$\boldsymbol{m}_1$	−0.75	−0.18	−0.04	0.64	0.13**	0.14**
	$\boldsymbol{m}_2$	0.27	−0.34	−0.89	0.16	0.01	0.02
	$\boldsymbol{m}_3$	−0.15	−0.89	0.21	−0.41	−0.14**	−0.03
	$\boldsymbol{m}_4$	0.59	0.30	0.41	0.63	0.07*	−0.07*
c. Mat. succ.	$\boldsymbol{m}_1$	0.69	0.40	−0.53	0.30	0.16	0.29**
	$\boldsymbol{m}_2$	−0.31	−0.53	−0.44	0.65	0.54**	0.22
	$\boldsymbol{m}_3$	0.15	0.16	0.71	0.67	0.24*	−0.14
	$\boldsymbol{m}_4$	0.64	−0.73	0.19	−0.16	−0.17	−0.18*

The linear ($\boldsymbol{\theta}_i$) and quadratic (λ_i) gradients of selection along each eigenvector are given in the last two columns. The quadratic selection gradients (λ_i) of each eigenvector ($\mathbf{m}_i$) are equivalent to the eigenvalue. Randomization tests: ** $p < .001$, * $p < .05$.

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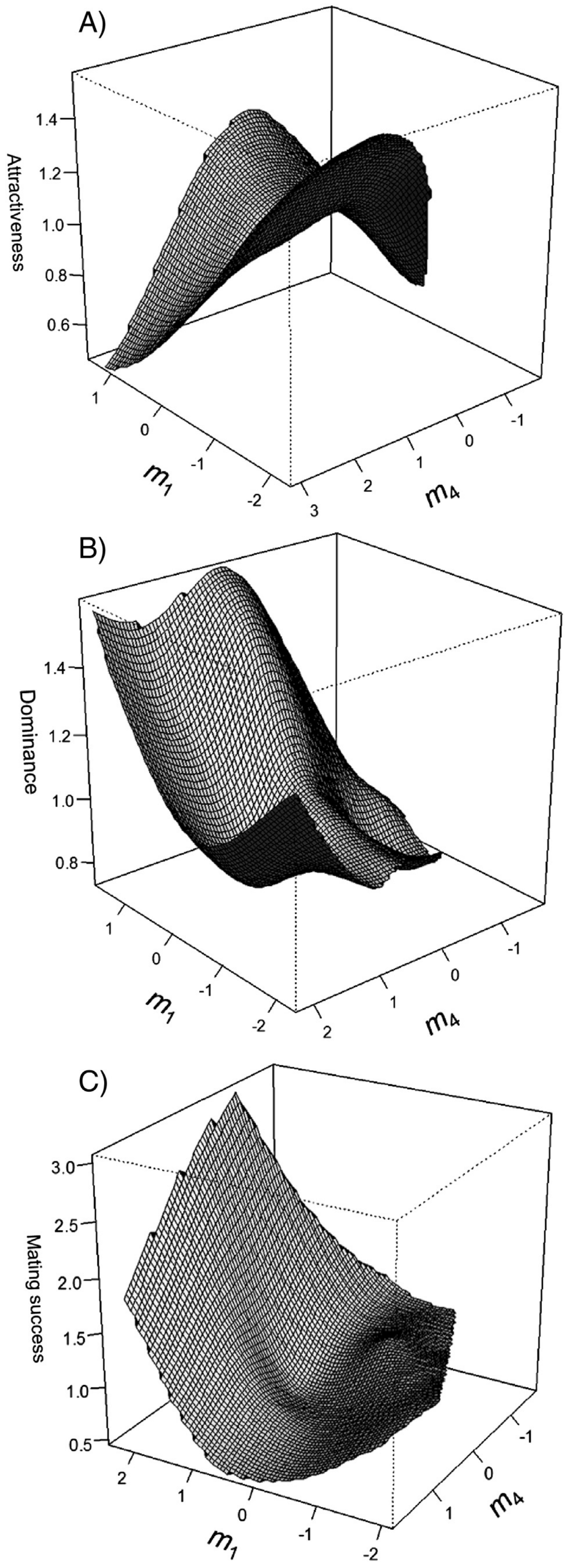

Fig. 2. Correlational selection on eigenvectors m_1 and m_4 (see Table 2) under (A) female choice, (B) male contests, and (C) mating success.

3.3. Female choice vs. contests

The strength and form of linear sexual selection acting on the four male traits differed significantly between female choice and male contests ($F_{4,106} = 3.44$, $p = 0.011$). This was due to selection for greater height through female choice ($F_{1,106} = 3.92$, $p = 0.050$) and greater girth through male contests ($F_{1,106} = 5.15$, $p = 0.025$). There was no difference in quadratic sexual selection ($F_{4,98} = 1.92$, $p = 0.113$). Correlational selection differed between these mechanisms of sexual selection ($F_{6,86} = 2.31$, $p = 0.041$) due to selection for negative covariance between girth and vocal masculinity through female choice ($F_{1,86} = 3.99$, $p = 0.049$).

3.4. Mating success

Mating success was measured by participants' self-reported numbers of sex partners. These numbers were highly correlated with average estimates made by their male peers ($r_{52} = 0.47$, $p < 0.0005$), suggesting reliability in assessing mating success. Mating success exerted directional selection favoring girth, negative correlational selection on girth and height, and positive correlational selection on facial and vocal masculinity (Table 1C).

Canonical analysis of γ revealed two eigenvectors with significant nonlinear sexual selection ($\mathbf{m_1}$ and $\mathbf{m_4}$, Table 2C). The dominant eigenvector of nonlinear selection ($\mathbf{m_1}$) had a positive eigenvalue and was heavily weighted by a positive loading from facial masculinity and a negative loading from height. The second eigenvector of nonlinear selection ($\mathbf{m_4}$) had a negative eigenvector and was heavily weighted by a positive loading from facial masculinity and a negative loading from vocal masculinity. As shown for female choice and male contests, the combination of significant positive and negative eigenvalues suggests that the fitness surface for mating success is best described as a multivariate saddle (Fig. 2C). There was also significant positive linear selection on $\mathbf{m_2}$ and $\mathbf{m_3}$, which favors increased girth and decreased vocal masculinity ($\mathbf{m_2}$) and increased height and girth ($\mathbf{m_3}$).

Despite evidence of selection on men's traits through female choice, linear sexual selection acting on the four male traits differed significantly between female choice and mating success ($F_{4,111} = 3.94$, $p = 0.005$). This was because female choice selected for greater height ($F_{1,111} = 3.95$, $p = 0.049$), and mating success selected for greater girth ($F_{1,111} = 12.30$, $p = 0.001$). Neither quadratic ($F_{4,103} = 1.75$, $p = 0.145$) nor correlational ($F_{6,91} = .82$, $p = 0.561$) sexual selection differed significantly between female choice and mating success. In contrast, the strength and form of linear ($F_{4,111} = 2.040$, $p = 0.093$), quadratic ($F_{4,103} = .962$, $p = 0.431$) and correlational sexual selection ($F_{6,91} = 1.192$, $p = 0.318$) imposed on male traits through male contests did not differ significantly from that imposed by mating success.

When mating success was used as the fitness measure and success under female choice (attractiveness) and male contests (dominance) were treated as traits, there was directional selection for dominance, but not attractiveness (Fig. 1, Table 3). Canonical analysis revealed that dominance loaded positively and attractiveness loaded negatively onto the first eigenvector, which exhibited positive linear

Table 3
The vector of standardized linear selection gradients (β) and the matrix of standardized quadratic and correlational selection gradients (γ) for the influence of men's attractiveness and dominance on mating success.

	β	γ	
		Dominance	Attractiveness
Dominance	.37**	.11	
Attractiveness	.07	−.11	.06

Randomization tests: ** $p < .001$.

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selection. Both dominance and attractiveness loaded positively onto the second eigenvector, which exhibited positive linear selection (Table 4).

3.5. Additional analyses

3.5.1. Subjective ratings of faces and voices

Because our measurements of facial and vocal masculinity could not capture all information available for perceptions of facial and vocal attractiveness and dominance, we performed a second set of analyses, similar to those above, substituting for objective masculinity measurements the subjective assessments of attractiveness and dominance made by independent raters.

Although facial and vocal attractiveness (Table E2a) and related eigenvectors (Table E3a: $\boldsymbol{m_1}$, $\boldsymbol{m_2}$) positively linearly predicted success under female choice, they did not predict mating success (Tables E2b, E3b). Again, linear, but not quadratic or correlational, sexual selection on male traits acting through female choice differed from that acting through mating success (see ESM).

When ratings of facial and vocal dominance were substituted for facial and vocal masculinity measurements, girth (Table E4a) and related eigenvectors (Tables E5a: $\boldsymbol{m_1}$, $\boldsymbol{m_3}$, $\boldsymbol{m_4}$; E5b: $\boldsymbol{m_1}$) again linearly predicted dominance and mating success. As above, there was no significant difference in linear or quadratic sexual selection acting on male traits under contests vs. mating success, although there was a significant difference in correlational selection acting on the covariance between height and vocal dominance and between height and girth (see ESM).

3.5.2. Sociosexuality

To control for the effects of sociosexual psychology on sexual behavior, we reran analyses involving mating success including the summed attitudes and desires components of the SOI-R. Girth, sociosexual psychology (Table E6), and related eigenvectors (Table E7: $\boldsymbol{m_1}$, $\boldsymbol{m_2}$, $\boldsymbol{m_4}$) positively linearly predicted mating success.

When mating success was used as the fitness measure and attractiveness, dominance, and sociosexual psychology were treated as traits, there was directional selection for dominance, sociosexuality (Table E8), and an eigenvector onto which dominance and sociosexuality loaded heavily (Table E9: m_1), but not attractiveness (Table E8). Dominance and sociosexuality also positively interacted in predicting mating success (Table E8).

4. Discussion

Female choice exerted positive directional selection on height and stabilizing selection on an eigenvector that was heavily weighted by girth. These results corroborate previous research finding that women prefer taller males particularly for short-term mating (Pawlowski & Jasienska, 2005), and that they prefer men of intermediate brawniness (Frederick & Haselton, 2007). Moreover, both multiple regression analysis and canonical analysis indicated selection under female choice for negative covariance between girth and facial and vocal masculinity, suggesting that the brawnier a man is, the more important it is for him to have a feminine face and voice, and vice versa. Female choice favored more attractive, but not more masculine, faces and voices, and facial attractiveness became more important as height increased. These results indicate that beyond height, masculine features tend not to make independent positive contributions to success under female choice, suggesting that other factors may have operated in the selection of masculine traits in men.

Table 4
The M matrix of eigenvectors from the canonical analysis of γ in Table 3.

	M		Selection	
	Dominance	Attractiveness	θ_i	λ_i
m_1	.78	-.62	.25*	.10
m_2	.62	.78	.28*	-.02

The linear (θ_i) and quadratic (λ_i) gradients of selection along each eigenvector are given in the last two columns. The quadratic selection gradients (λ_i) of each eigenvector (m_i) are equivalent to the eigenvalue. Randomization tests: $^*p < .05$.

In contrast, male contests exerted positive directional selection on girth and vocal masculinity. This was evident in the results of both our multiple regression and canonical analyses. These results support the notion that men's approximately 60% greater muscularity (Lassek & Gaulin, 2009) and voices approximately five standard deviations lower in pitch and timbre (Puts et al., 2012) evolved in the context of male contests (Puts, 2010). There was also disruptive selection for facial masculinity, and selection for negative covariance between facial masculinity and girth, indicating that men high in girth were more dominant if their faces were less masculine. Canonical analysis indicated disruptive selection on an eigenvector related to high girth and low facial masculinity, and stabilizing selection on an eigenvector related to high girth and high facial masculinity. Given little evidence that men generally deferred to, or that women preferred, men with masculine faces in the present study, perhaps facial masculinity evolved in men not so much as a dominance signal or sexual ornament but because robust facial skeletal structure was protective against facial fractures incurred in physical fights (Puts, 2010).

The selective surface under female choice differed from those under both male contests and mating success due to positive directional selection for height under female choice and for girth under male contests and mating success. The selective surfaces under male contests and mating success were largely similar. Overall success under male contests (male acquaintance-rated dominance) predicted mating success, but success under female choice (female acquaintance-rated attractiveness) did not. Moreover, there was positive correlational selection on dominance and sociosexual psychology, such that positive sociosexual attitudes and desires contributed more to mating success as men's dominance increased. This would be expected if dominant men can more readily satisfy their interests in uncommitted sex. Generally, dominance and the traits favored by male contests predicted mating success, but attractiveness and the traits favored by female choice did not.

These results suggest stronger sexual selection through male contests than female choice in the population studied. Much research in evolutionary psychology states or implies the contrary: stronger sexual selection in men through female choice (reviewed in Puts, 2010). Yet, male contests tend to evolve in terrestrial species, especially where females are social, as in humans (D. J. Emlen, 2008; S. T. Emlen & Oring, 1977; Puts, 2010), and frequent or intense male contests characterize all extant great apes (Plavcan & van Schaik, 1992). Large human sex differences in muscle mass and same-sex aggression also suggest the importance of male contests in shaping men's traits (Archer, 2009; Puts, 2010). Thus, the present findings are predicted from theory, as well as phylogenetic and functional analyses of men's traits.

At the same time, these results appear incompatible with the apparent autonomy with which Western women choose their mates. One possibility is that female choice determines men's mating success, but women choose dominant men (i.e., men's attractiveness and dominance are functionally equivalent). However, women preferred different traits from those favored under male contests, and dominance rather than attractiveness predicted men's mating success. Another possibility is that women choose from among dominant men—that is, men's attractiveness and dominance positively interact, so that the influence of attractiveness on mating success increases with increasing dominance. However, in predicting mating success, we observed no statistically significant selection for

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positive covariance between attractiveness and dominance: in fact, if anything, the correlational selection gradient was negative in sign. Nevertheless, perhaps women rate men's sexual attractiveness differently from how they ultimately choose (but see Burriss, Welling, & Puts, 2011 for correspondence between men's traits and their long-term mates' preferences). For example, attractiveness ratings may not adequately capture women's differential resistance to men's seduction attempts (Gangestad & Eaton, 2013; Kokko, Brooks, Jennions, & Morley, 2003). Finally, men's dominance may limit female choice in subtle ways. For example, in the bars, clubs, parties, and other venues in which sexual affairs are initiated, a dominant man may have little compunction against interfering with the mating attempts of a less dominant man, whereas the reverse would be less likely. These intriguing possibilities deserve future research, but certainly the present results provide strong evidence that dominance remains salient in men's competition for mates.

Despite the coherence of these results, we note several limitations. First, although we measured what we believe are some of the strongest candidates for sexually selected traits in men, traits that exhibit large sex differences that emerge at sexual maturity and have been implicated in men's mating competition, we did not assess all possible traits. Among those that we might have included are psychological traits, such as aggression (Archer, 2009) and humor (Miller, 2000). Second, the population that we sampled may differ in important ways from those in which men's sexually selected traits were shaped over human evolution. Yet, we note similarities between some traditional societies and American university social fraternities: both small groups of allied males with a high degree of social conformity and an ethos of hegemonic masculinity (Anderson, 2008; Chagnon, 1992) who interact regularly with the same females. It was also critical that we sample from a population in which participants view questions on sexual attitudes, desires, and behavior as minimally invasive or stressful (Yeater, Miller, Rinehart, & Nason, 2012). Third, the use of hormonal contraception may have affected some female participants' and raters' mate preferences (Roberts, Gosling, Carter, & Petrie, 2008) and decoupled male participants' copulatory patterns from their reproductive success. However, copulatory patterns can predict the reproductive success that would be realized in the absence of effective contraception (Perusse, 1993). Fourth, our data on mating success were based on self-report, which may be unreliable. However, we found a highly significantly correlation between self-reported numbers of sex partners and male peers' assessments of men's numbers of sex partners. Fifth, although we measured success under female choice and male contests, sexual selection in men likely involves other mechanisms, such as sperm competition and sexual coercion (Goetz & Shackelford, 2006). Finally, we measured men's mating success by their number of sex partners, but additional variables are clearly relevant to mating success, such as the quality of men's mates, the number of copulations with each, and mates' fecundability at the time. Nevertheless, the number of women with whom a man has copulated likely strongly reflects his ability to obtain mating opportunities (Faurie et al., 2004; Hodges-Simeon et al., 2011).

The present study begins to fill significant gaps regarding the mechanisms and forms of sexual selection in men and the relative salience of men's traits to different mechanisms of sexual selection. We do not, however, consider these questions resolved. Future research should explore additional traits and other measures of mating success in different populations, especially in traditional societies. We hope that the present study can help guide these future explorations.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2013.05.004.

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