**The relative importance of intra- and intersexual selection on human male sexually
dimorphic traits**

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Abstract

Recent evidence suggests that in sexual selection on human males, intrasexual competition plays a larger role than female choice. In a sample of men ($N = 164$), we sought to provide further evidence on the effects of men's physical dominance and sexual attractiveness on mating success and hence in sexual selection. Objective measures and subjective ratings of male sexually dimorphic traits purportedly under sexual selection (height, vocal and facial masculinity, upper body size from 3D scans, physical strength, and baseline testosterone) and observer perceptions of physical dominance and sexual attractiveness based on self-presentation video recordings were assessed and associated with mating success (sociosexual behaviour and number of potential conceptions) in a partly longitudinal design. Results from structural equation models and selection analyses revealed that physical dominance, but not sexual attractiveness, predicted mating success. Physical dominance mediated associations of upper body size, physical strength, as well as vocal and facial physical dominance and attractiveness with mating success. These findings thus suggest a greater importance of intrasexual competition than female choice in human male sexual selection.

Keywords sexual selection, mating success, physical dominance, sexual attractiveness

Introduction

Sexual selection favours traits that aid in competition for mates and has played a considerable role in the development of human sexual dimorphism (Puts, 2016). Mating competition is assumed to have been particularly intense among men, due to men's greater variance in fitness relative to women's, and an operational sex ratio (OSR; ratio of sexually active men to fecund women) that is male biased (Hill, Bailey, & Puts, 2017). Elevated mating and/or reproductive success in men has been associated with a range of sexually dimorphic traits that develop or increase in expression around sexual maturity, such as muscularity, height, and facial and vocal masculinity (Puts, Bailey, & Reno, 2015). These traits and others, such as agonistic behaviour and status-striving, may have evolved to aid in male intrasexual competition for mates, territory and resources (Puts, 2016; Puts, Bailey, & Reno, 2015). Another mechanism of sexual selection is female mate choice (intersexual selection), whereby females choose males as sexual partners based on preferences for males' traits (Puts, 2010). For a long time, female mate choice was assumed to be the primary mechanism of sexual selection driving the evolution of sexually dimorphic traits in men (Saxton, Mackey, McCarty, & Neave, 2016). Recent evidence, however, indicates that intrasexual (i.e., male-male) competition may have played a larger role than female mate choice (Hill, Bailey, & Puts, 2017).

Hill and colleagues (2013) investigated the influence of men's sexual attractiveness to women (as a proxy measure of female choice), physical dominance (indicating male-male competition) and related traits on mating success, and hence their relative importance in sexual selection ($N=63$ men). In particular, they assessed men's facial masculinity (a composite measure based on Penton-Voak & Perrett, 2001) and vocal masculinity (an aggregate of fundamental frequency (F_0 , the acoustic parameter closest to pitch) and formant frequencies (resonant frequencies that influence perceptions of vocal timbre)), body height, and girth (a composite body measure consisting of upper arm, chest and shoulder girth, and body weight). Hill and colleagues also obtained evaluations of men's sexual attractiveness and physical dominance made by familiar female and male acquaintances, respectively, as well as men's reported number of sexual partners

within the previous twelve months. Physical dominance and associated traits (in particular, girth and vocal masculinity), but not attractiveness, significantly and positively predicted mating success. In a further study on highly sexually dimorphic F0, the voice recordings of men ($N=175$) with lower F0 were rated to be more dominant (by males) and more sexually attractive (by females) (Puts et al., 2016). When analyzing both simultaneously, perceived physical dominance but not sexual attractiveness remained significantly associated with F0, again indicating a potentially stronger role of male-male competition than female mate choice. Saxton and colleagues (2016) investigated the effects of men's F0 and beard growth ($N=6$, for each four different beard growth stages and four voice manipulations, overall 96 stimuli) on perceptions of dominance and attractiveness based on video recordings. Masculine (lower) F0 and beard growth positively influenced dominance ratings, whereas the relationship between F0 and attractiveness was negatively curvilinear (i.e., intermediate values were most attractive). The authors interpreted these findings as suggesting context-dependent (intra- or intersexual selection) differential optimum levels of facial hair and F0. Similarly, Dixson and Vasey (2012) showed that men with full beards were judged to be more aggressive and higher in social status, but not more attractive, compared to when completely shaved ($N=19$, within-subject design). Antfolk and colleagues (2015) provided evidence for a role of female mate choice, in that men's sexual activity appeared to be more constrained by women than vice versa. Because no effects of intrasexual competition were estimated, the relative influence of these two mechanisms of sexual selection could not be ascertained from their study.

Overall, these studies suggest a larger influence of male-male competition versus female mate choice in men's sexual selection, yet important questions remain. Prior studies on human sexual selection have been limited in the number of relevant traits investigated, and the role of additional sexually selected traits, such as physical strength, or baseline testosterone (T) as a physiological basis of sexually dimorphic traits, has been largely ignored. Physical strength obviously is an influential trait in male-male contest competition (Sell, Hone, & Pound, 2012), increasing physical dominance and thus potentially augmenting mating success (Hill et al., 2013). T has been

proposed to underlie mechanisms facilitating trade-offs between mating and parenting efforts, especially in men (e.g., Muller, 2017; Puts et al., 2015), and has been associated with attractiveness (e.g., Roney et al., 2006; $N=39$ men), dominance (e.g., Dabbs, 1997; $N=119$ men) and mating success (Peters, Simmons, & Rhodes, 2008; $N=119$ men; but see Puts et al., 2015; $N=61$ men). Our study extends previous research by including these sexually dimorphic traits, which may have been central in men's sexual selection, as well as F0, upper body size/girth, and body height. Moreover, in previous studies, sample sizes were rather small ($N=19$ and 63 men, in Dixon & Vasey and Hill et al., respectively), and the samples in Hill and colleagues and Puts and colleagues had very low mean ages and narrow age ranges around 20 years, so that the robustness and generalizability of these findings remain to be investigated.

Hunt, Breuker, Sadowski and Moore (2009) emphasized the importance of assessing the form and strength of both male-male competition and female mate choice, as well as their interaction (i.e., correlational selection) simultaneously, in order to elucidate total sexual selection operating on male phenotypic traits. In addition, the effects of men's traits on attractiveness (e.g., Cunningham & Barbee, 1990; Neave & Shields, 2008; Saxton, Mackey, McCarty, & Neave, 2015), dominance (e.g., Saxton, Mackey, McCarty, & Neave; Wolff & Puts, 2010) and mating or reproductive success (e.g., Stulp, Pollet, Verhulst, & Buunk, 2012) are sometimes nonlinear, calling for an investigation of both linear and quadratic effects (i.e., stabilizing or disruptive selection), as well as the selection that targets the covariance between different traits (i.e., correlational selection).

Our study thus aimed to investigate the relative roles of male-male competition and female mate choice in men's mating competition by adding several study elements. First, we measured additional traits (baseline T, physical strength; Hill, Bailey, & Puts, 2017). Second, we obtained observer ratings of men's vocal, facial and bodily stimuli on sexual attractiveness and physical dominance (Dixon & Vasey, 2012; Hill et al., 2013; Puts et al., 2016). Third, we considered more complete operationalizations of mating success, in addition to men's number of sexual partners

within the previous twelve months, as in Hill and colleagues (2013). Specifically, we employed the full and hence more reliable sociosexual behaviour facet (adding the lifetime number of one-night stands and sexual partners without relationship interest; Penke & Asendorpf, 2008). We also estimated the number of conceptions that would likely have resulted from each man's pattern of copulatory behaviour over the past 18 months in the absence of reliable contraception (number of potential conceptions, NPC; Perusse, 1993). This integrated measure, which incorporates data on both a man's number of sexual partners and his number of copulations with each, should more closely reflect a man's expected reproductive success in a natural fertility population, such as those in which humans spent the vast majority of their evolution. Fourth, previous studies have predominantly employed a cross-sectional design, which makes causal interpretations difficult. We also investigated men's mating success assessed 18 months after the initial measurement of their traits. This partly longitudinal design enables us to examine potentially causal predictions of men's mating success by their objectively measured sexually dimorphic traits and subjective impressions on raters. Finally, we examined these relationships in a larger sample spanning a broader age range and from a different population (Germany). We hypothesize that dominance and related traits will more strongly predict men's mating success than attractiveness and associated variables (Hill et al., 2013; Puts et al., 2016). Moreover, we predict that perceived physical dominance, but not rated sexual attractiveness, will mediate the association between both objective traits and subjective ratings, and mating success (Hill et al., 2013).

Methods

Participants. We recruited 165 male heterosexual young adults with no hormonal disorders. One participant was excluded due to indicating a bisexual orientation, leaving a final sample of $N=164$ (age: $M=24.2$, $SD=3.2$, range: 18-34 years). The final sample size had sufficient power ($>.80$) to detect effect sizes of Pearson's $r>.21$ (Cohen, 1992). Ninety reported being single (including 11 who were in open relationships), 74 in relationships (66 committed, 4 engaged, 4 married), 88.4% were students (of which 2 were psychology students). On the 7-point Kinsey scale of sexual identity (0 =

exclusively heterosexual to 6 = exclusively homosexual; Kinsey, Pomeroy, & Martin, 1948), the mean was 0.17 (range 0-2; $SD=0.41$). All procedures received ethics approval from the Georg-Elias-Müller-Institute of Psychology's Ethics Committee (no. 111).

Procedure. For the first assessment (T1), participants visited the lab twice. During the first “pre-session” visit, participants provided informed consent and self-reports on personality traits. In addition, anthropometric measures (3D body and face scans, handgrip and upper body strength, body height and weight) were taken and their sexual history assessed (see below). A first saliva sample was taken approximately 20 minutes after arriving at the lab (to allow participants to calm down), to obtain a first measure of baseline T levels. To control for circadian variation in participants' hormonal levels, all testing was conducted between 2pm and 6pm (Idris, Wan, Zhang, & Punyadeera, 2017; Schultheiss & Stanton, 2009). During the second “main session” visit a few days after the pre-session, participants provided a second saliva sample for baseline T measures 12-15 minutes after arriving at the lab. Afterwards, they were escorted into the video laboratory to complete video recordings (one-minute recordings of participants talking about their personal strengths; see below). Participants subsequently engaged in further tasks not relevant to this study (see Kordsmeyer & Penke, 2017). At the end of the main session, participants were debriefed about the study's objective.

Hormonal assessment. For both samples, participants provided at least 2 ml of saliva via unstimulated passive drool through a straw (Schultheiss, Schiepe, & Rawolle, 2012; Fiers et al., 2014). The samples were immediately transported to an ultra-low temperature freezer (-80°C), where salivary T is stable for at least 36 months (Granger, Shirtcliff, Booth, Kivlighan, & Schwartz, 2004). At the end of data collection, saliva samples were shipped on dry ice to the Technical University of Dresden, where they were analyzed using chemiluminescence immunoassays with high sensitivity (IBL International, Hamburg, Germany). The intra- and inter-assay coefficients (CVs) for T are below 11 %. Outliers were winsorized to 3 SDs ($n=9$, in accordance with Mehta, Welker, Zilioli, & Carre, 2015; see also Pollet & van der Meij (2017) for an extensive discussion of the influence of

hormone outlier handling on significance testing). T values appeared to be positively skewed and to violate the assumption of normality (Shapiro-Wilk test $W<.96$, $ps<.001$). Consequently, both baseline T variables were log10-transformed (e.g., Mehta, Welker, Zilioli, & Carré, 2015). One participant had missing data for baseline T (decreasing the sample size for analyses involving this measure to $N=163$). Participants were asked to refrain from drinking alcohol, exercising, and taking recreational or non-prescribed clinical drugs on both days of the study; ingesting caffeine (coffee, tea, coke) or sleeping three hours before; and from eating, drinking (except for water), smoking or brushing teeth one hour before their scheduled appointment (Geniole, Busseri, & McCormick, 2013; Lopez, Hay, & Conklin, 2009). To check participants' adherence to these instructions and to assess further potential influences on the saliva samples and hormonal levels, a screening questionnaire was administered at the beginning of the session (Schultheiss & Stanton, 2009). None of the 163 participants indicated taking hormonal medication or supplements. Saliva samples were immediately controlled for blood traces and measures were repeated if necessary. Independent from this, 38 participants reported either recent gum bleedings or oral infections, which can lead to elevated steroid hormone concentrations (Schultheiss & Stanton, 2009). Baseline T levels were compared for these as a group with the remaining participants and no differences were detected (all $ts<0.44$, $ps>.66$). Finally, both T values were aggregated to form a more reliable measure of baseline T (Idris, Wan, Zhang, & Punyadeera, 2017).

Video recordings. Each participant was first told that the question he should answer while being videotaped within a one-minute time limit was, "What do you think right now, is great about yourself?". Then he was presented with one of two sets of eight terms about "life domains" (e.g., "humour" and "friendship"; Table S1) and instructed to choose three, which he would subsequently talk about. The participants were given these terms as hints for what to talk about and in order to ensure that they talked about a variety of different, but roughly comparable topics when presenting themselves. The three chosen domains were placed next to the camera, with the participant standing approximately four meters away from the camera (to have a full-body view). Participants

could start speaking whenever they wished and were gently notified when they passed the time limit, but not stopped abruptly.

Anthropometric measures. Participants were scanned three times during the pre-session using a Vitus Smart XXL 3D bodyscanner, running AnthroScan software (both Human Solutions GmbH, Kaiserslautern, Germany), while wearing tight underwear. Participants were instructed to stand upright with legs hip-width apart, arms extended and held slightly away from the body, making a fist with thumbs showing forward, the head positioned in accordance with the Frankfort Horizontal, and to breathe normally during the scanning process. Participants were asked to directly face the camera and show a neutral facial expression while two photos were taken of each participant's face in front of a white wall. The more suitable of the two photos (in terms of neutral facial expression and head angle) was chosen for the rating study (see below). Physical strength was operationalized as the average of upper body and handgrip strength. Both were measured using a hand dynamometer (Saehan SH5001). Each measurement was taken three times, starting with handgrip strength, for which participants were asked to use their dominant hand (88.2% used their right). Upper body strength was measured with the dynamometer following the procedure described in Sell, Cosmides, Tooby, Sznycer, von Rueden and Gurven (2009). A composite strength measure was formed by averaging the maximum values for each of the three measures of handgrip and upper body strength. Body height (in cm) was measured twice using a stadiometer while participants stood barefoot, and the two values were averaged. An aggregate indicator of upper body size (Price, Dunn, Hopkins, & Kang, 2012) was calculated by averaging z-standardized shoulder width, bust-chest girth, and upper arm girth (means of left and right arms), based on averages of automatic measurements extracted from the three body scans (measures according to ISO 20685:200). Reliabilities for the three body scans were high for all measures (ICCs>.90). To obtain fundamental frequency (F0) measurements, sound clips were extracted from the self-presentation video recordings (for which Line6 XD-V75 microphones were used) and cut to a length of five

seconds, beginning five seconds after the male participants started to speak. Sound files were analyzed as described in Study 2 of Puts et al. (2016) using PRAAT software (v. 6.0.14).

Sexual history. Men reported their sociosexual orientation (SOI-R; Penke & Asendorpf, 2008). Mating success was conceptualized as the behaviour facet of the SOI-R inventory, i.e., an aggregate of participants' number of sexual partners within the last twelve months, lifetime number of one-night stands and of sexual partners without relationship interest. In order to replicate the findings of Hill and colleagues (2013), results with only the first item of the SOI-R scale (i.e., participants' number of sexual partners within the last 12 months) are reported also.

Video ratings. For proxy measures of male-male competition and female mate choice, men's self-presentation video recordings were rated for physical dominance (by males, "How likely is it that this man would win a physical fight with another man?", using an 11-point Likert-scale, from -5="extremely unlikely" to +5="extremely likely") and sexual attractiveness (by females, "How sexually attractive is this man?", using an 11-point Likert-scale, from -5="extremely unattractive" to +5="extremely attractive"). We assessed perceptions of sexual attractiveness, rather than attractiveness for a long-term, committed relationship because men's masculine traits should be more strongly related to the former (Frederick & Haselton, 2007), and because we expected sexual attractiveness to more strongly influence sexual outcomes, such as number of sexual partners. One hundred and sixty raters (80 females; age: $M=24.1$, $SD=6.1$, range 18-63 years) were recruited from the local participant pool. The video stimuli were divided into eight sets, and each video was rated by ten independent female (for sexual attractiveness) and male (for physical dominance) raters. Because some target men exceeded the time limit of one minute, all videos were cut to a maximum length of one minute. The videos of seven participants were removed from the stimulus sample due to audio problems, leaving a final set of $N=157$ target men. Interrater agreements were high (Cronbach's $\alpha>.85$).

Additional ratings. In order to obtain further information on men's traits not captured by the objective trait measurements described above, naive observers provided judgments of physical

dominance and sexual attractiveness based on men's bodies, faces and voices. For bodily attractiveness and dominance ratings based on target men's 3D body scans, 44 participants (21 females; age $M=22.9$, $SD=5.7$, range 18-48 years) were recruited from the local participant pool. The 3D body scans of 13 target men had to be removed due to errors with the scans, leaving a final stimulus set of $N=151$ body scans. From each of the target men, one body scan was chosen by visual inspection (i.e., the scan coming closest to the standard posture). Body scans were truncated above the neck using the software Blender (version 2.75, www.blender.org), leaving an even plane just below the larynx. This was done in order to focus raters' attention on bodily features and to preserve anonymity of male participants. Animated videos of a body scan turning around its vertical axis ("beauty turns", duration: 8 sec. each; 960x540 pixels) were created. The 151 beauty turns were divided into two sets of 76 and 75 videos matched for BMI. After previewing all beauty turns (1 sec. each) to familiarize the raters with the stimulus material and range of bodies, ratings were conducted with the beauty turns being displayed in random order on 24" computer screens. Physical dominance and sexual attractiveness were assessed as with video ratings above. Each set of beauty turns was rated by 10-13 males and females each. Interrater reliabilities within each set and rater sex were high (Cronbach's $\alpha > .91$). For voice ratings, 60 participants (30 females; age: $M=19.7$, $SD 4.0$, range 18-48 years) were recruited at an US-American university. Raters provided information on their German language knowledge, which indicated that most raters had no comprehension of German language, ensuring our voice ratings were unbiased by spoken content. The five-second voice recordings (as described above) were played to raters using Sennheiser HD 280 Professional headphones. Overall each voice recording was judged by 15 male raters on physical dominance and 15 female raters on sexual attractiveness (mean ratings were used). Physical dominance was rated using the item "How likely is it that this man would win a physical fight against another man?" on a 7-point Likert scale, with the endpoints 1="very unlikely" to 7="very likely". Sexual attractiveness was rated using the item "How sexually attractive is this man?" on a 7-point Likert scale, with the endpoints 1="very unattractive" to 7="very attractive". Interrater reliabilities for both items were

good (Cronbach's $\alpha > .80$). Facial ratings were conducted on target men's facial photographs (frontal photos, with a neutral facial expression) by 23 independent raters (11 males; age: $M=27.3$, $SD=8.8$, range 19-54 years). Males rated physical dominance using the item "How likely is it that this man would win a physical fight against another man?" on an 11-point Likert scale, with the endpoints -5="very unlikely" to +5="very likely". Females rated sexual attractiveness using the item "How sexually attractive is this man?" on an 11-point Likert scale, with the endpoints -5="extremely unattractive" to +5="extremely attractive". Interrater reliabilities were good (Cronbach's $\alpha > .82$). Fourteen data points from 14 raters who indicated that they knew a given target man well were excluded from subsequent analyses.

Follow-up study. Exactly 18 months after T1, participants were invited to fill in an online questionnaire (T2), assessing their sexual history since the first study (using formr.org; Arslan & Tata, 2017). One hundred and nine participants (66.5 %) completed the questionnaire (age: $M=25.8$, $SD=3.2$ years). Corresponding to T1, mating success was conceptualized as the behaviour facet of the SOI-R. In addition, the number of potential conceptions (NPCs) were calculated according to the following formula by Perusse (1993), taking into account the number of (female) sexual partners within the last 18 months, the number of instances of vaginal intercourse (as indicated on a 9-point scale: 0, 1, 2, 3, 4, 5 to 6, 7 to 9, 10 to 19, 20 or more times), and a fixed estimated probability of conception for each sexual act (3%), yielding an estimate of number of conceptions (i.e., fertilized ova) that would have resulted if mating had occurred randomly across the ovulatory cycle and in the absence of contraception (see also Linton & Wiener, 2001):

$$NPC = \sum_{m=1}^n (1 - 0.97^{P_m})$$

where n is the number of sexual partners, and P_m the number of coital acts with partner m .

We chose to include the measure of NPCs, as it partially corrects for a confound of a simple measure of numbers of sexual partners: highly attractive or dominant men may eventually achieve a high reproductive fitness with one romantic partner, but this is not reflected in the recent number of

sexual partners (especially in light of socially imposed norms of monogamy; Perusse, 1993), whereas less attractive or dominant men who are single may have had a few more recent sexual partners (e.g., one-night stands), but in the end achieve a lower reproductive fitness. The NPCs adjusts for this by taking into account the number of copulations with each partner, which should be large for men in stable romantic relationships, compared to short-term sexual encounters. Finally, in line with T1 and to replicate Hill and colleagues' findings (2013), results with only the first item of the SOI-R inventory are reported as well.

Statistical analyses. To obtain relative fitness measures, the mating outcome variables (SOI-R items 1-3, NPCs) were divided by the sample mean (Hill et al., 2013). Trait measures and mean subjective ratings were z-standardized. Structural equation models were conducted to examine to what extent men's sexually dimorphic traits and observer impressions of their physical dominance and sexual attractiveness were associated with mating success. For these, the *lavaan* package in R (R Core Team, 2015; Rosseel, 2012) was used, including objective trait measures and subjective ratings (in separate models), video-rated physical dominance and sexual attractiveness, as well as mating success (T1 & T2: SOI-R items 1-3 loading on a latent factor sociosexual behaviour, SOI-R item 1; T2 only: NPCs; Fig. 1 and 2). Because all SOI-R items 1-3 and the NPC variable were positively skewed (Shapiro-Wilk test: $W < .87$, $p < .001$), maximum likelihood estimation with robust (Huber-White) standard errors (MLR) was used (except for the Vuong test reported below, for which regular maximum likelihood estimation is required). Quadratic effects were included by squaring the trait and rating measures. To find the model best fitting the data, we ran model comparisons employing the Scaled Chi-Square Difference Test (Satorra & Bentler, 2001) for nested models, and the Vuong test and calculated confidence intervals for BIC differences for non-nested models (R package *nonnest2*; Merkle, You, & Preacher, 2016; Vuong, 1989). Mediator analyses were conducted using the *lavaan* package in R. For robustness checks, we added men's relationship status (binary, single including "open relationship" vs. partnered; Linton & Wiener, 2001) and age (Thornhill & Gangestad, 1994) to the structural equation models.

The T2 measure of sociosexual behaviour partly overlaps with its T1 assessment (items 2 and 3 ask for the lifetime number of one-night stands and sexual partners without relationship interest; also evidenced by the correlation between T1 and T2, $r=.80$). This is not the case for the first item on the number of sexual partners within the previous twelve months, as it was assessed 18 months after T1. Due to the considerably larger sample size and consequently higher power at T1 ($N=164$; $T2\ n=109$), we decided to focus on sociosexual behaviour at T1 for further selection analyses (selection gradients and canonical analyses).

Selection analyses. Multivariate selection analysis (Lande & Arnold, 1983) was used to formally quantify the linear and nonlinear (i.e., quadratic and correlational selection) selection on men's traits. We applied a linear transformation to the variables rated physical dominance and sexual attractiveness (ranging from -5 to +5), adding a constant of five to each value, to avoid negative values, as differences in scale are known to alter estimated gradients in selection analyses (Brodie & Janzen, 1996). We employed two separate multiple regression models: the first to estimate standardized linear selection gradients (β), and the second to calculate quadratic and cross-product terms to estimate the matrix of standardized nonlinear selection gradients (γ) (Phillips & Arnold, 1989). Since interpreting individual effects in γ can underestimate the actual strength of sexual selection (Blows & Brooks, 2003), we performed canonical analyses of the γ matrix to find the major axes of the response surface, resulting in an M matrix with i eigenvectors (m_i ; where i is the number of traits), each describing a major axis of the response surface. The strength of linear selection along each eigenvector is indicated by θ_i , and the strength of nonlinear selection by its eigenvalue (λ_i) (Phillips & Arnold, 1989). We estimated θ_i using the double linear regression method (Bisgaard & Ankenman, 1996) and λ_i using the permutation procedure of Reynolds, Childers, and Pajewski (2010). 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 (Lewis, Wedell, & Hunt, 2011; Mitchell-Olds & Shaw, 1987). Major axes of the response surface extracted from the canonical analyses of γ were visualized

using thin plate splines when two or more axes showed statistically significant nonlinear selection (Green & Silverman, 1994). The response surface was created using the lambda value that minimized the generalized cross-validation (GCV) score was fit employing the *Tps* function in the *fields* package of R (version 3.2.2). When significant selection only targeted a single axis, we visualized this using a univariate spline employing the *splines* package in R. A sequential model-building approach was used to compare mechanisms of sexual selection to each other and to mating success (Draper & John, 1988). A hierarchical model was run to first compare 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. To determine which individual traits contributed to any overall significant difference, univariate interaction terms from the complete models were used (Lewis, Wedell, & Hunt, 2011).

Results

Preliminary Analyses.

Descriptive statistics for all measured variables and bivariate Pearson correlations between all main variables can be found in the online supplementary material (Tables S2 and S3).

Structural equation models and mediation analyses.

Model selection. We compared different structural equation models (SEMs) in order to find out which model fit our data best. First, we built a complete model including linear and quadratic effects (on video-rated physical dominance and sexual attractiveness, and on mating success), as well as direct effects of the five objective traits and six subjective ratings on each of the mating success variables separately (corresponding to Hill et al., 2013; see Fig. 1 and 2). As video-rated dominance and attractiveness were substantially correlated (for both T1/T2 samples: $r_s=.55$, $p_s<.001$, $N=164/107$), possibly due to halo effects, we included the covariance between these two as a next step. Model comparison (nested models, Scaled Chi-Square Difference Test; Satorra & Bentler, 2001) showed a clearly better fit of the latter model including the covariance (for model comparison statistics see Tables 1 and S4). Even though the effects of objective traits and subjective

ratings may be mediated by perceived attractiveness and dominance, Hill and colleagues (2013) showed direct effects of objective traits (girth) on mating success. We analyzed whether model fit would significantly improve when removing these direct effects and it did (at least for objective traits; Tables 1 and S4). As previous studies showed quadratic effects on mating success (Hill et al., 2013; Saxton, Mackey, McCarty, & Neave, 2015), we examined if model fit would improve when retaining these terms. Model comparison showed that model fit improved significantly when excluding quadratic effects on rated dominance and attractiveness, and on mating success. However, previous research has shown that there may still be quadratic effects of men's traits on either sexual attractiveness or physical dominance, but not both (e.g., Saxton et al., 2015 found nonlinear associations of fundamental frequency (F0) with attractiveness, but only linear effects on dominance; Hill et al., 2013 found a positive quadratic effect of facial masculinity on rated physical dominance). Thus, we additionally tested models including quadratic effects of objective traits and subjective ratings on either video-rated dominance or attractiveness in two separate models. Results showed that model fit was significantly better excluding any quadratic effects (Table 1). The models with the best fit overall are shown in Fig. 1 and 2 (mating success measured as sociosexual behaviour at T1).

Table 1

Structural equation model comparison statistics for different versions of model 1.

Nested model comparisons	χ^2 difference	p	Result			
Full model: include covariance between sexual attractiveness and physical dominance?	25.58	<.001	better fit including covariance			
Include “long paths” (direct effects of traits on mating success)?	35.34	<.001	better fit excluding “long paths”			
Non-nested model comparisons	Vuong test		AIC difference		BIC difference	
	z	p	CI lower	CI upper	CI lower	CI upper
Include quadratic besides linear effects?	-37.11 → exclude	<.001	3749.87	4165.42	3787.06	4202.61
Full model vs. excluding long paths & quadratic effects	-38.05 → exclude	<.001	3744.39	4146.29	3812.58	4214.49
Include quadratic effects on sexual attractiveness only?	29.97 → exclude	<.001	-3186.57	-2796.58	-3202.07	-2812.08
Include quadratic effects on physical dominance?	30.04 → exclude	<.001	3187.41	-2798.18	-3202.90	-2813.69

Note: sociosexual behaviour at T1 as outcome, objective traits as predictors; χ^2 = chi-square; AIC =

Akaike information criterion; BIC = Bayesian information criterion; CI = confidence interval;

lower/upper = lower/upper bound.

Table 2

Fit statistics of all ten final structural equation models.

Predictors	Outcome	χ^2	p	CFI	TLI	$RMSEA$
Objective traits	Sociosexual behaviour T1	26.23	.12	0.98	0.96	.059
Subjective ratings	Sociosexual behaviour T1	28.98	.15	0.99	0.97	.045
Objective traits	Sexual partners 12 months T1	9.20	.10	0.96	0.86	.073
Subjective ratings	Sexual partners 12 months T1	8.08	.23	0.99	0.97	.046
Objective traits	Sociosexual behaviour T2	16.01	.66	1.00	1.02	.000
Subjective ratings	Sociosexual behaviour T2	20.39	.56	1.00	1.01	.000
Objective traits	Sexual partners 12 months T2	7.11	.21	0.97	0.90	.060
Subjective ratings	Sexual partners 12 months T2	4.81	.57	1.00	1.03	.000
Objective traits	NPCs T2	3.65	.60	1.00	1.07	.000
Subjective ratings	NPCs T2	4.36	.63	1.00	1.05	.000

Note: T1/T2 = time point 1/2; NPCs = number of potential conceptions; χ^2 = chi-square; CFI = robust

Comparative Fit Index; TLI = robust Tucker-Lewis Index; $RMSEA$ = robust Root Mean Square Error of

Approximation.

Model 1: sociosexual behaviour at T1 as outcome, objective traits as predictors. Results of this final model revealed a negative effect of F0 and a positive effect of physical strength on video-rated sexual attractiveness, and positive effects of upper body size and physical strength, as well as a

negative effect of F0 on rated physical dominance (Fig. 1). Video-rated physical dominance positively predicted sociosexual behaviour, and mediated associations of upper body size and physical strength with mating success (Table 3; all unsigned indirect effects for video-rated sexual attractiveness $<.01$, $ps>.13$). Results were virtually identical with no changes in significance of effects when including participants' age and relationship status (Fig. S1).

Model 2: sociosexual behaviour at T1 as outcome, subjective ratings as predictors. Results of this final model showed positive effects of rated facial and bodily sexual attractiveness and facial physical dominance on video-rated sexual attractiveness (Fig. 2). Facial sexual attractiveness, vocal, facial and bodily physical dominance were positively related to video-rated physical dominance. Rated physical dominance was positively associated with sociosexual behaviour. Moreover, video-rated physical dominance mediated associations of vocal and facial physical dominance as well as vocal and facial attractiveness with mating success (Table S5). Video-rated sexual attractiveness mediated the association between bodily sexual attractiveness and mating success (Table S6). Results were virtually identical with no changes in significance when including age and relationship status (Fig. S2).

Fig. 1. Structural equation model 1, sociosexual behaviour (SOI-R behaviour) at T1 as outcome and objective traits as predictors; baseline T = baseline testosterone; F0 = fundamental frequency; SOI-R 1/2/3 = items 1/2/3 of the sociosexual orientation inventory; for model fit statistics see Table 2; * $p<.05$, ** $p<.01$, *** $p<.001$.

Fig. 2. Structural equation model 2, sociosexual behaviour (SOI-R behaviour) at T1 as outcome and subjective ratings as predictors. Sex. attr. = sexual attractiveness; phys. dom. = physical dominance; SOI-R 1/2/3 = items 1/2/3 of the revised sociosexual orientation inventory; for model fit statistics see Table 2; * $p < .05$, ** $p < .01$, *** $p < .001$.

Models 3 and 4: number of sexual partners during last twelve months at T1 as outcome, objective traits or subjective ratings as predictors. To replicate findings of Hill and colleagues (2013), we applied the number of sexual partners in previous 12 months as the mating success measure. Results were virtually identical to models 1 and 2 with no changes in effects (Fig. S3 and S4), also when including age and relationship status (Fig. S5 and S6).

Models 5 and 6: sociosexual behaviour at T2 as outcome, objective traits or subjective ratings as predictors. For a quasi-longitudinal design predicting men's mating success, we assessed men's number of sexual partners in the twelve months before T2, their lifetime number of one-night stands and sexual partners without relationship interest (thus having some overlap with sociosexual behaviour at T1 for the latter two items; sociosexual behaviour at T1 and T2 correlated $r = .80$, $p < .001$). We replicated effects of models 1 and 2 of video-rated physical dominance, but not sexual attractiveness, on sociosexual behaviour (for details and for effects of objective traits/subjective ratings, see Fig. S7 and S8). Results were unchanged when including age and relationship status (Fig. S9 and S10).

Models 7 and 8: number of sexual partners in twelve months at T2 as outcome and objective traits or subjective ratings as predictors. For an actual longitudinal design, we employed men's number of sexual partners in the twelve months previous to T2 as the dependent variable. No effects of video-rated physical dominance or sexual attractiveness were found, either in the model including objective traits or when including subjective ratings (all unsigned β s < .17, p s > .08; for details and for effects of objective traits/subjective ratings, see Fig. S11 and S12). Again, results were unchanged when including age and relationship status (Fig. S13 and S14).

Models 9 and 10: number of potential conceptions (NPCs) at T2 as outcome and objective traits or subjective ratings as predictors. Alternatively using NPCs at T2 as the mating success outcome revealed no effects of video-rated physical dominance or sexual attractiveness (all unsigned β s < .18, p s > .11; for details and for effects of objective traits/subjective ratings, see Fig. S15 and S16). Results were virtually unchanged when including age and relationship status (Fig. S17 and S18).

Table 3

Mediation analyses for association between objective trait and sociosexual behaviour (T1), mediator: video-rated physical dominance.

Independent variable:	Indirect effect	SE	CI lower	CI upper	z
Height	.01	.01	-.01	.03	0.71
Fundamental frequency (F0)	-.02	.01	-.04	.003	-1.73
Upper body size	.03	.01	.001	.06	2.06*
Physical strength	.04	.01	.01	.06	2.49*
Baseline T	.004	.01	-.01	.02	0.51

Note: SE = standard error; CI = confidence interval; * p < .05.

Selection analysis with objective traits as predictors.

To further examine linear and nonlinear, we employed selection gradient and canonical analyses. We focussed on the outcome variable sociosexual behaviour at T1, as explained above.

Female mate choice. Female choice exerted directional (linear) selection favouring physical strength (Table 4A). There was also significant stabilizing (negative quadratic) selection on upper

body size (Table 4A), but no significant correlational selection (Table 4A). Canonical analysis of selection gradients γ revealed one eigenvector with significant negative nonlinear sexual selection (m_5 , Table 5A), indicative of stabilizing selection. It was heavily weighted by a negative loading from upper body size (Table 5A; Fig. 3A, in line with regression analyses; Table 4A). This eigenvector was also subject to significant negative linear selection (Table 5A). In addition, there was significant negative linear selection on m_2 , facilitating increased physical strength and body height (due to the negative contribution of these traits to this eigenvector; Table 5A).

Male-male competition. Male-male competition exerted directional selection favouring increased upper body size and physical strength (Table 4B). There was also significant disruptive (positive quadratic) selection on body height and stabilizing (negative quadratic) selection on upper body size (Table 4B), as well as negative correlational selection between physical strength and body height, and positive correlational selection between physical strength and F0 (Table 4B): as physical strength increased, shorter men and those with higher voices were perceived as more physically dominant. Canonical analysis of γ revealed two eigenvectors with significant nonlinear sexual selection (m_1 and m_5 , Table 5B). The first eigenvector of nonlinear selection (m_1) had a positive eigenvalue (indicative of disruptive selection) and was heavily weighted by a positive loading from body height and a negative loading from physical strength (Table 5B). This eigenvector was also subject to significant negative linear selection, favouring decreased body height and increased physical strength (Table 5B). This result parallels results of the regression analysis in that it signifies negative correlational selection between height and physical strength. The second eigenvector of nonlinear selection (m_5) had a negative eigenvalue (indicative of stabilizing selection) and was heavily weighted by upper body size (Table 5B). There was also significant positive linear selection on m_4 , selecting for increased upper body size, physical strength and decreased baseline T (Table 5B). The combination of significant positive and negative eigenvalues suggests that the fitness surface for male-male competition is best described as a multivariate saddle (Fig. 3B).

Table 4

The vector of standardized linear selection gradients (β) and the matrix of standardized quadratic and correlational selection gradients (γ) for body height, fundamental frequency (F0), upper body size, physical strength and baseline testosterone (T) operating through female choice, male-male competitions and mating success (sociosexual behaviour at time point 1).

	β	γ				
		Height	F0	Body size	Phys. str.	T
A. Female choice						
Height	.03 (.03)	-.02 (.06)				
F0	-.06 (.03)	.01 (.04)	-.02 (.04)			
Body size	-.07 (.04)	.04 (.05)	-.04 (.04)	-.22* (.08)		
Phys. str.	.09* (.04)	.00 (.04)	.03 (.04)	.02 (.06)	.02 (.06)	
T	-.01 (.03)	-.01 (.04)	-.04 (.03)	.03 (.05)	-.03 (.04)	.04 (.06)
B. Male-male competition						
Height	-.03 (.03)	.12* (.04)				
F0	-.05 (.03)	.03 (.03)	.02 (.04)			
Body size	.09* (.03)	-.00 (.04)	-.08 (.04)	-.14* (.06)		
Phys. str.	.10* (.03)	-.08* (.03)	.07* (.04)	.04 (.05)	.02 (.04)	
T	-.00 (.03)	.02 (.03)	-.04 (.03)	.01 (.04)	-.00 (.03)	.01 (.04)
C. Mating success						
Height	-.02 (.05)	-.10 (.08)				
F0	-.06 (.05)	.05 (.06)	.12 (.06)			
Body size	.17* (.06)	.06 (.07)	.09 (.06)	-.12 (.10)		
Phys. str.	.06 (.05)	.01 (.06)	.02 (.06)	.03 (.09)	.10 (.08)	
T	.06 (.05)	.04 (.06)	-.05 (.05)	.02 (.07)	-.06 (.06)	-.06 (.08)

Note: Randomization tests: * $p < .05$.

Table 5

The M matrix of eigenvectors from the canonical analysis of γ in Table 4 for female choice, male-male competitions and mating success (sociosexual behaviour at T1).

	M					Selection	
	Height	F0	Body size	Phys. str.	T	θ_i	λ_i
A. Female choice							
m_1	.07	.42	-.09	.44	-.79	.03	.09
m_2	-.49	.13	-.24	-.74	-.37	-.07*	-.00
m_3	.83	-.11	.09	-.47	-.26	-.01	-.01
m_4	.18	.88	-.11	-.14	.41	-.05	-.04
m_5	.18	-.18	-.96	.12	.09	.10*	-.25*
B. Male-male competition							
m_1	.85	-.06	-.07	-.51	.12	-.08*	.17*
m_2	-.28	-.82	.24	-.32	.31	.04	.09
m_3	.21	.08	.16	.52	.81	.05*	.01
m_4	.38	-.37	.49	.50	-.48	.10*	-.05
m_5	.12	-.43	-.82	.35	-.04	-.02	-.19*
C. Mating success							
m_1	.18	.77	.30	.49	-.22	.02	.18
m_2	-.15	-.49	-.14	.83	-.19	.05	.10
m_3	.52	-.17	.33	.22	.74	.11*	-.03
m_4	-.69	.31	-.21	.16	.60	.01	-.15
m_5	.45	.21	-.86	.08	.09	-.16*	-.18

Note: 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: * $p < .05$.

Female mate choice vs. male-male competition. The strength and form of linear sexual selection acting on the five male traits differed significantly between female choice and male-male competition ($F_{5,300}=2.60$, $p=.03$; Table 6). This was due to selection for greater upper body size through male-male competition ($F_{1,300}=9.78$, $p<.01$). There was no difference in quadratic ($F_{5,290}=1.21$, $p=.30$) or correlational ($F_{10,270}=0.61$, $p=.81$; Table 6) sexual selection.

Table 6

Hierarchical sequential model comparing sexual selection through male-male competitions versus female choice.

	SS_R	SS_C	Df_1	Df_2	F	p
Linear	40.06	38.39	5	300	2.60	.03 ^A
Quadratic	35.74	35.01	5	290	1.21	.30
Correlational	33.25	32.52	10	270	0.61	.81

Note: ^AContribution of individual traits: upper body size: $F_{1,300}=9.78$, $p<.01$; body height: $F_{1,300}=2.30$, $p=.13$; F0: $F_{1,300}=0.04$, $p=.85$; physical strength: $F_{1,300}=0.11$, $p=.74$; baseline testosterone: $F_{1,300}=0.02$, $p=.88$.

Fig. 3. A) Spline surface, showing quadratic selection for m_5 under female choice (see Table 5A); B) correlational selection on eigenvectors m_1 and m_5 under male-male competition (see Table 5B).

Mating success. Mating success (sociosexual behaviour) exerted directional selection favouring an increased upper body size, but no stabilizing, disruptive or correlational selection (Table 4C). Canonical analysis of γ revealed two eigenvectors with significant linear sexual selection (m_3 and m_5 ; Table 5C), which favoured increased body height and baseline T (m_3) as well as increased upper body size and decreased body height (m_5 ; due to negative and positive contributions of these traits to the negative eigenvectors, respectively; Table 5C). No significant nonlinear selection was detected (Table 5C).

When mating success was used as the fitness measure and video-rated sexual attractiveness (as a proxy of male-male competition) and video-rated physical dominance (as an indicator of female

choice) were treated as traits, there was directional selection for success in male-male competition, but not female mate choice (Table 7). Canonical analysis revealed one significant eigenvector with significant linear selection (m_1), favouring both male-male competitions and female choice (due to negative contributions to the negative eigenvector; Table 8), of which male-male competition showed a slightly greater weight. No significant nonlinear selection was detected (Table 8).

Table 7

The vector of standardized linear selection gradients (β) and the matrix of standardized quadratic and correlational selection gradients (γ) for female choice and male-male competitions operating through mating success (sociosexual behaviour at T1).

	β	γ	
		Male comp.	Fem. choice
Mating success			
Male comp.	.19* (.06)	.03 (.10)	
Fem. choice	.01 (.06)	.07 (.08)	-.01 (.10)

Note: Male comp. = male-male competition; fem. choice = female choice; randomization tests:

* $p < .05$.

Table 8

The M matrix of eigenvectors from the canonical analysis of γ in Table 7 for mating success (sociosexual behaviour at T1).

	M		Selection	
	Male comp.	Fem. choice	θ_i	λ_i
Mating success				
m_1	-.79	-.62	-.15*	.08
m_2	.62	-.79	.11	-.06

Note: 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. Male comp. = male-male competition; fem. choice = female choice; randomization tests: * $p < .05$.

Selection analyses when using subjective ratings as predictors. Following Hill and colleagues (2013), we substituted the objectively measured sexually dimorphic traits by target men's observer-rated bodily, facial and vocal sexual attractiveness and physical dominance (see also

models 2, 4, 6, 8, and 10 above), in order to capture subjective impressions, which may yield information beyond the specificity of the measured objective traits.

Facial, bodily and vocal attractiveness were under positive linear selection due to female mate choice (in terms of selection gradients for the former two, and selection on the eigenvector m_3 for the latter; Tables S7A and S8A). Facial and vocal attractiveness were positively, and bodily attractiveness was negatively, linearly associated with success under male-male competition (selection gradients and/or related eigenvectors; Tables S7B and S8B). However, none of these observer-rated attractiveness variables or related eigenvectors showed associations with mating success (Tables S7C and S8C). One significant eigenvector each revealed a positive (m_3) and a negative effect (m_5) of bodily dominance on female mate choice (Table S8A). Facial, bodily and vocal dominance were positively linearly related to male-male competition (in terms of selection gradients and/or an eigenvector m_2 , m_3 and m_5 ; Tables S7B and S8B), of which only bodily and facial dominance were positively linearly related to mating success (selection gradients and the related eigenvector m_4 , respectively; Tables S7C and S7C). No nonlinear selection was detected under female choice, male-male competition or mating success (Tables S7A/B/C and S8A/B/C). As with objective traits, the strength and form of linear sexual selection acting on the six male traits differed significantly between female choice and male-male competition ($F_{6,272}=5.08$, $p<.001$; Table S9). This was due to selection for greater facial attractiveness ($F_{1,272} = 7.36$, $p < .01$), bodily dominance ($F_{1,272} = 6.20$, $p = .01$) and bodily attractiveness ($F_{1,272} = 4.08$, $p = .04$) through male-male competition. There was no difference in quadratic ($F_{6,260}=0.18$, $p=.98$) or correlational sexual selection ($F_{15,230}=0.62$, $p=.86$; Table S9).

Data availability. The data and analysis scripts associated with this research are available at osf.io/z4dxa.

Discussion

Employing a partly longitudinal design and an extensive set of both objectively measured and observer-rated putative sexually dimorphic traits, we provide evidence for a stronger role of

male-male competition than female mate choice in sexual selection on German men. Our main findings are that physical dominance rated by men based on videos (as a proxy measure of male-male competition), but not female-judged sexual attractiveness (as a measure of female mate choice), predicts men's mating success, measured as their sociosexual behaviour (Penke & Asendorpf, 2008). This association held both cross-sectionally (T1) and quasi-longitudinally (T2, 18 months after T1) and was shown using structural equation modelling (SEM), as well as multivariate selection analysis and canonical analyses (for T1 only). Using the number of sexual partners in the previous twelve months as an alternative indicator of mating success (as in Hill et al., 2013) with no overlap between T1 and T2, this association could be replicated only cross-sectionally, but not longitudinally. Neither male-male competition nor female choice longitudinally predicted an alternative measure of men's mating success, the number of potential conceptions (NPCs; Perusse, 1993). The sociosexual behaviour measures overlapped at T1 and T2, since two out of the three items asked for the lifetime number of partners. Consequently, these analyses are only quasi-longitudinally. In contrast, for the number of sexual partners within the previous twelve months and the NPC index there is no overlap, so that these are longitudinal results, providing insight into potential causation. Not surprisingly due to the strong correlation between sociosexual behaviour at T1 and T2, we could replicate the positive effect of physical dominance on sociosexual behaviour at both time points. However, this was not the case for the number of sexual partners, which might be a false negative, explicable by the considerably lower power at T2. In addition, the twelve months represent a rather short time frame, so that for most men there are only few occurrences of new sexual partners, reducing the variable's variance and decreasing the likelihood of finding an effect. For the NPC index we found no effects of male-male competition or female choice, for which there are several possible reasons. First, T2 sample size and thus power was also low for analyses involving NPCs. Also, four participants did not fully complete this measure but did indicate comparatively large numbers of sexual partners by T2. Thus their NPCs values could not be calculated, but would presumably have been towards the upper end of the distribution, so that this measure is somewhat

biased. It should also be noted that the NPC index has not been used very often in empirical studies since its publication 25 years ago, so that it cannot be seen as well validated. Alternatively, assuming the index and our findings are valid, it may mean that male-male competition predicts male number of sexual partners, but is unrelated to the frequency of sexual intercourse with them. This argument may be related to the diminishing returns in terms of conception for repeated copulations with the same woman (Kanazawa, 2003). Our findings could imply that men's traits related to mating competition function primarily to increase the number of mates, but not copulation frequency. Despite our null results, the NPCs may be a promising candidate for future studies on human sexual selection, capturing mating success more thoroughly.

Regarding the objectively measured sexually dimorphic traits, both kinds of statistical analyses consistently indicated a positive linear effect of men's physical strength, and a negative curvilinear effect of upper body size on female mate choice, suggesting stabilizing selection. Some inconclusive significant effects on female mate choice were shown for body height (positive linear), vocal fundamental frequency and upper body size (negative linear for both), which need to be replicated in further research. These results for upper body size and body height are partly in line with Hill and colleagues (2013), who found a curvilinear effect of girth and a positive linear effect of body height. Moreover, Puts and colleagues (2016) reported a small negative linear effect of fundamental frequency on perceived dominance, which we replicated here. Both kinds of analyses converged on positive associations of upper body size and physical strength, as well as positive curvilinear (disruptive) and negative curvilinear associations of body height and upper body size, respectively, with male-male competition. The positive linear association for upper body size aligns with Hill and colleagues' finding for their aggregate measure girth. Inconsistent findings for selection under male-male competition were detected for fundamental frequency and body height (negative linear), baseline testosterone (T, both negative and positive linear loadings on eigenvectors), and physical strength (negative curvilinear), as well as negative correlational selection between body height and physical strength and positive correlational selection between fundamental frequency

and physical strength. Although these results partly support previous findings (at least for fundamental frequency: Hill et al., Puts et al., Saxton, Mackey, McCarty, & Neave., 2016), they need to be replicated in future research. Consistent positive linear effects on mating success (sociosexual behaviour at T1) were found for male-male competition and upper body size, both supporting findings by Hill and colleagues. Partly significant positive linear effects on mating success were shown for female mate choice, body height, and baseline T, providing some support for Hill and colleagues' positive linear effect of body height. Finally and importantly, canonical analyses suggested the association of mating success (sociosexual behaviour at T1) with male-male competition was significantly stronger than with female mate choice (replicating Hill and colleagues' finding).

Thus, we could only partly replicate results regarding fundamental frequency (Puts et al., 2016; Saxton et al., 2016), which has been described as one of the most highly sexually dimorphic traits in humans (Puts, Doll, & Hill, 2014). Our lack of detecting a significant effect of body height on mating success converges with previous studies showing a mixture of positive and negative, linear and quadratic associations between height and reproductive success (e.g., Nettle, 2002; Stulp, Pollet, Verhulst, & Buunk, 2012). On the contrary, negative linear selection of height under male-male competition (at least in the canonical analyses) contradicts some previous findings indicating that taller men on average are more aggressive, physically stronger and are perceived to have better fighting ability (for a review see Stulp & Barrett, 2016). This result may be explained as an oddity of our sample. Our sample of target men seems to be characterized by a slight overrepresentation of short men who are muscular and hence appear dominant, and tall but slim men who were rated as low in physical dominance. Thus, this study's finding regarding the link between height and male-male competition should be treated cautiously and clarified in further studies.

We provide novel evidence for a likely influence of physical strength in men's sexual selection. In contrast, baseline T does not appear to be selected for under either female mate choice, male-male competition or mating success. Even though baseline T levels are highly sexually

dimorphic (e.g., Cohen's $d=3.20$; Edelman, Chopik, & Kean, 2011), and T has been suggested to be an underlying mechanism for trade-offs between mating and parenting effort in males (e.g., Muehlenbein & Bribiescas, 2005; Muller, 2017), and hence meets important criteria to be considered a sexually selected variable, we do not provide additional evidence for associations with men's perceived attractiveness (cf. Roney, Hanson, Durante, & Maestripieri, 2006), dominance (cf. Dabbs, 1997), or mating success (cf. Peters, Simmons, & Rhodes 2008; Puts et al., 2015). Thus, there may be no direct and unambiguous positive association between T levels and mating success, and further psychological variables may mediate or moderate the link. Alternatively, effects of T or any other sexually dimorphic trait mediating men's reproductive success (Puts, 2016) may not satisfactorily be captured by a simple measure of men's number of sexual partners. Instead, more qualitative assessment of men's reproductive effort, or a more complete investigation of their reproductive success, may deliver insights into the exact role of T levels and other traits in sexual selection. Furthermore, rather than current baseline T levels, pubertal and/or perinatal T levels may be more relevant in this context (e.g., Whitehouse et al., 2015), due to developmental links with traits implicated in sexual selection (Hill, Bailey, & Puts, 2017), such as physical strength (Lassek & Gaulin, 2009). Alternatively, acute fluctuations in T have been suggested to be more strongly related to behaviours and traits than baseline T (Carre & Olmstead, 2015).

Some of our traits showed nonlinear selection, such as upper body size and body height, suggesting differential optimum levels (Saxton, Mackey, McCarty, & Neave, 2016). Our results indicate that women seem to favour men with medium levels of upper body size over very large and very small men, with a similar trend under male-male competition. In contrast, for body height, we found the opposite: in this study it appeared both small and tall, but not medium-sized men are selected for under male-male competition. The latter, however, may also be interpreted as a false positive finding, especially taking into account this sample's apparent oddity regarding body height (see above).

The physical dominance and sexual attractiveness of bodily, facial and vocal stimuli was also judged by unacquainted raters in order to capture subjective impressions of men's traits, complementing our objective measurements. We found robust positive linear selection for facial attractiveness under both female choice and male-male competition (supporting Hill et al., 2013 for female choice, but contradicting their result for male-male competition), as well as selection for increased facial and bodily dominance under male-male competition, but not consistently under female mate choice. These findings are somewhat in line with previous suggestions that men's facial masculinity may not be preferred by women, since it conveys impressions of aggressiveness and may hence be more functional in male contests (Puts et al., 2012; Scott et al., 2014). Neither facial dominance nor attractiveness predicted mating success, partly contradicting previous findings (e.g., Mueller & Mazur, 1997). Regarding observer perceptions of vocal stimuli, we detected only an inconsistent effect of vocal dominance on male-male competition, partly backing previous findings on objective measures of vocal characteristics (e.g., Hill et al., 2013; Puts et al., 2016; Saxton, Mackey, McCarty, & Neave, 2016). Overall, facial attractiveness robustly predicted female choice, and bodily dominance, facial dominance and attractiveness were related to male-male competition, which predicted mating success. These somewhat mixed findings regarding the role of men's facial dominance and attractiveness in sexual selection require further investigation.

Mediation analyses revealed that male-male competition mediated the association of men's sociosexual behaviour with objectively measured upper body size and physical strength, and observer-judged vocal dominance, facial dominance and attractiveness. Female mate choice did not have mediating effects. The mediation effects concerning upper body size and physical strength nicely show how men's formidability may lead to success in male-male competition and subsequently higher mating success. This reveals how these two putative sexually selected traits may have been and are currently under positive linear selection, by augmenting men's access to mates and thereby increasing reproductive success. These findings converge with two more ecologically valid results from two studies in small scale societies. In one Western African population,

men involved in traditional ritual fights (wrestling) had a higher number of offspring, but were not especially preferred by local women (Llaurens, Raymond, & Faurie, 2009). In another traditional society, men's success in turtle hunting predicted earlier onset of reproduction and higher reproductive success, but again this activity did not appear to be valued by women (Smith, Bliege Bird, & Bird, 2003). Thus, traits related to physical dominance may enhance men's access to opposite-sex mates and increase their mating and reproductive success, supporting a strong influence of male-male competition and related traits in men's sexual selection.

Our study offers several improvements over previous studies. Besides including men's sexually dimorphic traits examined in earlier studies (e.g., fundamental frequency, body height, upper body size; Hill et al., 2013; Puts et al., 2016), we included additional relevant traits, such as physical strength and baseline T. We extended Hill and colleagues' approach of assessing subjective impressions of men's vocal and facial traits by asking male and female raters to judge men's bodily dominance and attractiveness from valid 3D body stimuli, which likely capture more information than simple objective measures, thus strengthening the validity of findings on sexual selection mechanisms (Doll, Cardenas, Burriss, & Puts, 2016). We employed additional mating success measures to more thoroughly characterize men's mating success. Besides using sociosexual behaviour (SOI-R; Penke & Asendorpf, 2008), we conducted our analyses with the number of sexual partners in the previous twelve months, in order to directly replicate findings by Hill and colleagues. Additionally, we assessed NPCs (Perusse, 1993), an index that takes into account the number of copulations with each partner.

Our indices of mating success, despite possibly being broader than in previous studies, should still be considered indirect proxies of reproductive success. It may well be that some men have a large number of sexual partners during their young adulthood, but may not convert this quantitative mating success into a high reproductive success later in life. Although NPCs (Perusse, 1993) may be a more valid proxy of mating success than a simple count of sexual partners, it is still far from measuring actual reproductive success, and closer to fertility than to reproductive success

(Steven, 1993). Still, previous evidence suggests that measures of mating success may be moderately related to men's reproductive success (Puts, Bailey, & Reno, 2015). Relatedly, our mating success measures were self-reports, which have been shown to be biased in some cases, especially for men (e.g., Smith, 1992). Such a bias may be moderated by personality, in that more dominant men may exaggerate their self-reported number of sexual partners even more, consequently inflating the association between rated physical dominance and sociosexual behaviour.

In addition to objective measures, men's sexually dimorphic traits were assessed via subjective ratings. Whereas our objective measures assessed a single or a few cues of men's traits (e.g., vocal fundamental frequency, handgrip and upper body strength, baseline T), our subjective ratings focussed on a more integrated assessment of different aspects based on separate entities of a man's phenotype. For example, raters judging vocal dominance and attractiveness (unconsciously) base their assessment on traits' perceptual components beyond fundamental frequency, such as formants or harmonics. Hence, these subjective ratings provide a more complete assessment of men's phenotype with a focus on two crucial emergent characteristics (dominance and attractiveness) of three aspects (faces, bodies, voices). The validity of attractiveness and dominance ratings based on facial photographs and vocal stimuli has been supported in previous studies (e.g., Doll et al., 2014). Relatedly, the video-based judgments of physical dominance and sexual attractiveness, as proxy measures of the two primary mechanisms of sexual selection, were based on an even larger number of cues, since raters observed an individual's behavioural sequence, including visual and verbal information. Thus, these judgments are more complete and valid assessments of a target man's physical dominance and sexual attractiveness, which justifies their positioning as a potential mediator of the association between objective traits or subjective ratings and mating success. Still, reports from well-acquainted peers, as used in Hill and colleagues' study (2013), are likely even more valid ways of capturing real-life physical dominance and sexual attractiveness.

In this study we focused on men's sexually dimorphic, objectively measured traits, which have partly been investigated in previous research, as well as subjectively judged impressions of attractiveness and dominance, based on stimuli which were assumed to be the most important in mate choice and intrasexual competitions (voices, faces and bodies). Besides these traits and observer impressions, men's self-reported psychological traits could be assessed in relation to their mating and reproductive success and a potential influence of perceptions of physical dominance and sexual attractiveness. For example, propensity for same-sex aggression, pain tolerance, risk-taking, interest in physical competition and coalition formation (Puts, Bailey, & Reno, 2015) could be investigated, which presumably are more strongly implicated in male-male competition, but may also affect perceptions of attractiveness. Vall and colleagues (2016) found seven dimensions of personality pathology to be under sexual selection in men and women. For example, persistence-compulsivity was shown to have positive effects on men's reproductive success (mediated by relationship duration, fatherhood and number of offspring). Thus, future studies could focus on the role of relevant personality traits in sexual selection.

To further disentangle the relative contributions of male-male competition versus female choice to sexual selection in men generally, further research could investigate females' perceptions of men's physical dominance, to pinpoint if it is actually more physical dominance amongst men which leads to increased access to potential female partners (as in our study), or whether females prefer and choose more dominant men directly. This would also yield additional insights into female mate choice, enabling us to examine whether female-rated physical dominance predicts men's mating success, and more so than female-rated sexual attractiveness. On the other hand, though it has been suggested that sexual selection may have affected men more than women (Puts, 2010, 2016), intrasexual competition and male mate choice likely also influenced the evolution of women's phenotypic traits (Arnocky & Vaillancourt, 2017; Fink, Klappauf, Brewer, & Shackelford, 2014). To our knowledge, there is no comprehensive study on women comparable to the current study or Hill and

colleagues (2013). Presumably, male mate choice would be more influential here, but female competition should not be underestimated (Arnocky, 2016).

An important question concerns whether there are cross-cultural differences in the relative contributions of different mechanisms and sexually dimorphic traits to sexual selection, especially given that societies differ in potentially influential moderating variables such as mating systems and subsistence types (Hill et al., 2013; Schmitt, 2015). This study could be replicated in more traditional and collectivistic societies (in contrast to the highly industrialized and individualistic German population) to further explore the complex evolutionary dynamics underpinning sexual selection.

Finally, a study on sexual selection remains incomplete until the full array of possible mechanisms has been investigated. Besides mate choice and direct intrasexual competition, these include scrambles, sexual coercion, and sperm competition (Puts, 2016). Though the latter three mechanisms may have played some role over human evolution and are prominent in nonhuman animals (Puts, 2010), direct intrasexual competition and mate choice are arguably the primary mechanisms in human sexual selection. Our study adds further evidence that of these, direct intrasexual competition may be more influential. Still, future research could investigate to what extent scrambles, sexual coercion and sperm competition are related to men's sexually dimorphic traits and affect mating and reproductive success (Barbaro & Shackelford, 2016; Goetz & Shackelford, 2006; Leivers, Rhodes, & Simmons, 2014). Our findings of men's formidable traits affecting success in male-male competition, which subsequently predicted mating success, point towards male intrasexual competition remaining still playing a role in this contemporary industrialized Western population. The intensity of men's contest competition throughout human evolution may be underestimated when examining traits such as upper body size and physical strength, due to the invention of tools enabling to aggress from a distance, such as handheld weapons, limiting the usefulness of anatomical weaponry (Hill, Bailey, & Puts, 2017). With modern laws and societal norms suppressing overt aggressiveness, such formidable traits may no longer function in direct male contests. Instead, these traits may lead to elevated prestige and respect in

dyadic relationships and groups, which may subsequently enhance a man's access to potential female partners. This is supported by earlier findings that men's social dominance and status are related to mating and reproductive success (Puts, 2016; Vall et al. 2016; von Rueden & Jaeggi, 2016; see Arnocky & Carré, 2016, for a discussion of different kinds of male-male competition). For example, a study by von Rueden, Gurven and Kaplan (2011) examined the relative influence of both physical and social dominance on men's reproductive success in the Tsimane. They showed that whereas both predicted a higher reproductive success, the effect of social dominance was somewhat stronger. Further sexual selection studies could investigate variables such as prestige, popularity or social status as potential mediators between success in male-male competition and mating/reproductive success, as these may explain such relationships in contemporary societies characterized by reduced overt aggressiveness (Puts, Bailey, & Reno, 2015; see von Rueden & Jaeggi, 2016, for a comprehensive meta-analysis in nonindustrialized societies). Moreover, rather than physical prowess, traits like intelligence and humor may influence status, dominance and subsequently mating success, and may hence be under sexual selection in modern societies (Miller, 2000; Prokosch, Coss, Scheib, & Blozis, 2009). Still, considering the complexity of contemporary social interactions generally and mate choice specifically, our finding of positive effects of male-male competition and (inconsistently) female choice on sociosexual behaviour also point towards the likelihood of intrasexual competition and female choice acting in concert, for instance that women find dominant men attractive, or seek their protection and provisioning abilities, and subsequently choose them as their partners (Puts, Bailey, & Reno, 2015). Our lack of finding an interaction between male-male competition and female choice on mating success shows that their effects may well be additive, questioning previous claims of correlational selection for these two mechanisms of sexual selection (Hunt, Breuker, Sadowski, & Moore, 2009). Additional work is required to disentangle the contributions of female mate choice and male-male competition to men's sexual selection.

An important question surrounds the distinction between current selection and adaptation (i.e., past selection): Do we provide evidence for selection in progress or rather selection during humans' early evolution, which may not necessarily be ongoing (Puts, Bailey, & Reno, 2015)? It has been argued that trait-related approaches, as ours, are more useful to provide insights into adaptation rather than current selection (Grafen, 1987). Different types of evidence are required to conclude that a trait has been influenced by sexual selection in the past. Traits should develop or increase in expression around sexual maturity, and show sexual dimorphism (Hill, Bailey, & Puts, 2017). These preconditions are likely fulfilled for all five objectively measured traits in this study (fundamental frequency, baseline T, upper body size, body height, and physical strength; e.g., Mehta & Josephs, 2010; Price, Dung, Hopkins, & Kang, 2012; Puts, Doll, & Hill, 2014; Puts et al., 2016). Moreover, a trait should affect success in one or more mechanisms of sexual selection and eventually mating success. We provide further evidence for such effects at least for upper body size and physical strength. Thus, under these assumptions there appears to be strong indication of past sexual selection on increased upper body size and physical strength (Hill, Bailey, & Puts), replicating and extending previous research (e.g., Hill et al., 2013). However, on the contrary, since we assessed men's current mating success and hence a proxy for adaptiveness, we cannot be sure that these traits were adaptive throughout humans' environment of evolutionary adaptedness. This is complicated by the fact that developments in modern industrial environments such as contraception and normative monogamy may confound associations between dominance- and attractiveness-related traits and reproductive success, and even mating success (Perusse, 1993). Therefore, our approach is more a behavioural ecological one, though we still assume that our findings provide insight into past sexual selection on men's traits (Hill et al., 2013; Hill, Bailey, & Puts, 2017).

Overall, we provide evidence for a stronger influence of male-male competition, compared to female mate choice in sexual selection on men. Men with higher physical dominance, but not sexual attractiveness, indicated higher mating success. Moreover, male-male competition mediated effects of upper body size, physical strength, facial attractiveness, as well as vocal and facial

dominance on mating success. We hence deliver novel insights for an important role of physical strength, but not for baseline testosterone, in sexual selection on men. Thus, access to female mates may be predominantly determined by intimidating, competing with and winning against male rivals, rather than by being perceived as attractive and chosen by females.

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Online supplementary

Table S1

The two sets of eight “life domains” each for the video-recorded self-presentations in Study 1; presented in counterbalanced order.

1 st set	2 nd set
leisure time	sports
team	companionship/communion
party	social life
energy/strength	vigour
success with women	physical attractiveness
humour	creativity
friendship	family
success in studies/job	ambition

Table S2

Descriptive statistics for all variables measured.

	<i>M</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
Age T1/T2	24.2/25.8	3.2/3.3	18/19	34/36
Relationship status T1/T2				
Body height (cm)	180.92	7.40	160.50	202.00
Fundamental frequency	119.51	15.13	87.76	180.92
Physical strength (kg)	48.24	7.88	26.00	77.50
Baseline T	78.47	30.93	24.10	180.37
Upper body size	0.00	0.88	-2.06	3.04
Vocal attractiveness	3.58	0.70	1.87	4.90
Vocal dominance	4.13	0.84	1.70	5.87
Facial attractiveness	-1.63	1.41	-4.27	2.18
Facial dominance	0.39	1.43	-3.64	3.91
Bodily attractiveness	-0.09	2.00	-4.90	4.00
Bodily dominance	0.38	1.66	-4.30	4.00
Video-rated physical dominance	0.08	1.80	-4.50	4.30
Video-rated sexual attractiveness	-0.46	1.84	-4.80	3.40
Sociosexual behaviour T1/T2	3.10/3.44	1.85/2.00	1.00/1.00	8.33/8.33
Number sexual partners previous 12 months T1/T2	2.80/2.85	1.52/1.65	1.00/1.00	7.00/8.00
Number of potential conceptions T2	0.55	0.45	0.00	3.22

Note: T1/T2 = time point 1/2; baseline T = baseline testosterone.

Table S3

Bivariate Pearson correlations between all main variables measured.

	Height	F0	Strength	Baseline T	Body size	Vocal attr.	Vocal dom.	Facial attr.	Facial dom.	Bodily attr.	Bodily dom.	Phys. dom.	Sex. attr.	SOIR behav.	Sex. partn.	NPCs
Height	-	-.13	.24*	.28**	.26**	.11	.16	.13	.01	-.07	-.19	.11	.11	.10.	.13	.07
F0	-.13	-	-.07	-.03	-.03	-.44***	-.38***	-.14	-.10	-.13	-.21*	-.11	-.14	.01	.03	-.09
Strength	.19*	-.02	-	.20*	.41***	.03	.19	.15	.33***	.06	.38***	.30**	.15	.23*	.18	.12
Baseline T	.19*	-.04	.13	-	.12	.12	.20*	.14	.18	-.02	-.04	.02	-.03	.05	.03	.09
Body size	.27***	-.09	.41***	.05	-	.14	.26**	-.08	.47***	-.39***	.39***	.36***	-.05	.36***	.26***	.08
Vocal attr.	.08	-.44***	.01	.09	.10	-	.58***	.27**	.22*	.17	.29**	.30**	.25*	.10	.02	.01
Vocal dom.	.15	-.39***	.20*	.17*	.26***	.57***	-	.16	.22*	.06	.33**	.42***	.16	.19	.08	.01
Facial attr.	.08	-.12	.13	.16*	-.08	.25**	.16*	-	.21*	.37***	.22*	.42***	.58***	.05	.10	-.04
Facial dom.	-.05	-.12	.28***	.15	.43***	.12	.21**	.11	-	.09	.50***	.45***	.22*	.34***	.23*	.11
Bodily attr.	-.09	-.06	.02	.00	-.43***	.15	.03	.37***	.00	-	.39***	.28**	.42***	-.01	.08	.01
Bodily dom.	-.23**	-.14	.35***	-.02	.36***	.20*	.25**	.21*	.46***	.38***	-	.58***	.25*	.33***	.20	-.05
Phys. dom.	.05	-.17*	.37***	.03	.33***	.25**	.35***	.32***	.51***	.16*	.52***	-	.55***	.33***	.24*	.06
Sex. attr.	.12	-.15	.16*	.02	-.02	.29***	.18*	.57***	.22**	.37***	.25**	.55***	-	.19	.20*	.16
SOIR behav.	.12	-.16*	.20*	.13	.29***	.15	.22**	.13	.30***	.00	.30***	.33***	.19*	-	.78***	.54***
Sex. partn.	.13	-.18*	.15	.16*	.20*	.17*	.20*	.21**	.20*	-.01	.20*	.28***	.21**	.79***	-	.37***

Note: bottom-left: time point 1, top-right: time point 2; F0=fundamental frequency; strength = physical strength; baseline T = baseline testosterone; body size = upper body size; attr. = attractiveness; dom. = dominance; phys. dom. = video-rated physical dominance; sex. attr. = video-rated sexual attractiveness; SOIR behav. = sociosexual behaviour; sex. partn. = number of sexual partners within previous 12 months; NPCs = number of potential conceptions; * $p < .05$, ** $p < .01$, *** $p < .001$.

Table S4

Structural equation model comparison statistics (for sociosexual behaviour at T1 and subjective ratings; further tables see online supplementary).

Nested model comparisons	χ^2 difference	p	Result
Full model: include covariance between sexual attractiveness and physical dominance?	26.02	<.001	better fit including covariance
Include “long paths” (direct effects of traits on mating success)?	19.59	.075	similar fit, use more parsimonious model excluding “long paths”
Non-nested model comparisons	Vuong test	AIC difference	BIC difference
	z	p	CI lower CI upper CI lower CI upper
Include quadratic besides linear effects?	-40.47 → exclude	<.001	3758.41 4138.11 3801.80 4181.51
Full model vs. excluding long paths & quadratic effects	-40.30 → exclude	<.001	3761.83 4141.13 3842.43 4221.72
Include quadratic effects on sexual attractiveness only?	38.47 → exclude	<.001	-3147.31 -2843.35 -3165.91 -2861.95
Include quadratic effects on physical dominance?	38.64 → exclude	<.001	3145.45 -2842.93 -3164.05 -2861.53

Note: χ^2 = chi-square; AIC = Akaike information criterion; BIC = Bayesian information criterion; CI = confidence interval.

Fig. S1. Structural equation model 1 robustness analyses including age and relationship status; sociosexual behaviour (SOI-R behaviour) at T1 as outcome and objective traits as predictors; baseline T = baseline testosterone; F0 = fundamental frequency; relationship status = binary, single including “open relationship” vs. partnered; SOI-R 1/2/3 = items 1/2/3 of the revised sociosexual orientation inventory; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; RMSEA = Robust Root Mean Square Error of Approximation; * p <.05, ** p <.01, *** p <.001.

Table S5

Mediation analyses for association between sociosexual behaviour (T1) and subjective ratings,
mediator: physical dominance.

Independent variable:	Indirect effect	<i>SE</i>	<i>CI lower</i>	<i>CI upper</i>	<i>z</i>
Vocal attractiveness	.03	.01	.001	.06	2.03*
Facial attractiveness	.04	.01	.01	.06	2.87**
Bodily attractiveness	.02	.01	-.004	.04	1.66
Vocal dominance	.04	.01	.01	.07	2.57*
Facial dominance	.04	.02	.001	.07	2.03*
Bodily dominance	.04	.02	.06	-.002	1.86

Note: SE = standard error; *CI* = confidence interval; * $p < .05$, ** $p < .01$.

Table S6

Mediation analyses for association between sociosexual behaviour (T1) and subjective ratings,
mediator: sexual attractiveness.

Independent variable:	Indirect effect	<i>SE</i>	<i>CI lower</i>	<i>CI upper</i>	<i>z</i>
Vocal attractiveness	.02	.01	-.003	.04	1.67
Facial attractiveness	.04	.02	-.001	.08	1.91
Bodily attractiveness	.03	.01	.001	.06	2.02*
Vocal dominance	.01	.01	-.003	.02	1.50
Facial dominance	.01	.01	-.01	.02	1.27
Bodily dominance	.01	.01	-.01	.02	1.21

Note: SE = standard error; *CI* = confidence interval; * $p < .05$.

Fig. S2. Structural equation model 2 robustness analyses including age and relationship status; sociosexual behaviour (SOI-R behaviour) at T1 as outcome and subjective ratings as predictors; sex. attr. = sexual attractiveness; phys. dom. = physical dominance; relationship status = binary, single including “open relationship” vs. partnered; SOI-R 1/2/3 = items 1/2/3 of the revised sociosexual orientation inventory; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; RMSEA = Robust Root Mean Square Error of Approximation; * $p < .05$, ** $p < .01$, *** $p < .001$.

Fig. S3. Structural equation model 3, number of sexual partners within previous 12 months (SOI-R # sexual partners) at T1 as outcome and objective traits as predictors; baseline T = baseline testosterone; F0 = fundamental frequency; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; RMSEA = Robust Root Mean Square Error of Approximation; * $p < .05$, ** $p < .01$, *** $p < .001$.

Fig. S4. Structural equation model 4, number of sexual partners within previous 12 months (SOI-R # sexual partners) at T1 as outcome and subjective ratings as predictors; sex. attr. = sexual attractiveness; phys. dom. = physical dominance; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; $RMSEA$ = Robust Root Mean Square Error of Approximation; * $p < .05$, ** $p < .01$, *** $p < .001$.

Fig. S5. Structural equation model 3 robustness analyses including age and relationship status; number of sexual partners within previous 12 months (SOI-R # sexual partners) at T1 as outcome and objective traits as predictors; baseline T = baseline testosterone; F0 = fundamental frequency; relationship status = binary, single including “open relationship” vs. partnered; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; $RMSEA$ = Robust Root Mean Square Error of Approximation; * $p < .05$, ** $p < .01$, *** $p < .001$.

Fig. S6. Structural equation model 4 robustness analyses including age and relationship status, number of sexual partners within previous 12 months (SOI-R # sexual partners) at T1 as outcome and subjective ratings as predictors; sex. attr. = sexual attractiveness; phys. dom. = physical dominance; relationship status = binary, single including “open relationship” vs. partnered; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; $RMSEA$ = Robust Root Mean Square Error of Approximation; * $p<.05$, ** $p<.01$, *** $p<.001$.

Fig. S7. Structural equation model 5, sociosexual behaviour (SOI-R behaviour) at T2 as outcome and objective traits as predictors; baseline T = testosterone; F0 = fundamental frequency; SOI-R 1/2/3 = items 1/2/3 of the sociosexual orientation inventory; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; $RMSEA$ = Robust Root Mean Square Error of Approximation; * $p < .05$, ** $p < .01$, *** $p < .001$.

Fig. S8. Structural equation model 6, sociosexual behaviour (SOI-R behaviour) at T2 as outcome and subjective ratings as predictors; sex. attr. = sexual attractiveness; phys. dom. = physical dominance; SOI-R 1/2/3 = items 1/2/3 of the sociosexual orientation inventory; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; $RMSEA$ = Robust Root Mean Square Error of Approximation; * $p < .05$, ** $p < .01$, *** $p < .001$.

Fig. S9. Structural equation model 5 robustness analyses including age and relationship status, sociosexual behaviour (SOI-R behaviour) at T2 as outcome and objective traits as predictors; baseline T = baseline testosterone; F0 = fundamental frequency; relationship status = binary, single including “open relationship” vs. partnered; SOI-R 1/2/3 = items 1/2/3 of the sociosexual orientation inventory; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; $RMSEA$ = Robust Root Mean Square Error of Approximation; * $p<.05$, ** $p<.01$, *** $p<.001$.

Fig. S10. Structural equation model 6 robustness analyses including age and relationship status, sociosexual behaviour (SOI-R behaviour) at T2 as outcome and subjective ratings as predictors; sex. attr. = sexual attractiveness; phys. dom. = physical dominance; relationship status = binary, single including “open relationship” vs. partnered; SOI-R 1/2/3 = items 1/2/3 of the sociosexual orientation inventory; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; RMSEA = Robust Root Mean Square Error of Approximation; * $p < .05$, ** $p < .01$, *** $p < .001$.

Fig. S11. Structural equation model 7, number of sexual partners within previous 12 months (SOI-R # sexual partners) at T2 as outcome and objective traits as predictors; baseline T = baseline testosterone; F0 = fundamental frequency; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; RMSEA = Robust Root Mean Square Error of Approximation; * $p < .05$, ** $p < .01$, *** $p < .001$.

Fig. S12. Structural equation model 8, number of sexual partners within previous 12 months (SOI-R # sexual partners) at T2 as outcome and subjective ratings as predictors; sex. attr. = sexual attractiveness; phys. dom. = physical dominance; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; $RMSEA$ = Robust Root Mean Square Error of Approximation; * $p < .05$, ** $p < .01$, *** $p < .001$.

Fig. S13. Structural equation model 7 robustness analyses including age and relationship status; number of sexual partners within previous 12 months (SOI-R # sexual partners) at T2 as outcome and objective traits as predictors; baseline T = baseline testosterone; F0 = fundamental frequency; relationship status = binary, single including “open relationship” vs. partnered; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; $RMSEA$ = Robust Root Mean Square Error of Approximation; * $p < .05$, ** $p < .01$, *** $p < .001$.

Fig. S14. Structural equation model 8 robustness analyses including age and relationship status, number of sexual partners within previous 12 months (SOI-R # sexual partners) at T2 as outcome and subjective ratings as predictors; sex. attr. = sexual attractiveness; phys. dom. = physical dominance; relationship status = binary, single including “open relationship” vs. partnered; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; $RMSEA$ = Robust Root Mean Square Error of Approximation; * $p<.05$, ** $p<.01$, *** $p<.001$.

Fig. S15. Structural equation model 7, number of potential conceptions (NPCs) at T2 as outcome and objective traits as predictors; baseline T = baseline testosterone; FO = fundamental frequency; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; $RMSEA$ = Robust Root Mean Square Error of Approximation; * $p < .05$, ** $p < .01$, *** $p < .001$.

Fig. S16. Structural equation model 8, number of potential conceptions (NPCs) at T2 as outcome and subjective ratings as predictors; sex. attr. = sexual attractiveness; phys. dom. = physical dominance; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; $RMSEA$ = Robust Root Mean Square Error of Approximation; * $p < .05$, ** $p < .01$, *** $p < .001$.

Fig. S17. Structural equation model 7 robustness analyses including age and relationship status; number of potential conceptions (NPCs) at T2 as outcome and objective traits as predictors; baseline T = baseline testosterone; F0 = fundamental frequency; relationship status = binary, single including “open relationship” vs. partnered; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; $RMSEA$ = Robust Root Mean Square Error of Approximation; * $p < .05$, ** $p < .01$, *** $p < .001$.

Fig. S18. Structural equation model 8 robustness analyses including age and relationship status, number of potential conceptions (NPCs) at T2 as outcome and subjective ratings as predictors; sex. attr. = sexual attractiveness; phys. dom. = physical dominance; relationship status = binary, single including “open relationship” vs. partnered; χ^2 = chi-square; CFI = Robust Comparative Fit Index; TLI = Robust Tucker-Lewis Index; $RMSEA$ = Robust Root Mean Square Error of Approximation; * $p<.05$, ** $p<.01$, *** $p<.001$.

Table S7

The vector of standardized linear selection gradients (β) and the matrix of standardized quadratic and correlational selection gradients (γ) for vocal, facial and bodily dominance (VoDom, FaDom, BoDom) and attractiveness (VoAttr, FaAttr, BoAttr) operating through female choice, male-male competitions and mating success (sociosexual behaviour at time point 1).

β		γ					
		VoDom	VoAttr	FaDom	FaAttr	BoDom	BoAttr
A. Female choice							
VoDom	0.01 (0.03)	-0.04 (0.06)					
VoAttr	0.03 (0.03)	0.08 (0.05)	-0.07 (0.07)				
FaDom	0.05 (0.03)	-0.03 (0.05)	-0.02 (0.05)	0.01 (0.06)			
FaAttr	0.17* (0.03)	-0.07 (0.04)	0.05 (0.05)	0.02 (0.04)	-0.10 (0.06)		
BoDom	-0.00 (0.03)	0.03 (0.05)	0.03 (0.05)	-0.01 (0.05)	0.06 (0.05)	-0.04 (0.08)	
BoAttr	0.08* (0.03)	0.04 (0.04)	-0.09* (0.04)	0.02 (0.04)	0.02 (0.05)	0.02 (0.06)	0.05 (0.08)
B. Male-male competition							
VoDom	0.07* (0.03)	0.00 (0.06)					
VoAttr	0.01 (0.03)	0.01 (0.04)	0.02 (0.06)				
FaDom	0.10* (0.03)	-0.04 (0.04)	0.05 (0.04)	-0.00 (0.06)			
FaAttr	0.06* (0.03)	-0.05 (0.04)	0.08* (0.04)	-0.02 (0.03)	-0.06 (0.04)		
BoDom	0.11* (0.03)	0.02 (0.05)	-0.05 (0.04)	0.04 (0.04)	0.08 (0.04)	-0.07 (0.06)	
BoAttr	-0.01 (0.03)	0.05 (0.04)	-0.04 (0.04)	0.04 (0.04)	-0.06 (0.04)	0.01 (0.05)	0.04 (0.06)
C. Mating success							
VoDom	0.06 (0.06)	0.12 (0.12)					
VoAttr	0.02 (0.06)	0.02 (0.09)	0.03 (0.12)				
FaDom	0.11 (0.06)	0.07 (0.08)	0.01 (0.08)	0.05 (0.10)			
FaAttr	0.03 (0.05)	0.05 (0.07)	0.02 (0.08)	-0.15* (0.07)	0.10 (0.10)		
BoDom	0.15* (0.06)	-0.13 (0.09)	-0.05 (0.09)	-0.02 (0.09)	0.14 (0.08)	0.02 (0.12)	
BoAttr	-0.08 (0.06)	0.03 (0.07)	-0.02 (0.08)	-0.02 (0.08)	-0.03 (0.09)	-0.00 (0.11)	-0.02 (0.13)

Note: Randomization tests: * $p < .05$.

Table S8

The M matrix of eigenvectors from the canonical analysis of γ in Table S7 for female choice, male-male competitions and mating success (sociosexual behaviour at T1).

	M						Selection	
	VoDom	VoAttr	FaDom	FaAttr	BoDom	BoAttr	θ_i	λ_i
A. Female choice								
m_1	-.08	-.48	.31	.02	.00	.82	.06	.11
m_2	.64	.25	-.48	-.06	.37	.40	.01	.06
m_3	-.09	.34	.45	.56	.61	-.00	.13*	.02
m_4	-.56	-.19	-.69	.38	.17	.09	.02	-.03
m_5	-.02	-.51	.03	-.45	.67	-.30	-.12*	-.11
m_6	.52	-.55	-.01	.58	-.14	-.28	.06	-.24
B. Male-male competition								
m_1	.37	-.49	-.05	-.48	-.01	.62	-.02	.14
m_2	.01	.51	.73	-.00	.05	.45	.08*	.06
m_3	.67	.55	-.33	-.09	-.36	-.07	-.03	.03
m_4	.43	-.02	-.12	.52	.72	.13	.13*	-.01
m_5	.41	-.21	.51	-.33	.18	-.62	.08*	-.07
m_6	.25	-.39	.29	.62	-.56	.04	.02	-.22
C. Mating success								
m_1	.41	.09	.47	-.58	-.52	.07	-.02	.31
m_2	.74	.25	-.19	.57	-.17	.02	.02	.18
m_3	-.33	.83	-.17	-.06	-.25	-.32	-.04	.04
m_4	-.09	-.15	-.72	-.21	-.44	.47	-.19*	.01
m_5	.04	-.44	-.22	-.00	-.35	-.80	-.02	-.05
m_6	.41	.14	-.40	-.55	.57	-.19	.06	-.21

Note: 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: * $p < .05$.

Table S9

Hierarchical sequential model comparing sexual selection through male-male competitions versus female choice.

	SS_R	SS_C	Df_1	Df_2	F	p
Linear	26.59	23.91	6	272	5.08	< .001 ^A
Quadratic	23.61	23.51	6	260	0.18	.98
Correlational	20.93	20.12	15	230	0.62	.86

Note: ^Asignificant contribution of individual ratings: facial attractiveness: $F_{1,272} = 7.36$, $p < .01$; bodily dominance: $F_{1,272} = 6.20$, $p = .01$; bodily attractiveness: $F_{1,272} = 4.08$, $p = .04$.