Evolution and Human Behavior 39 (2018) 424–436

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.elsevier.com/locate/ens

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

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ARTICLE INFO

Keywords:
Sexual selection
Mating success
Physical dominance
Sexual attractiveness

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.

1. 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 amongst 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, et al., 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 et al., 2017).

Hill et al. (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). They assessed men's facial masculinity (a composite measure based on Penton-Voak et al., 2001) and vocal masculinity (an aggregate of fundamental frequency (F0, 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 (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

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https://doi.org/10.1016/j.evolhumbehav.2018.03.008
Received 18 December 2017; Received in revised form 20 March 2018; Accepted 21 March 2018
1090-5138/

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 et al. (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 the perception of dominance, whereas the relationship between F0 and attractiveness was negatively curvilinear (i.e., intermediate values were most attractive), 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 et al. (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.

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 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, Pope, et al., 2015), and has been associated with attractiveness (e.g., Roney, Hanson, Durante, & Maestripieri, 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, Pope, 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 Dixson & 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, to elucidate total sexual selection operating on male phenotypic traits. In addition, the effects of men's traits on attractiveness (e.g., Cunningham, Barbee, & Pike, 1990; Neave & Shields, 2008; Saxton et al., 2016), 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 investigated 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 et al., 2017). Second, we obtained observer ratings of men's vocal, facial and bodily stimuli on sexual attractiveness and physical dominance (Dixson & Vasey, 2012; Hill et al., 2013; Puts et al., 2016). Third, we considered more complete operationalizations of quantitative mating success, in addition to men's number of sexual partners within the previous twelve months, as in Hill et al. (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; Pérusse, 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. Fourth, previous studies have predominantly employed a cross-sectional design. We also investigated men's mating success assessed 18 months after the initial measurement of their traits, enabling us to rule out interpretations of reversed causality of men's mating success predicted 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 physical dominance (as an indicator of male-male competition) and related traits will more strongly predict men's quantitative mating success than attractiveness (as an indicator of female choice) 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).

2. Methods

2.1. 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 (> 0.80) to detect effect sizes of Pearson's $r > 0.21$ (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).

2.2. 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 min 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 2 pm and 6 pm (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 min 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.

2.3. Hormonal assessment

For both samples, participants provided at least 2 ml of saliva via unstimulated passive drool through a straw (Fiers et al., 2014; Schultheiss, Schiepe, & Rawolle, 2012). 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 *SD*s ($n = 9$, in accordance with Mehta, Welker, Zilioli, & Carré, 2015; see also Pollet and 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 $W < 0.96$, $ps < .001$). Consequently, both baseline T variables were log10-transformed (e.g., Mehta et al., 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 3 h before; and from eating, drinking (except for water), smoking or brushing teeth 1 h 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 et al., 2017).

2.4. 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.

2.5. 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 et al. (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 (*ICC*s > 0.90). 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 5 s, beginning 5 s 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).

2.6. 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 et al. (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.

2.7. 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 1 min, all videos were cut to a maximum length of 1 min. 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 $\alpha > 0.85$).

2.8. 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 s each; 960 × 540 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 s 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 $\alpha > 0.91$). 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 would the speaker win a physical fight against an average male college student?" on a 7-point Likert scale, with the endpoints 1 = "very unlikely" to 7 = "very likely". Sexual attractiveness was rated using the item "How attractive does the speaker sound for a short-term, uncommitted sexual relationship?" 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 $\alpha > 0.80$). 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 $\alpha > 0.82$). Fourteen data points from 14 raters who indicated that they knew a given target man well were excluded from subsequent analyses.

2.9. 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 Pérusse (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):

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

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; Pérusse, 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 et al.'s (2013) findings, results with only the first item of the SOI-R inventory are reported as well.

2.10. 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; Figs. 1 and 2). Because all SOI-R items 1–3 and the NPC variable were positively skewed (Shapiro-Wilk test: $W < 0.87$, $p < .001$), 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, $r = 0.80$). 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).

2.11. Selection analyses

To further examine sexual selection on men's sexually dimorphic

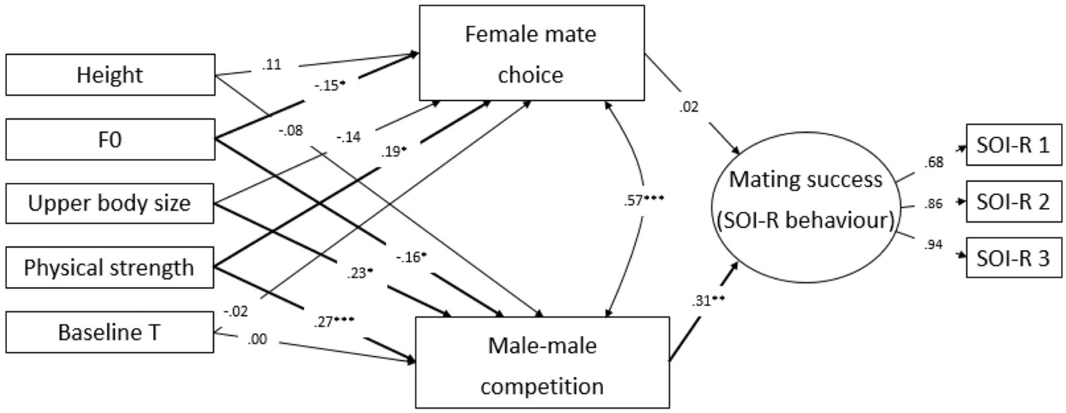

Fig. 1. Structural equation model 1, sociosexual behaviour (SOI-R behaviour) at T1 as outcome and objective traits as predictors; baseline T = baseline testosterone; F0 = fundamental frequency; SOI-R 1/2/3 = items 1/2/3 of the sociosexual orientation inventory; for model fit statistics see Table 2; *$p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

traits we employed selection analyses, which are regularly used in evolutionary biology (e.g., Hunt et al., 2009). For these, we investigated selection under male-male competition and female mate choice (assuming physical dominance and sexual attractiveness can be seen as proxy measures of these, respectively), as well as mating success (in line with previous research, e.g., Hill et al., 2013). 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 Θi, and the strength of nonlinear selection by its eigenvalue (λi) (Phillips & Arnold, 1989). We estimated Θi using the double linear regression method (Bisgaard & Ankenman, 1996) and λi 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 emplyoing 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 et al., 2011).

2.12. Data availability

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

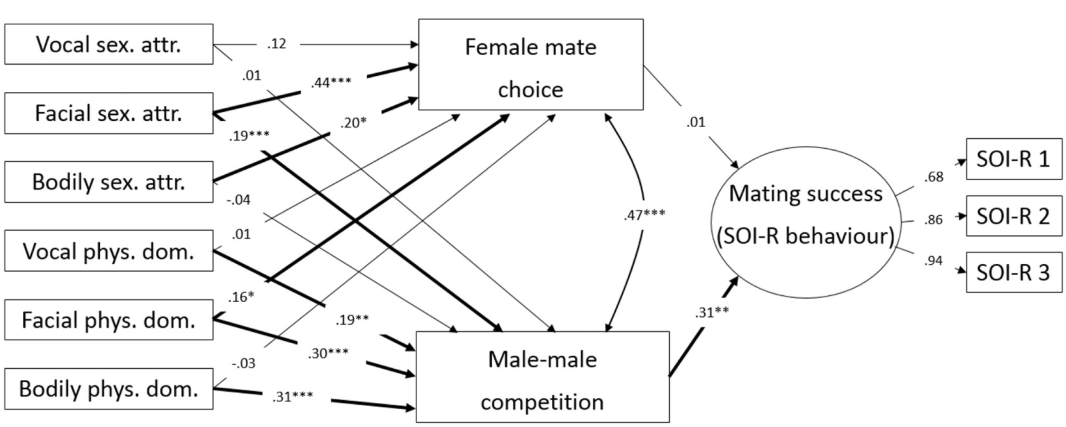

Fig. 2. Structural equation model 2, sociosexual behaviour (SOI-R behaviour) at T1 as outcome and subjective ratings as predictors. Sex. attr. = sexual attractiveness; phys. dom. = physical dominance; SOI-R 1/2/3 = items 1/2/3 of the revised sociosexual orientation inventory; for model fit statistics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

3. Results

3.1. 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).

3.2. Structural equation models and mediation analyses

3.2.1. Model selection

We compared different structural equation models (SEMs) 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 (corresponding to Hill et al., 2013; Figs. 1 and 2). As video-rated dominance and attractiveness were substantially correlated (for both T1/T2 samples: *rs* = 0.55, *ps* < .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 when 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 et al. (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 et al., 2016), 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., 2016 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 Figs. 1 and 2 (mating success measured as sociosexual behaviour at T1).

3.2.2. 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 < 0.01, *ps* > .13). Results were virtually identical with no changes in significance of effects when including participants' age and relationship status (Fig. S1).

3.2.3. Model 2: sociosexual behaviour at T1 as outcome, subjective ratings as predictors

Results 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).

3.2.4. 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 et al. (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 (Figs. S3 and S4), also when including age and relationship status (Figs. S5 and S6).

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	< 0.001	Better fit including covariance
Include "long paths" (direct effects of traits on mating success)?	35.34	< 0.001	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	< 0.001	3749.87	4165.42	3787.06	4202.61
Full model vs. excluding long paths & quadratic effects	−38.05 →exclude	< 0.001	3744.39	4146.29	3812.58	4214.49
Include quadratic effects on sexual attractiveness only?	29.97 →exclude	< 0.001	−3186.57	−2796.58	−3202.07	−2812.08
Include quadratic effects on physical dominance?	30.04 →exclude	< 0.001	−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	0.12	0.98	0.96	0.059
Subjective ratings	Sociosexual behaviour T1	28.98	0.15	0.99	0.97	0.045
Objective traits	Sexual partners 12 months T1	9.20	0.10	0.96	0.86	0.073
Subjective ratings	Sexual partners 12 months T1	8.08	0.23	0.99	0.97	0.046
Objective traits	Sociosexual behaviour T2	16.01	0.66	1.00	1.02	0.000
Subjective ratings	Sociosexual behaviour T2	20.39	0.56	1.00	1.01	0.000
Objective traits	Sexual partners 12 months T2	7.11	0.21	0.97	0.90	0.060
Subjective ratings	Sexual partners 12 months T2	4.81	0.57	1.00	1.03	0.000
Objective traits	NPCs T2	3.65	0.60	1.00	1.07	0.000
Subjective ratings	NPCs T2	4.36	0.63	1.00	1.05	0.000

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.

Table 3
Mediation analyses for association between objective traits and sociosexual behaviour (T1), mediator: video-rated physical dominance.

Independent variable	Indirect effect	*SE*	*CI* lower	*CI* upper	*z*
Height	0.01	0.01	−0.01	0.03	0.71
Fundamental frequency (F0)	−0.02	0.01	−0.04	0.003	−1.73
Upper body size	0.03	0.01	0.001	0.06	2.06*
Physical strength	0.04	0.01	0.01	0.06	2.49*
Baseline T	0.004	0.01	−0.01	0.02	0.51

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

3.2.5. Models 5 and 6: sociosexual behaviour at T2 as outcome, objective traits or subjective ratings as predictors

In a quasi-longitudinal design on the prediction of mating success, we replicated effects of models 1 and 2 of video-rated physical dominance on sociosexual behaviour (for details and for effects of objective traits/subjective ratings, see Figs. S7 and S8). Results were unchanged when including age and relationship status (Figs. S9 and S10).

3.2.6. 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 before 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 *ß*s < 0.17, *p*s > .08; for details and for effects of objective traits/subjective ratings, see Figs. S11 and S12). Again, results were unchanged when including age and relationship status (Figs. S13 and S14).

3.2.7. Models 9 and 10: number of potential conceptions (NPCs) at T2 as outcome and objective traits or subjective ratings as predictors

Using NPCs at T2 as the mating success outcome revealed no effects of video-rated physical dominance or sexual attractiveness (all unsigned *ß*s < 0.18, *p*s > .11; for details and for effects of objective traits/subjective ratings, see Figs. S15 and S16). Results were virtually unchanged when including age and relationship status (Figs. S17 and S18).

3.3. Selection analysis with objective traits as predictors

To further examine linear and nonlinear selection, we employed

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 competition and mating success (sociosexual behaviour at time point 1).

	β	γ				
		Height	F0	Body size	Phys. str.	T
A. Female choice						
Height	0.03 (0.03)	−0.02 (0.06)				
F0	−0.06 (0.03)	0.01 (0.04)	−0.02 (0.04)			
Body size	−0.07 (0.04)	0.04 (0.05)	−0.04 (0.04)	−.22* (0.08)		
Phys. str.	.09* (0.04)	0.00 (0.04)	0.03 (0.04)	0.02 (0.06)	0.02 (0.06)	
T	−0.01 (0.03)	−0.01 (0.04)	−0.04 (0.03)	0.03 (0.05)	−0.03 (0.04)	0.04 (0.06)
B. Male-male competition						
Height	−0.03 (0.03)	.12* (0.04)				
F0	−0.05 (0.03)	0.03 (0.03)	0.02 (0.04)			
Body size	.09* (0.03)	−0.00 (0.04)	−0.08 (0.04)	−.14* (0.06)		
Phys. str.	.10* (0.03)	−.08* (0.03)	.07* (0.04)	0.04 (0.05)	0.02 (0.04)	
T	−0.00 (0.03)	0.02 (0.03)	−0.04 (0.03)	0.01 (0.04)	−0.00 (0.03)	0.01 (0.04)
C. Mating success						
Height	−0.02 (0.05)	−0.10 (0.08)				
F0	−0.06 (0.05)	0.05 (0.06)	0.12 (0.06)			
Body size	.17* (0.06)	0.06 (0.07)	0.09 (0.06)	−0.12 (0.10)		
Phys. str.	0.06 (0.05)	0.01 (0.06)	0.02 (0.06)	0.03 (0.09)	0.10 (0.08)	
T	0.06 (0.05)	0.04 (0.06)	−0.05 (0.05)	0.02 (0.07)	−0.06 (0.06)	−0.06 (0.08)

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 competition 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	0.07	0.42	−0.09	0.44	−0.79	0.03	0.09
m_2	−0.49	0.13	−0.24	−0.74	−0.37	−.07*	−0.00
m_3	0.83	−0.11	0.09	−0.47	−0.26	−0.01	−0.01
m_4	0.18	0.88	−0.11	−0.14	0.41	−0.05	−0.04
m_5	0.18	−0.18	−0.96	0.12	0.09	.10*	−.25*
B. Male-male competition							
m_1	0.85	−0.06	−0.07	−0.51	0.12	−.08*	.17*
m_2	−0.28	−0.82	0.24	−0.32	0.31	0.04	0.09
m_3	0.21	0.08	0.16	0.52	0.81	.05*	0.01
m_4	0.38	−0.37	0.49	0.50	−0.48	.10*	−0.05
m_5	0.12	−0.43	−0.82	0.35	−0.04	−0.02	−.19*
C. Mating success							
m_1	0.18	0.77	0.30	0.49	−0.22	0.02	0.18
m_2	−0.15	−0.49	−0.14	0.83	−0.19	0.05	0.10
m_3	0.52	−0.17	0.33	0.22	0.74	.11*	−0.03
m_4	−0.69	0.31	−0.21	0.16	0.60	0.01	−0.15
m_5	0.45	0.21	−0.86	0.08	0.09	−.16*	−0.18

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

selection gradient and canonical analyses. We focussed on the outcome variable sociosexual behaviour at T1, as explained above.

3.3.1. 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, 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).

3.3.2. 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, as well as negative correlational selection between physical strength and body height, and positive correlational selection between physical strength and F0 (Table 4B): the positive influence of strength on perceptions of physical dominance was stronger in shorter men with higher voices than in tall men with deep voices. 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. This eigenvector was also subject to significant negative linear selection, favouring decreased body height and increased physical strength. 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. 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).

3.3.3. 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.

3.3.4. 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). No significant nonlinear selection was

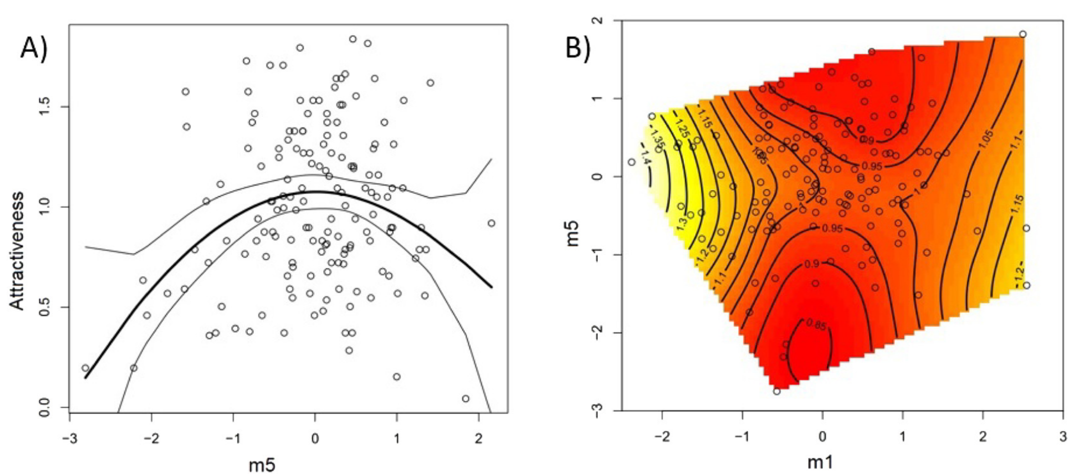

Fig. 3. A) Spline surface, showing quadratic selection for m_5 under female choice (see Table 5A); B) correlational selection on eigenvectors m_1 and m_5 under male-male competition (see Table 5B).

Table 6
Hierarchical sequential model comparing sexual selection through male-male competition versus female choice.

	SS_R	SS_C	Df_1	Df_2	F	p
Linear	40.06	38.39	5	300	2.60	0.03[A]
Quadratic	35.74	35.01	5	290	1.21	0.30
Correlational	33.25	32.52	10	270	0.61	0.81

Note:
[A] Contribution 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: $F_{1,300} = 0.02$, $p = .88$.

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 competition operating through mating success (sociosexual behaviour at T1).

	β	γ	
		Male competition	Female choice
Mating success			
Male competition	**0.19*** (**0.06**)	0.03 (0.10)	
Female choice	0.01 (0.06)	0.07 (0.08)	−0.01 (0.10)

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

detected (Table 5C).

When mating success was used as the fitness correlate, and video-rated sexual attractiveness as a proxy of female choice and video-rated male-male competition as an indicator of physical dominance 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 competition 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.

3.3.5. Selection analyses when using subjective ratings as predictors

Following Hill et al. (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 (m_5) effect 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 S8C). 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).

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 competition	Female choice	Θ_i	λ_i
Mating success				
m_1	−0.79	−0.62	**−.15***	0.08
m_2	0.62	−0.79	0.11	−0.06

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

4. Discussion

Employing a partly longitudinal design and an extensive set of both objectively measured and observer-rated sexually dimorphic traits, our main finding is 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 quantitative mating success, measured as their sociosexual behaviour (Penke & Asendorpf, 2008). This could be interpreted as indicating a stronger role of male-male competition than female mate choice in sexual selection on men. The 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 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 mating success, the number of potential conceptions (NPCs; Pérusse, 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 NPCs there is no overlap, so that these are longitudinal results, ruling out reverse causality. 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 NPCs 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 NPCs has not been used very often in empirical studies since its publication 25 years ago, so that it cannot be seen as well validated. 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, structural equation models, including mediation analyses, and selection analyses consistently indicated that both physical strength and upper body size augmented men's mating success by increasing other men's perceptions of their physical dominance. This directly replicates Hill et al.'s (2013) result for upper body size ("girth" in their study), and underlines that upper body size may be sexually selected and enhance men's mating success. Positive selection under female choice was shown for body height in the selection analyses only, thus partly replicating the effect of Hill et al. (2013). Puts et al. (2016) and Saxton et al. (2016) reported negative linear effects of fundamental frequency on perceived dominance, which we replicated here, albeit inconsistently (no effect in selection analyses). Hence, further replication studies are required to see whether effects of body height and fundamental frequency turn out to be robust. 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 et al., 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. Alternatively, height differences between the men may not have been sufficiently salient for observers judging physical dominance based on video-recordings presented on computer screens, so that an alternative rating procedure might have yielded different results. 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, which appears to increase other men's perceptions of physical dominance and may support men in intrasexual competition. In contrast, baseline T does not appear to be favoured for under female mate choice, male-male competition or mating success. Although baseline T levels are highly sexually dimorphic (e.g., Cohen's $d = 3.20$; Edelstein, 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 et al., 2006), dominance (cf. Dabbs, 1997), or mating success (cf. Peters et al., 2008; Puts, Pope, 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 et al., 2017), such as physical strength (Lassek & Gaulin, 2009). Finally, developmental influences of T may be a confounding factor in the relationship between physical dominance and mating success. If higher developmental T increases both physical dominance and unrestricted sociosexual desire, then men with higher developmental T might lower their quality threshold for sexual partners to satisfy their sociosexual desire, thereby increasing their quantitative mating success and creating a spurious association with physical dominance. However, the existing indirect evidence does not seem to support a link between developmental T and sociosexuality (Charles & Alexander, 2011; Manning & Fink, 2008).

The physical dominance and sexual attractiveness of bodily, facial and vocal stimuli was also judged by unacquainted raters 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, Jones, & DeBruine, 2012; Scott et al., 2014). Neither facial dominance nor attractiveness predicted mating success, partly contradicting previous findings (e.g., Mueller & Mazur, 1997).

Male-male competition mediated the association of men's sociosexual behaviour with upper body size and physical strength, and 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 currently are 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 did not seem to be valued by women (Smith, 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 formidable 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, 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, Cárdenas, Burriss, & Puts, 2016). We employed additional measures to more thoroughly characterize men's mating success. Besides using sociosexual behaviour (SOI-R; Penke & Asendorpf, 2008), we included the number of sexual partners in the previous twelve months, in order to directly replicate findings by Hill and colleagues. Additionally, we assessed NPCs (Pérusse, 1993), an index that takes into account the number of copulations with each partner.

Our indices of mating success, though broader than those utilized in some previous studies, do not capture all components of mating success. Although NPCs (Pérusse, 1993) may more precisely measure mating success than a simple count of sexual partners, this measure remains incomplete, and closer to fertility (Steven, 1993). We did not assess components of mating success related to partner mate quality (including fecundability, residual reproductive value, parental ability, and genetic quality) or to relationship quality, which could influence relationship longevity, cuckoldry risk, and quality of parental care. Men who are successful in competition for mates may also obtain higher quality female mates and/or longer, more stable, faithful, and sexually active relationships. Indeed, both empirical data (e.g., Jones & Hunter, 1993) and mathematical models (Hooper & Miller, 2008) indicate that mate choice can drive evolution even under conditions of perfect monogamy. Thus, although measures of mate quantity are moderately related to men's reproductive success across a variety of cultural contexts (Puts, Bailey, et al., 2015), future studies should measure the quality of men's relationships and mates, ideally in combination with mate quantity and coital frequency, and examine relative influences of female choice and male-male competition on these various components of mating success. Relatedly, we measured mating success via self-report, which has been shown to be biased in some cases, especially for men (e.g., Smith, 1992). Such bias may be moderated by personality, in that more dominant men may more greatly exaggerate their self-reported number of sexual partners, inflating the association between rated physical dominance and sociosexual behaviour.

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 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 et al. (2013). Presumably, male mate choice would be more influential here, but female intrasexual competition should not be underestimated (Arnocky, 2016; Campbell, 2013).

Our findings of men's formidable traits affecting success in male-male competition, which subsequently predicted mating success, point towards male intrasexual competition 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 et al., 2017). With modern laws and societal norms suppressing overt aggression, 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, 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 stronger. Besides the sexually dimorphic traits and observer impressions investigated here, variables such as prestige, popularity or social status as potential mediators between success in male-male competition and components of mating success and reproductive success should be incorporated, as these may explain such relationships in contemporary societies characterized by reduced overt aggression (Puts, Bailey, et al., 2015; see von Rueden & Jaeggi, 2016, for a comprehensive meta-analysis in nonindustrialized societies). Moreover, traits such as intelligence and humour may influence status, and subsequently mating success (Miller, 2000; Prokosch, Coss, Scheib, & Blozis, 2009), perhaps by moderating the influence of dominance (Muller & Mazur, 1997), and may hence be under sexual selection in modern societies. Finally, additional 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, coalition formation (Puts, Bailey, et al., 2015), or personality traits (Vall et al., 2016) may also influence success in intra- and intersexual competition for mates.

Considering the complexity of contemporary social interactions generally and mate choice specifically, despite our null-findings for female choice, there is the possibility of intrasexual competition and female choice acting in concert, such as when women find dominant men attractive, or seek their protection and provisioning abilities, and subsequently choose them as their partners (Puts, Bailey, et al., 2015). 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, et al., 2015)? It has been argued that trait-related approaches, such as ours, are more useful for providing insights into adaptation rather than current selection (Grafen, 1987). Traits influenced by past sexual selection typically develop or increase in expression around sexual maturity, and show sexual dimorphism (Hill et al., 2017). These preconditions likely characterize all five objectively measured traits in this study (e.g., Mehta & Josephs, 2010; Price et al., 2012; Puts et al., 2016; Puts, Doll, & Hill, 2014). 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, indicating past sexual selection on these traits (Hill et al., 2017), replicating and extending previous research (e.g., Hill et al., 2013). However, because we assessed men's current mating success and hence a proxy for adaptiveness, we cannot conclude that these traits were adaptive ancestrally. 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 (Pérusse, 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 et al., 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, reported higher quantitative mating success. Moreover, physical dominance mediated effects of upper body size, physical strength, facial attractiveness, as well as vocal and facial dominance on mating success. We deliver novel insights for an important role of physical strength, but not for baseline testosterone concentrations, in sexual selection on men. Our results provide further evidence to suggest that in modern populations, and hence perhaps ancestrally, men's access to female mates is determined in part by intimidating and winning deference from male rivals, and that this influence may be independent of and even exceed that of mate attraction.

Open practices

The study in this article earned Open Materials and Open Data badges for transparent practices. Materials and data for the experiment are available at osf.io/z4dxa.

Acknowledgements

We acknowledge support by the Leibniz Association through funding for the Leibniz ScienceCampus Primate Cognition. We thank Rike Arkenau, Julia Jünger and Christoph Schild for support with the data collection.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.evolhumbehav.2018.03.008.

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