Is male dimorphism under sexual selection in humans? A meta-analysis

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Abstract

Humans are sexually dimorphic: men and women differ in body build and composition, craniofacial structure, and voice pitch, likely mediated in part by developmental testosterone. Sexual selection hypotheses posit that, ancestrally, more 'masculine' men may have acquired more mates and/or sired more viable offspring. Thus far, however, evidence for either association is unclear. Here, we meta-analyze the relationship between six masculine traits and mating/reproductive outcomes (96 studies, 474 effects, N = 177,044). Voice pitch, height, digit ratios, and testosterone all predicted mating; however, strength/muscularity was the strongest and only consistent predictor of both mating and reproduction. Facial masculinity did not significantly predict either. There was insufficient evidence for any effects of masculinity on offspring viability. Our findings support arguments that strength/muscularity can be considered sexually selected in humans, but raise concerns over other forms of masculinity and highlight the need to increase tests of evolutionary hypotheses outside of industrialized populations.

Introduction

Sexual dimorphism refers to sex differences in morphological and behavioral traits, excluding reproductive organs (1), with particular emphasis on traits thought to have evolved through sexual selection (2). Humans are a sexually dimorphic species (1). Sexual selection is commonly argued to have acted more strongly on male traits, as a consequence of greater variance in males' reproductive output (3) and a male-biased operational sex ratio, i.e. a surplus of reproductively available males relative to fertile females (e.g. 4).

Dimorphic traits that are exaggerated in males are typically referred to as masculine. In humans, masculine faces are characterized by features such as a pronounced brow ridge, a longer lower face, and wide mandibles, cheekbones, and chins (5). Men are, on average, 7-8% taller than women (6) and weigh approximately 15% more (7). Relative to this fairly modest body size dimorphism, upper body musculature and strength are highly dimorphic in humans: compared to women, men have 61% more overall muscle mass, and 90% greater upper body strength (8). Men's bodies tend to have a V- or wedge-shape; their shoulders are broader in relation to their hips than those of women, showing a greater shoulder-to-hip ratio (9, 10). A closely related measure which also contributes to the impression of a V-shaped torso, is the waist-to-chest ratio (11, 12). Second-to-fourth finger (digit) length ratios are also sexually dimorphic, with men showing a lower 2D:4D than women (13; but see also 14), particularly in the right hand (15). In addition, fundamental frequency, commonly referred to as voice pitch, is produced by vibration of the vocal folds and is influenced by the vocal tract's size and shape (16). Under the influence of androgen production in puberty the vocal fold length in boys increases, thus deepening the voice (17) and resulting in an adult male voice pitch approximately six standard deviations lower than women's (18). The development of these dimorphic traits in men is influenced by exposure to androgens, particularly testosterone. With the exception of 2D:4D, which is commonly claimed to be influenced primarily by prenatal testosterone levels and is present at birth (19; but see 20), masculine traits generally

develop or become exaggerated following a surge in testosterone production at sexual maturity (21-23) – although it is not necessarily clear whether the size of that surge corresponds directly to the extent of trait expression.

Key to the assumption that men's masculine traits are sexually selected is that masculine traits should be reliably associated with greater biological fitness. Men may increase fitness by producing a greater quantity of offspring overall (i.e. greater *fertility*), by acquiring a greater number of partners which may in turn mediate offspring numbers (greater *mating success*), and/or by producing more *surviving* offspring (greater *reproductive success*). Several mechanisms have been proposed to explain such putative associations between masculinity and fitness outcomes. For example, according to the *immunocompetence handicap hypothesis* (26), masculine traits index heritable immunocompetence, i.e. good genetic quality. This hypothesis rests upon the notion that testosterone has immunosuppressive properties, increasing vulnerability to pathogens (see 27). Hence, only men whose immune systems are sufficiently robust to cope with the negative impact of high testosterone levels should be able to develop masculine traits, rendering such traits costly signals of genetic quality. Masculine men should therefore produce better quality, more viable offspring. To increase their own fitness, women should preferentially select masculine men as mates, and thus masculine men should be able to attract a greater number of partners which should also result in greater offspring numbers. This suggests that masculinity in men is intersexually selected and evolved and/or was maintained through female choice.

The immunocompetence hypothesis has been widely applied to facial masculinity in particular (although there are no *a priori* reasons to expect this putative mechanism to act more strongly on men's faces than on their bodies). However, there is inconsistent evidence for two key predictions of the hypothesis, namely that testosterone and testosterone-dependent traits will be positively associated with health outcomes, and that masculine traits are

attractive to women. For example, recent evidence suggests that testosterone may have a modulating rather than suppressive effect on immune functioning (28), and facial masculinity is not consistently linked to better health (e.g. 29-31). Evidence is similarly mixed regarding the claim that women are attracted to masculinity in men's faces (32, 33 – see also evidence regarding the perceived attractiveness of men's body masculinity below).

Under the *male-male competition hypothesis*, formidable (i.e. physically strong and imposing) men are better equipped to compete with other men for resources, status, and partners (25, 34). This may work, for example, through direct physical contests or by deterring rivals indirectly (25, 35). Increased stature and physical strength, especially in the upper body, is arguably advantageous in combat, and strength cues such as increased musculature are likely to intimidate competitors. Indeed, people treat physical strength as a proxy of fighting prowess (36) and, in assessing overall strength, favor cues found in the upper body (37). Other traits, such as facial masculinity and voice pitch, do not directly impact fighting prowess, but may have an indirect relationship with formidability (38-43).

Importantly, while male-male competition is often framed as an alternative to female choice, these two drivers of selection may work in conjunction through a 'sexy son' mechanism (44) if women preferentially mate with competitive men (rather than with immunocompetent men, as predicted by the immunocompetence handicap hypothesis), and male competitiveness is cued by formidability (33). While some studies have shown that women are attracted to formidable traits, such as strength cues/muscularity (45-48), other studies have indicated that formidability increases men's mating success through male-rated dominance rather than female-rated attractiveness (49, 50, 51). Under this notion, formidable men are perceived by other men to be more competitive and this in turn creates circumstances under which women may select them as partners. Thus, regardless of whether the driving mechanism is intra- or intersexual selection (or a combination thereof), formidable men

should be able to acquire more partners over their lifetime, which should in turn result in more offspring. Whether formidable men should also have a greater proportion of surviving offspring is unclear. High-quality men may be better able to offer physical protection, contributing to increased survival rates of offspring (52). At the same time, men high in testosterone/masculinity are sometimes claimed to show reduced investment in romantic relationships and in offspring (53-56). If this is the case, this suggests that women 'trade off' a partner's competitiveness against parental investment.

If masculine men do show reduced parental/relationship investment, they may still reap fitness benefits if they increase reproductive output by investing more in mating efforts. This suggestion relies on the assumption that masculine men have higher levels of circulating testosterone, which in turn motivates sexual behavior (57, 58). There are two potential issues with this suggestion, which it shares with the immunocompetence handicap hypothesis. First, the relationship between men's testosterone levels in adolescence, when most masculine traits become exaggerated, and in adulthood is exceedingly weak (59). Second, masculine trait expression in adulthood is not consistently correlated with adult testosterone levels (e.g. 60, 61).

The hypotheses described above therefore suggest that masculine men should show greater offspring numbers, more surviving offspring, and/or more partners. Having thus reviewed multiple proposed mechanisms underlying this association above (which should neither be considered exhaustive nor as mutually exclusive), we turn now to evidence that the association exists. Demonstrating this empirically is key to showing that masculinity is under present selection in men. In societies without effective contraception, reproduction can be measured directly in terms of offspring numbers and/or offspring survival. In most industrialized populations, where offspring numbers are typically constrained by contraceptive use and modern medicine reduces child mortality, mating-based proxies of

reproduction are often used instead. These include preferences for casual sex, number of sexual partners, and age at first sexual intercourse (earlier sexual activity allows for a greater lifetime number of sexual partners), as these are assumed to have correlated with reproductive success in men under ancestral conditions (62). Previous studies testing the relationships between masculine traits and such fitness outcomes have produced a mixture of positive, negative, and null results (e.g. 63-65), highlighting the need for meta-analytic evidence. To date, however, such analyses are rare, and typically exclude many aspects of masculinity in addition to focusing exclusively on either mating or reproductive outcomes.

Van Dongen and Sprengers (66) meta-analyzed the relationships between men's handgrip strength (HGS) and sexual behavior in only three industrialized populations (showing a weak, positive association [r = .24]). Across 33 non-industrialized societies, von Rueden and Jaeggi (67) found that male status (which included, but was not limited to, measures of height and strength) weakly predicted reproductive success (overall r = .19); in contrast, Xu and colleagues (68) reported no significant association between men's height and offspring numbers across 16 studies. Lastly, a meta-analysis of 16 effects by Grebe et al. (57) showed that men with high testosterone levels invested more in mating effort, indexed by mating with more partners and showing greater interest in casual sex (r = .22). Facial masculinity, voice pitch, and 2D:4D have never been meta-analyzed in relation to mating/reproduction.

The present article is the first to meta-analyze the relationships between six masculine traits in men (facial masculinity, body masculinity, 2D:4D, voice pitch, height, and testosterone levels) and both mating and reproductive outcomes. We included testosterone levels because according to the immunocompetence handicap hypothesis, the association between masculine traits and mating/reproductive outcomes occurs because masculine traits index testosterone levels. We emphasize that our aim in the present analysis was not to

identify precise selection mechanisms, but rather to establish the essential grounding principle of whether masculine traits are under present sexual selection in men, as indicated by masculine traits being associated with increased mating success, increased fertility, and/or increased reproductive success. We make no attempt to evaluate the hypotheses described above against each other.

Mating measures included behavioral measures such as number of sexual partners, number of marital spouses, and age at first sexual intercourse. Since increased mating effort is an additional possible route to increased reproductive output, we also included mating attitudes, such as preferences for casual sex. Reproductive measures included: fertility measures, such as number of children/grandchildren born and age at the birth of the first child; and reproductive success measures, i.e. number of offspring surviving childhood. Since offspring mortality is a measure specifically of offspring viability, we included this as a separate measure (i.e. mortality rate and/or number of deceased offspring).

Methods

Literature search and study selection

A systematic search was carried out between November 2017 and February 2018 using the databases PsycINFO, PubMed, and Web of Science; the searches were saved and search alerts ensured inclusion of subsequently published studies. Studies were also retrieved through cross-referencing, citation searches/alerts, and by asking for data on social media. Studies submitted up to 1 May 2020 were accepted. Eligible studies included at least one of the following predictors: facial masculinity, body masculinity (strength, body shape, or muscle mass/non-fat body mass), 2D:4D, voice pitch, height, or testosterone levels. The following outcome measures were included:

- Mating domain: global sociosexuality (i.e. preferences for casual sex: 69, 70) and specific

measures of mating attitudes and mating behaviors where:

i. Mating attitudes included: preferences for short-term relationships, and sociosexual attitudes and desires.

ii. Mating behaviors included: number of sexual partners, one-night-stands/short-term relationships, potential conceptions, sociosexual behaviors, extra-pair sex, age at first sexual intercourse, and number of marital spouses.

- Reproductive domain: including both fertility and reproductive success, described below.

i. Fertility: number of children and grandchildren born, and age at the birth of the first child.

ii. Reproductive success: number of surviving children/grandchildren.

- Offspring mortality: mortality rate and number of deceased offspring.

Both published and unpublished studies were eligible. We restricted our sample to studies with adult participants (≥17 years old). If key variables were collected but the relevant analyses were not reported, we contacted authors to request effect sizes or raw data. If data were reported in more than one study, we selected the analysis with the larger sample size or which included appropriate control variables, such as age. Studies using measures that were ambiguous and/or not comparable to measures used in other studies were excluded. Twin studies where participants were sampled as pairs, population level studies, and studies analyzing both sexes together were also discarded, as well as articles that were not written in English. Multiple measures from the same study were retained if they met the other criteria. We chose Pearson's *r* as our effect size measure and effect sizes not given as *r* were converted; if effect sizes were not convertible, the study was excluded. Where effect sizes for non-significant results were not stated in the paper and could not be obtained, an effect size of 0 was assigned. Excluding those effects from the analyses had no effect on any of the results except for 2D:4D and mating, presented below, and will therefore not be discussed otherwise.

In total, 96 studies were selected (8, 9, 12, 15, 45, 47, 49, 50, 61, 63-66, 71-153), comprising 474 effect sizes from 99 samples and 177,044 unique participants. This exceeds the number of studies for each of the meta-analyses published previously (57, 66-68). See the Supporting Information (SI), sections 1.1.-1.3., for full details about the literature search, study/measure selection decisions, effect size conversions, and the study list (S3).

Statistical analyses

We used the *metafor* package (154) in R 3.6.2 (147). *metafor* transforms Pearson's *r* to Fisher's *Z* for analysis; for ease of interpretation, effect sizes were converted back to *r* for presentation of results. For 2D:4D and voice pitch, effects were reverse coded prior to analysis because low values denote greater masculinity and these traits should therefore be negatively associated with fitness outcomes. Similarly, effects were reverse coded for all offspring mortality outcomes as well as the outcomes age at first birth and age at first sexual intercourse/contact, as low values denote increased fitness. Thus, a positive value of *r* denotes a positive relationship between masculinity and fitness outcomes, and all predicted relationships were positive. Analyses were conducted using random-effects models, as we expected the true effect to vary across samples. A threshold of .05 was used for determining significance.

The analyses were conducted on three levels for both predictor traits and outcomes (Figure 1). For predictor traits, all six masculine traits were first combined and analyzed together at the *global masculinity level*. At the *trait level*, each masculine trait was then

analyzed separately. Lastly, each masculine trait was further divided into separate *trait indices*, which were analyzed as potential moderators (see below).

Overall analyses (all traits & all samples combined)

- Global masculinity (all masculine traits) predicting:
  - Total fitness
    - Mating domain
    - Reproductive domain
    - Offspring viability domain

Main analyses (separating masculine traits; all samples combined)

- Each masculine trait predicting:
  - Mating domain
  - Reproductive domain

Subgroup analyses (separating sample type & outcome measure type)

- Low fertility samples:
  Each masculine trait predicting:
  - Mating domain
    - Mating attitudes
    - Mating behaviors
  - Reproductive domain
    - Fertility
    - Reproductive success
- High fertility samples:
  Each masculine trait predicting:
  - Mating domain
    - Mating attitudes
    - Mating behaviors
  - Reproductive domain
    - Fertility
    - Reproductive success

Moderation analyses (full details in SI)

- Domain type (mating vs reproduction)
  - Mating measure type (attitudes vs behaviors)
  - Reproductive measure type (fertility vs reproductive success)
- Sample type (low vs high fertility)
  - Low fertility sample type (student vs non-student sample)
  - High fertility sample type (traditional vs industrialized sample)
- Ethnicity
- Marriage system
- Publication type
- Peer-review status
- Sexual orientation
- Transformation of variables
- Conversion of effect size
- Age control
- Other control variables

Figure 1. Overall analysis structure.

For the outcomes, mating, reproduction, and offspring mortality were first analyzed together at the *total fitness level*. Given the widespread use of mating measures as proxies of reproductive outcomes, it is imperative (wherever possible) to test (and ideally compare) both mating and reproduction, to ensure that we are not relying on proxies that do not measure

what they are assumed to measure. The *domain level* therefore divided outcomes into the *mating domain*, the *reproductive domain*, and the *offspring mortality domain* and analyzed them separately. The last level, the *measures level*, further divided mating and reproduction into the separate measures, which were analyzed as subgroups.

The mating domain thus comprised mating attitudes and mating behaviors. This is because, where a man has a high mating success, it might result from increased mating efforts (reflected in favorable attitudes towards short-term mating). Alternatively, it might result from being presented with more mating opportunities (reflected in mating behaviors) without actively seeking them; the latter suggests female choice. It is therefore necessary to divide these two measures.

The reproductive measures fertility and reproductive success are closely related: a man who has sired more offspring, i.e. has higher fertility, is also likely to have a higher number of surviving offspring, i.e. greater reproductive success. To tease apart these two measures, we performed separate subgroup analyses of them. Offspring mortality, on the other hand, is largely a measure of mortality *rate* (only two studies comprised measures of number of dead offspring – which may be correlated with total offspring numbers - rather than mortality rate, and it made no difference to the results whether those studies were included or not) and is therefore neither directly nor indirectly a measure of offspring numbers. Since this prediction is theoretically different from our other predictions, offspring mortality was analyzed as a separate domain. There were also too few observations of offspring mortality to test predictor traits separately, and this outcome was therefore only analyzed at the global masculinity level (see Table 1).

In addition to analyzing all samples together, we also analyzed low and high fertility samples separately to assess whether results differed between populations. We used a cut-off of three or more children per woman on average within that sample, which roughly

corresponds to samples with vs without widespread access to contraception. Samples therefore had two levels: *all samples*, and the two sample types *low fertility* and *high fertility*.

The analysis structure was therefore as follows: in the first *overall analyses*, we analyzed global masculinity as a predictor of total fitness, as well as the three domains mating, reproduction, and offspring mortality, separately, across all samples. In our *main analyses*, we analyzed masculinity at the trait level, in relation to the mating, reproductive, and offspring mortality domains. In the following *subgroup analyses*, low and fertility samples were analyzed separately. For those analyses, we analyzed masculine traits predicting the mating and reproductive domains in addition to also dividing outcomes into their respective measures mating attitudes vs mating behaviors, and fertility vs reproductive success.

Lastly, we performed a series of exploratory meta-regressions to test for potential moderator variables. Such moderation analyses make it possible to compare effect sizes across categories of studies as determined by a particular study characteristic, e.g. monogamous vs polygynous marriage systems. This process thus allowed us to determine if effect sizes were equivalent across these categories in addition to indicating how robust the results were to variance in study characteristics. Since power was often low, we ran moderation analyses separately for each study characteristic. For all masculine traits, moderation analyses included domain type (mating vs reproduction), mating measure type (attitudes vs behaviors), reproductive measure type (fertility vs reproductive success), sample type (low vs high fertility), low fertility sample type (student vs non-student), high fertility sample type (traditional vs industrialized), ethnicity, marriage system, publication status, peer-review status, sexual orientation, transformation of variables, conversion of effect sizes, age control, and other control variables. For each masculine trait, we also conducted trait-specific moderation analyses some of which indexed study quality (e.g. subjectively rated vs

morphometric facial masculinity). For description of trait-specific moderators, refer to the SI, section 1.4.; overall, no trait-specific moderators significantly affected the results, except for type of body masculinity on mating (presented below). In the Results section, we therefore summarize results from moderation analyses of outcome domain and outcome measure type (mating vs reproduction, mating attitudes vs behaviors, and fertility vs reproductive success) and low vs high fertility samples; see also Table 5 for an overview of general moderators. For complete moderation analysis results, including trait-specific moderators, see the SI, section 2.1.

Analyses sometimes included more than one observation from the same study/sample. In all analyses, therefore, effect sizes were clustered both by sample and by study. For all analyses, only relationships with a minimum of three independent samples from a minimum of two separate studies were analyzed. For moderation analyses, this meant that *each category* of the moderator needed observations from at least three samples from at least two studies; in many cases, there were not enough observations to test for moderators. Additional details and full results of all analyses can be found in the SI, section 2.

Results

Summary of results. To reiterate, various proposed (and non-mutually exclusive) hypotheses suggest that more masculine men should show increased mating success (indexed by more matings and/or preferences for short-term mating), increased reproductive output (indexed by fertility and/or reproductive success), and/or lower offspring mortality. Our results showed partial support for these predictions. Global masculinity (i.e. all masculine traits combined) significantly predicted both the mating domain and the reproductive domain, but not the offspring mortality domain. When we analyzed each masculine trait separately, all traits except facial masculinity significantly predicted the mating domain, where the strongest

associations were seen for body masculinity, voice pitch, and testosterone levels. In terms of the reproductive domain, the only significant predictor was body masculinity. Effect sizes were overall small, with significant associations ranging between r = .03 and .17.

Below, we present in further detail the results of the effect of global masculinity on each of the three outcome domains: mating, reproduction, and offspring mortality. We then present the associations between each masculine trait and mating and reproductive measures, separately. We also present results for subgroup and selected moderation analyses; for complete results, see the SI, section 2.

Due to few observations, we could only analyze offspring mortality as predicted by global masculinity, but it should be noted that in these analyses, masculinity was largely measured as a function of height (see full results in SI, section 2.2.). Note that this also means that no further analyses could be conducted for offspring mortality, and it is therefore not reported further in the Results.

Overall analyses of global masculinity. In the initial overall analyses, global masculinity was weakly but significantly associated with greater total fitness (i.e. mating and reproduction combined) (r = 0.080 (95% CI: [0.061, 0.101]). When we divided the outcome measures into their three domains, the positive (albeit weak) associations with global masculinity remained significant for mating and reproduction, but not for offspring mortality (mating: r = .090 (95% CI: [0.071, 0.110]; reproduction: r = .047 (95% CI: [0.004, 0.090]; offspring mortality: r = .002 (95% CI: [-0.011, 0.015]). While the effect was thus strongest for mating, the differences between effects were not significant, but we note that sample sizes differed considerably between domains.

Mating

Main analyses of each masculine trat. This set of analyses tested the prediction that individual masculine traits are positively associated with mating. In terms of the overall mating domain (i.e. mating attitudes and behaviors combined), all masculine traits showed the predicted positive relationships with mating and all effects were significant except for facial masculinity (Tables 1 and 2). Some of these effects were very weak, however. The strongest associations with the mating domain were seen in terms of body masculinity (r = .133, 95% CI: [0.091, 0.176]), voice pitch (r = .132, 95% CI: [0.061, 0.204]), and testosterone levels (r = .093, 95% CI: [0.066, 0.121]); moderation analyses showed that these three effects did not significantly differ from each other (p > .05). Height and 2D:4D showed significantly smaller effect sizes than body, voice, or testosterone (height: r = .057, 95% CI: [0.027, 0.087]; 2D:4D: r = .034, 95% CI: [0.000, 0.069]). While not the weakest association, the relationship between facial masculinity and mating was nonsignificant (r = 0.080, 95% CI: [-0.003, 0.164]); it significantly differed from the stronger predictors.

Table 1
Facial masculinity, body masculinity, and 2D:4D predicting mating: main analyses and subgroup analyses of mating attitudes vs mating behaviors and low vs high fertility samples. Pearson's r (95% CI); number of observations (k), samples (s), and unique participants (n); test for heterogeneity (Q) (p-value refers to the latter). Statistically significant associations are bolded: note that significant meta-analytic associations and significant heterogeneity are bolded separately.

	Mating		
Outcome Sample	Facial masculinity	Body masculinity	2D:4D
Mating domain All samples	r = .080 (-0.003, 0.164) k = 30, s = 11, n = 948 **Q(df = 29) = 54.834, p = .003**	**r = .133 (0.091, 0.176)** k = 121, s = 32, n = 7939 **Q(df = 120) = 297.472, p < .001**	**r = .034 (0.000, 0.069)** k = 84, s = 23, n = 66807 Q(df = 83) = 101.994, p = .077
Mating attitudes All samples	r = .095 (-0.072, 0.263) k = 5, s = 4, n = 407 Q(df = 4) = 8.684, p = .070	**r = .078 (0.002, 0.155)** k = 20, s = 9, n = 922 Q(df = 19) = 17.606, p = .549	r = .035 (-0.061, 0.132) k = 19, s = 7, n = 504 Q(df = 18) = 24.141, p = .151

Mating behaviors All samples	*r* = .025 (-0.059, 0.109) *k* = 22, *s* = 8, *n* = 755 **Q(df = 21) = 37.044, *p* = .017**	***r* = .142 (0.099, 0.187)** *k* = 91, *s* = 31, *n* = 7738 **Q(df = 90) = 267.876, *p* < .001**	*r* = .038 (-0.002, 0.078) *k* = 51, *s* = 19, *n* = 1607 Q(df = 50) = 64.049, *p* = .087
Mating domain Low fert. samples	*r* = .089 (-0.001, 0.179) *k* = 28, *s* = 10, *n* = 913 **Q(df = 27) = 54.287, *p* = .001**	***r* = .135 (0.091, 0.180)** *k* = 117, *s* = 28, *n* = 7572 **Q(df = 116) = 289.080, *p* < .001**	***r* = .038 (0.002, 0.073)** *k* = 82, *s* = 22, *n* = 66751 Q(df = 81) = 101.369, *p* = .063
Mating attitudes Low fert. samples	*r* = 0.095 (-0.072, 0.262) *k* = 5, *s* = 4, *n* = 407 Q(df = 4) = 8.684, *p* = .070	***r* = .078 (0.002, 0.155)** *k* = 20, *s* = 9, *n* = 922 Q(df = 19) = 17.606, *p* = .549	*r* = .035 (-0.061, 0.132) *k* = 19, *s* = 7, *n* = 504 Q(df = 18) = 24.141, *p* = .151
Mating behaviors Low fert. samples	*r* = .028 (-0.063, 0.119) *k* = 20, *s* = 7, *n* = 720 **Q(df = 19) = 36.610, *p* = .009**	***r* = .145 (0.100, 0.193)** *k* = 87, *s* = 27, *n* = 7371 **Q(df = 86) = 259.448, *p* < .001**	***r* = .042 (0.001, 0.083)** *k* = 49, *s* = 19, *n* = 1551 Q(df = 48) = 62.941, *p* = .073
Mating domain High fert. samples	*s* = 1	*r* = .105 (-0.069, 0.280) *k* = 4, *s* = 4, *n* = 367 Q(df = 3) = 7.282, *p* = .063	*s* = 1
Mating attitudes High fert. samples	*s* = 0	*s = 0*	*s* = 0
Mating behaviors High fert. samples	*s* = 1	*r* = .105 (-0.069, 0.280) *k* = 4, *s* = 4, *n* = 367 Q(df = 3) = 7.282, *p* = .063	*s* = 1

Note. fert. = fertility; k = number of observations; n = number of unique participants; Q = Cochran's Q test of heterogeneity; s = number of samples.

Table 2

Voice pitch, height, and testosterone (T) levels predicting mating: main analyses and subgroup analyses of mating attitudes vs mating behaviors and low vs high fertility samples.
Pearson's r (95% CI); number of observations (k), samples (s), and unique participants (n); test for heterogeneity (Q) (p-value refers to the latter). Statistically significant associations are bolded: note that significant meta-analytic associations and significant heterogeneity are bolded separately.

	Mating		
	Voice pitch	Height	T levels
Outcome Sample			

Mating domain All samples	***r* = .132 (0.061, 0.204)** *k* = 8, *s* = 5, *n* = 443 Q(df = 7) = 2.334, *p* = .939	***r* = .057 (0.027, 0.087)** *k* = 62, *s* = 25, *n* = 43686 **Q(df = 61) = 263.247, *p* < .001**	***r* = .093 (0.066, 0.121)** *k* = 66, *s* = 21, *n* = 7083 Q(df = 65) = 66.090, *p* = .439
Mating attitudes All samples	*s* = 0	*r* = .028 (-0.013, 0.068) *k* = 9, *s* = 6, *n* = 4232 Q(df = 8) = 5.137, *p* = .743	***r* = .099 (0.026, 0.173)** *k* = 21, *s* = 11, *n* = 1039 Q(df = 20) = 25.379, *p* = .187
Mating behaviors All samples	***r* = .124 (0.043, 0.206)** *k* = 7, *s* = 5, *n* = 443 Q(df = 6) = 2.162, *p* = .904	***r* = .054 (0.021, 0.087)** *k* = 48, *s* = 24, *n* = 42179 **Q(df = 47) = 247.032, *p* < .001**	***r* = .084 (0.058, 0.110)** *k* = 32, *s* = 17, *n* = 6765 Q(df = 31) = 28.558, *p* = .592
Mating domain Low fert. samples	***r* = .129 (0.055, 0.204)** *k* = 7, *s* = 4, *n* = 388 Q(df = 6) = 2.234, *p* = .897	***r* = .055 (0.024, 0.086)** *k* = 58, *s* = 21, *n* = 43310 **Q(df = 57) = 259.576, *p* < .001**	***r* = .099 (0.069, 0.129)** *k* = 58, *s* = 20, *n* = 6795 Q(df = 57) = 61.443, *p* = .320
Mating attitudes Low fert. samples	*s* = 0	*r* = .028 (-0.013, 0.068) *k* = 9, *s* = 6, *n* = 4232 Q(df = 8) = 5.137, *p* = .743	***r* = .108 (0.021, 0.195)** *k* = 17, *s* = 10, *n* = 751 Q(df = 16) = 20.017, *p* = .220
Mating behaviors Low fert. samples	***r* = .119 (0.034, 0.205)** *k* = 6, *s* = 4, *n* = 388 Q(df = 5) = 2.017, *p* = .847	***r* = .051 (0.017, 0.086)** *k* = 44, *s* = 20, *n* = 41803 Q(df = 43) = 243.392, *p* < .001	*r* = .088 (0.058, 0.119) *k* = 30, *s* = 16, *n* = 6477 Q(df = 29) = 27.793, *p* = .529
Mating domain High fert. samples	*s* = 1	*r* = .089 (-0.016, 0.193) *k* = 4, *s* = 4, *n* = 376 Q(df = 3) = 3.388, *p* = .336	*s* = 1
Mating attitudes High fert. samples	*s* = 0	*s* = 0	*s* = 1
Mating behaviors High fert. samples	*s* = 1	*r* = .089 (-0.016, 0.193) *k* = 4, *s* = 4, *n* = 376 Q(df = 3) = 3.388, *p* = .336	*s* = 1

Note. fert. = fertility; k = number of observations; n = number of unique participants; Q = Cochran's Q test of heterogeneity; s = number of samples; T = testosterone.

Inclusion bias/heterogeneity. Since the analysis included unpublished data, the distribution of effects in the funnel plots (shown in Figure 2) shows availability bias rather than publication bias. Apart from voice pitch, for which we did not have many effects, visual inspection of

funnel plots indicated that they were generally symmetric, suggesting that the analysis did not systematically lack studies with unexpected effects. There was significant heterogeneity of effect sizes for facial masculinity, body masculinity, and height, all of which are accounted for in a random-effects analysis.

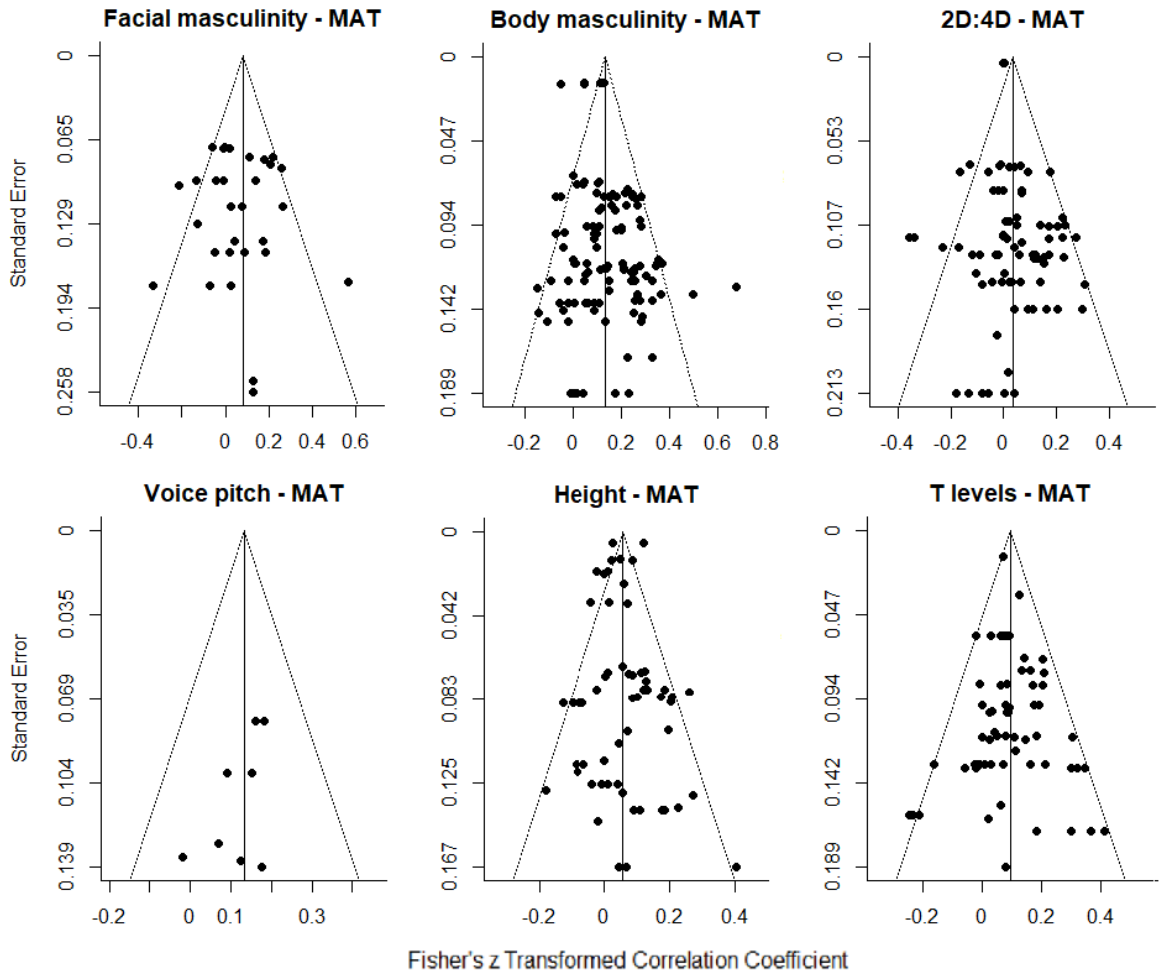

Figure 2. Funnel plots of effect sizes for mating measures (MAT). T = testosterone.

Subgroup and moderation analyses. In this step of the analyses, we tested the hypothesis that each of the six masculine traits are positively associated with the two mating domain measures, mating attitudes and mating behaviors. In this step, we also analyzed low and high fertility samples separately, and conducted moderation analyses. Results of subgroup analyses

can be viewed in Tables 1 and 2; full results of all moderation analyses are reported in the SI, section 2.1.

Across all masculine traits, most effect sizes (94 %) came from low fertility samples. Even though the size of the effects on mating attitudes and mating behaviors differed for some traits, type of mating measure was never a significant moderator. Moderation analyses of sample type could only be run for body masculinity and height; neither was significant. We note, however, that sample sizes are small in some of these analyses.

For facial masculinity, effect sizes were larger for mating attitudes than for mating behaviors, but neither was significant. All samples bar one were from low fertility populations.

Body masculinity significantly predicted both mating attitudes and mating behaviors in the full sample; the effect was stronger for behaviors (attitudes: r = .078, 95% CI: [0.002, 0.155]; behaviors: r = .142, 95% CI: [0.099, 0.187]). While the positive relationship between body masculinity and the mating domain was significant in the 28 low fertility samples and non-significant in the 4 high fertility samples, moderation analysis did not show the strength of relationship to differ between these two population types. Furthermore, moderation analyses of type of body masculinity (strength, body shape, and muscle/non-fat mass) showed that strength and muscle mass did not predict overall mating domain or mating behaviors differently (mating attitudes could not be analyzed due to too few observations), but for both outcomes, body shape was a significantly weaker predictor than strength (B = -0.099, p = .003 and B = -0.105, p = .009, respectively).

For 2D:4D, all samples except one were from low fertility populations. Although the relationship with the mating domain was significant (but very weak), this was no longer significant when excluding non-significant effect sizes not reported in the paper, where we

had assigned an effect size of 0. When mating domain measures were divided into mating attitudes and mating behaviors, neither was significantly related to 2D:4D. The mating domain and mating behaviors, but not mating attitudes, showed significant results in low fertility samples (r = .03, 95% CI: [0.002, 0.073] and r = .042, 95% CI: [0.001, 0.083], respectively). Effect sizes were, however, identical across mating measures. There was no significant difference between left and right 2D:4D (see SI, section 2.1., for results).

Voice pitch was measured in four low fertility samples and one high fertility sample. No effects came from studies measuring overall mating attitudes. All associations (for the overall mating domain and mating behaviors) were significant and of equal strength (r ~ .125).

For height, there were 21 low fertility and 4 high fertility samples. Height had a weak and significant effect on mating behaviors (r = .054, 95% CI: [0.021, 0.087]) but not mating attitudes; the results were identical when analyses were restricted to low fertility samples. Results for high fertility samples were not significant.

Testosterone significantly predicted mating attitudes and mating behaviors to a similar degree: r = .099, 95% CI: (0.026, 0.173) and r = .084, 95% CI: (0.058, 0.110), respectively. One of the 21 samples was from a high fertility population.

Reproduction

Main analyses of each masculine trait. In this set of analyses, we tested the hypothesis that individual masculine traits positively predict reproduction. As Tables 3 and 4 show, relationships were generally in the predicted direction, but body masculinity was the strongest and only significant predictor (r = .143, 95% CI: [0.076, 0.212]; Figure 2). The only trait with an effect size significantly smaller than body masculinity was height (B = -0.107, p = .005).

Table 3

Facial masculinity, body masculinity, and 2D:4D predicting reproduction: main analyses and subgroup analyses of fertility vs reproductive success (RS) and low vs high fertility samples. Pearson's r (95% CI); number of observations (k), samples (s), and unique participants (n); test for heterogeneity (Q) (p-value refers to the latter). Statistically significant associations are bolded: note that significant meta-analytic associations and significant heterogeneity are bolded separately.

	Reproduction		
Outcome Sample	Facial masculinity	Body masculinity	2D:4D
Reproductive domain All samples	*r* = .099 (-0.012, 0.211) *k* = 5, *s* = 5, *n* = 1411 Q(df = 4) = 8.799, *p* = .066	***r* = .143 (0.076, 0.212)** *k* = 14, *s* = 8, *n* = 897 Q(df = 13) = 16.356, *p* = .230	*r* = .074 (-0.006, 0.154) *k* = 19, *s* = 10, *n* = 84558 **Q(df = 18) = 31.704,** ***p* = .024**
Fertility All samples	*r* = .003 (-0.253, 0.260) *k* = 3, *s* = 3, *n* = 437 Q(df = 2) = 5.416, *p* = .067	***r* = .130 (0.060, 0.201)** *k* = 8, *s* = 6, *n* = 813 Q(df = 7) = 4.840, *p* = .679	*r* = .032 (-0.065, 0.130) *k* = 13, *s* = 5, *n* = 84128 Q(df = 12) = 17.757, *p* = .123
RS All samples	*s* = 2	*r* = .192 (-0.052, 0.441) *k* = 6, *s* = 4, *n* = 205 **Q(df = 5) = 11.344,** ***p* = .045**	***r* = .174 (0.085, 0.267)** *k* = 6, *s* = 5, *n* = 430 Q(df = 5) = 0.976, *p* = .965
Reproductive domain Low fert. samples	*s* = 0	*s* = 1	*r* = .083 (-0.023, 0.190) *k* = 8, *s* = 4, *n* = 84034 Q(df = 7) = 13.988, *p* = .051
Fertility Low fert. samples	*s* = 0	*s* = 1	*r* = .052 (-0.065, 0.169) *k* = 7, *s* = 3, *n* = 83845 Q(df = 6) = 8.335, *p* = .215
RS Low fert. samples	*s* = 0	*s* = 0	*s* = 1
Reproductive domain High fert. samples	*r* = .099 (-0.012, 0.211) *k* = 5, *s* = 5, *n* = 1411 Q(df = 4) = 8.799, *p* = .066	***r* = .163 (0.104, 0.225)** *k* = 13, *s* = 7, *n* = 626 Q(df = 12) = 12.347, *p* = .418	*r* = .083 (-0.039, 0.205) *k* = 11, *s* = 6, *n* = 524 Q(df = 10) = 12.595, *p* = .247
Fertility High fert. samples	*r* = .003 (-0.253, 0.260) *k* = 3, *s* = 3, *n* = 437 Q(df = 2) = 5.416, *p* = .067	***r* = .165 (0.095, 0.237)** *k* = 7, *s* = 5, *n* = 542 Q(df = 6) = 0.988, *p* = .986	*s = 2*

RS High fert. samples	*s* = 2	*r* = .192 (-0.052, 0.441) *k* = 6, *s* = 4, *n* = 205 **Q(df = 5) = 11.344,** ***p* = .045**	***r* = .170 (0.053, 0.291)** *k* = 5, *s* = 4, *n* = 241 Q(df = 4) = 0.965, *p* = .915

Note. fert. = fertility; k = number of observations; n = number of unique participants; Q = Cochran's Q test of heterogeneity; RS = reproductive success; s = number of samples.

Table 4

Voice pitch, height, and testosterone levels predicting reproduction: main analyses and subgroup analyses of fertility vs reproductive success (RS) and low vs high fertility samples.
Pearson's r (95% CI); number of observations (k), samples (s), and unique participants (n); test for heterogeneity (Q) (p-value refers to the latter). Statistically significant associations are bolded: note that significant meta-analytic associations and significant heterogeneity are bolded separately.

	Reproduction		
Outcome Sample	Voice pitch	Height	T levels
Reproductive domain All samples	*r* = .136 (-0.053, 0.328) *k* = 5, *s* = 3, *n* = 143 Q(df = 4) = 5.378, *p* = .251	*r* = .006 (-0.049, 0.062) *k* = 35, *s* = 25, *n* = 22326 **Q(df = 34) = 433.359,** ***p* < .001**	*r* = .039 (-0.067, 0.145) *k* = 3, *s* = 3, *n* = 351 Q(df = 2) = 0.387, *p* = .824
Fertility All samples	*s* = 2	*r* = .011 (-0.039, 0.062) *k* = 26, *s* = 23, *n* = 22242 **Q(df = 25) = 400.038,** ***p* < .001**	*s* = 2
RS All samples	*s* = 2	*r* = -0.044 (-0.201, 0.113) *k* = 9, *s* = 9, *n* = 603 **Q(df = 8) = 33.311,** ***p* < .001**	*s* = 1
Reproductive domain Low fert. samples	*s* = 0	*r* = -0.037 (-0.112, 0.038) *k* = 8, *s* = 8, *n* = 17135 **Q(df = 7) = 244.970,** ***p* < .001**	*s* = 2
Fertility Low fert. samples	*s* = 0	*r* = -0.037 (-0.112, 0.038) *k* = 8, *s* = 8, *n* = 17135 **Q(df = 7) = 244.970,** ***p* < .001**	*s* = 2
RS Low fert. samples	*s* = 0	*s* = 0	*s* = 0

Reproductive domain High fert. samples	*r* = .136 (-0.053, 0.327) *k* = 5, *s* = 3, *n* = 143 Q(df = 4) = 5.378, *p* = .251	*r* = .034 (-0.041, 0.109) *k* = 27, *s* = 17, *n* = 5191 **Q(df = 26) = 70.216, *p* < .001**	*s* = 1
Fertility High fert. samples	*s* = 2	***r* = .059 (0.007, 0.111)** *k* = 18, *s* = 15, *n* = 5107 Q(df = 17) = 26.458, *p* = .067	*s* = 0
RS High fert. samples	*s* = 2	*r* = -.044 (-0.201, 0.113) *k* = 9, *s* = 9, *n* = 603 **Q(df = 8) = 33.311, *p* < .001**	*s* = 1

Note. fert. = fertility; k = number of observations; n = number of unique participants; Q = Cochran's Q test of heterogeneity; RS = reproductive success; s = number of samples; T = testosterone.

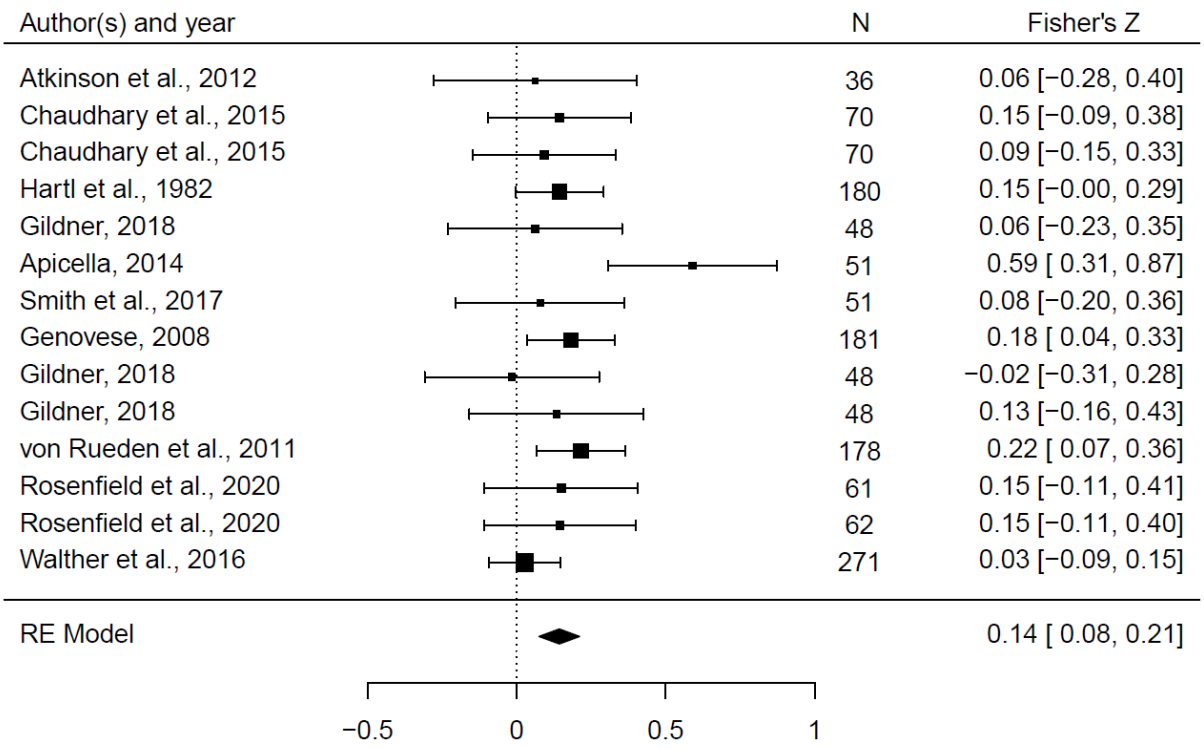

Figure 3. Forest plot of the association between body masculinity and reproductive domain. Effect sizes are shown as *Z*-transformed *r*, with 95% confidence intervals in brackets. The width of the diamond corresponds to the confidence interval for the overall effect.

Inclusion bias/heterogeneity. Visual inspection of funnel plots (Figure 3) suggested that while the effects for voice pitch, height, and testosterone levels were symmetrically distributed, our analysis may have lacked studies for the other traits. Facial masculinity and height showed significant heterogeneity.

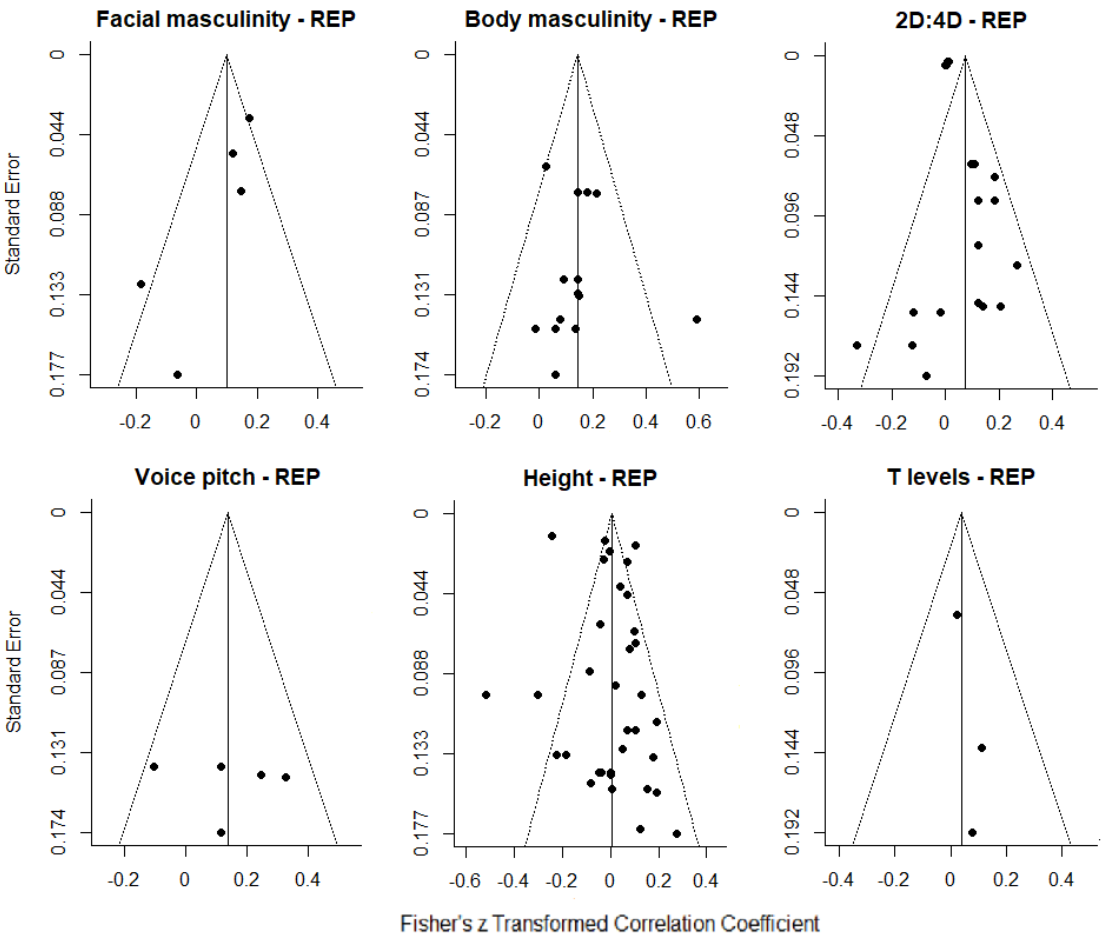

Figure 4. Funnel plots of effect sizes for reproductive measures (REP). T = testosterone levels.

Subgroup and moderator analyses. In this step of the analyses, we tested the hypothesis that masculine traits positively predict the two reproductive domain measures fertility and reproductive success. We also report results of subgroup analyses of low vs high fertility samples and moderation analyses. Subgroup analyses are reported in Tables 3 and 4; moderation analyses in the SI, section 2.2.

The majority (77 %) of observations of reproduction were from high fertility samples. Moderation analyses of low versus high fertility samples could only be conducted for 2D:4D and height; effect sizes did not differ significantly between sample types.

All five effects for facial masculinity came from high fertility samples. Three of these effects were fertility measures; the relationship with fertility was close to zero and non-

significant. No subgroup analyses of reproductive success/low fertility samples or moderation analyses could be conducted.

For body masculinity, all samples except one came from high fertility populations. The effect on fertility was significant (r = .130, 95% CI: [0.060, 0.201]) but not the effect on reproductive success. Although the latter showed a larger effect; the effects did not significantly differ, however. Type of body masculinity (strength vs muscle mass) did not moderate the results.

2D:4D was sampled from four low fertility and six high fertility populations. The only significant association was seen in terms of reproductive success (four out of five samples from high fertility populations: r = .174, 95% CI: [0.085, 0.267]); although a larger effect, it did not significantly differ from fertility. There was no difference between left and right hand 2D:4D.

Effects of voice pitch on reproductive outcomes were measured exclusively in high fertility samples. As there were only two samples each for fertility and reproductive success, no subgroup or moderation analysis could be conducted.

For height, there were observations from 9 low fertility and 17 high fertility samples. Height significantly predicted fertility outcomes in high fertility samples (r = .059, 95% CI: [0.007, 0.111]). No other subgroup and no moderation analyses were significant. As can be seen with reproductive success, height was the only trait in our analyses showing relationships in the negative direction.

Testosterone levels were measured in just three samples, out of which two were low fertility samples for which fertility was measured. Thus, no subgroup or moderation analyses could be conducted.

Moderation analyses of domain type (mating versus reproduction) for each trait showed that height and testosterone levels had weaker associations with reproduction than

mating and body masculinity slightly stronger, but the differences were not significant. However, there were generally far fewer observations for reproductive measures, so this may reflect lack of power. For facial masculinity, voice pitch, and 2D:4D, effect sizes for global mating and reproductive measures were identical.

Table 5

Overview of moderation analyses for the mating vs reproductive domains. Ticks indicate significant moderation (i.e. that the impact of masculinity is likely affected by the moderator), crosses no significant moderation, and NA that power was too low to run that specific analysis. Note that this table only shows general moderators shared by all masculine traits; for trait-specific moderation analyses, see the SI, section 2.1. Likewise, for moderation analyses of the two mating domain measures attitudes vs behaviors, and the two reproductive domain measures fertility and reproductive success, we also refer to the SI, section 2.1.

	Facial masc.		Body masc.		2D:4D		Voice pitch		Height		T levels	
Moderator	Mat	Rep	Mat	Rep	Mat	Rep	Mat	Rep	Mat	Rep	Mat	Rep
Mating vs reproductive domain	✗		✗		✗		✗		✗		✗	
Mating attitudes vs behaviors	✗	NA	✗	NA	✗	NA	NA	NA	✗	NA	✗	NA
Fertility vs reproductive success	NA	NA	NA	✗	NA	✗	NA	NA	NA	✗	NA	NA
Low vs high fertility sample	NA	NA	✗	NA	NA	✗	NA	NA	✗	✗	NA	NA
Low fertility: student vs non-student sample	NA	NA	√	NA	✗	NA	NA	NA	✗	NA	✗	NA
High fertility: traditional vs industrialized sample	NA	NA	NA	NA	NA	✗	NA	NA	NA	✗	NA	NA
Ethnicity	✗	NA	✗	NA	√	✗	NA	NA	✗	✗	✗	NA
Marriage system	NA	NA	✗	NA	NA	✗	NA	NA	NA	✗	NA	NA
Publication status	✗	NA	√	✗	✗	✗	NA	NA	✗	✗	✗	NA
Peer-review status	NA	NA	✗	NA	✗	NA	NA	NA	✗	NA	NA	NA
Sexual orientation	✗	NA	√	NA	✗	✗	NA	NA	✗	√	√	NA
Transformation of variables	NA	NA	✗	✗	√	√	NA	NA	✗	✗	√	NA
Conversion of effect sizes	NA	NA	✗	√	NA	NA	NA	NA	✗	✗	✗	NA

Age control	✗	NA	√	NA	✗	✗	NA	NA	✗	✗	✗	NA
Other control variables	NA	NA	NA	✗	NA	NA	NA	NA	NA	✗	✗	NA

Note. Masc = masculinity; mat = mating; rep = reproduction; T = testosterone.

Discussion

We conducted the first comprehensive meta-analysis of the relationships between men's masculine traits and outcomes related to mating and reproduction. Mating outcomes (indexed by mating attitudes and mating behaviors) were predominantly measured in low fertility populations. Here, they were positively associated with all the masculine traits we assessed, apart from facial masculinity. The strongest correlations were r = .13 for both body masculinity and voice pitch and r = .09 for testosterone levels. Reproductive outcomes (indexed by fertility and reproductive success) were measured mainly in high fertility populations. Here, they were correlated only with body masculinity (r = .14); 2D:4D was significantly associated only with reproductive success (r = .17), and height showed a weak significant correlation with fertility in high fertility samples. Offspring mortality was not associated with masculinity (indexed primarily by height in this analysis), but we note a severe lack of relevant data from which to draw conclusions.

The effects mentioned above are potentially meaningful in an evolutionary context. As benchmarks for interpreting correlations, Funder and Ozer (156) suggest that a correlation of .10, while being a small effect, has the potential to be influential over a long time period, and a medium-size correlation of .20 can be consequential both in the short- and long-term. The cumulative effect of relatively 'weak' correlations can therefore be of real consequence, particularly when considered in terms of selection acting over many generations.

Compared to previous meta-analyses, assessing associations between handgrip strength and mating outcomes (66), height/strength and reproductive outcomes (67, 68), and testosterone levels and mating effort (57), our analysis benefits from more comprehensive

measures of masculinity, larger sample sizes, and inclusion of more unpublished effects. With the exception of (68), we observe smaller effect sizes than previous meta-analyses, which suggests that the association between masculinity and fitness outcomes has previously been overestimated.

Body masculinity (i.e. strength/muscularity) is the only trait in our analysis that was consistently correlated with fitness outcomes across populations, and the effects of body masculinity on these outcomes were among the strongest in the analysis. Body masculinity is therefore the trait for which we have the most compelling evidence for present selection in naturally fertile populations. Height and 2D:4D showed inconsistent relationships with fertility and reproductive success: in three high fertility samples, men with a more masculine 2D:4D had more surviving children, but such men did not show greater fertility in either low or high fertility populations. Height, on the other hand, showed a weak, positive association with fertility – but not child survival – in naturally fertile populations, suggesting a role of female choice and/or intrasexual competition. Overall, since traits such as body size, strength, and muscularity are associated with formidability, our findings could be interpreted as lending support to the male-male competition hypothesis. In species with male intrasexual competition, males tend to evolve to become larger, stronger, and more formidable than females, as they are in humans. Some authors argue that male-male violence has influenced human evolution (25, 157), and male intergroup aggression increases mating/reproductive success in both non-industrialized human societies and in non-human primates (158, 159). For example, in the Yanomamö Indians, killing increases men's reproductive success (160). A relationship between formidable traits and fitness outcomes need not be a direct one, however. It might, as mentioned in the introduction, be mediated by other factors that are important in mate choice, such as interpersonal status and dominance. For example, features that are advantageous in intraspecies conflicts may also be advantageous when hunting game (35);

Smith and colleagues (134) reported that in a hunter-gatherer population, men with greater upper body strength and a low voice pitch had increased reproductive success, but this relationship was explained by hunting reputation.

It is of course possible that different selection pressures may have contributed to the evolution of different masculine traits. Male-male competition for resources and mates, female choice, and intergroup violence are all plausible, non-mutually exclusive explanations (24). In this article, we have focused on the effect of men's own traits on their fitness, but it is of course equally possible that men varying in masculinity may differ in the quality of the partners they acquire. If masculine men are able to secure partners who are more fertile and/or better parents, this may also increase their fitness. Traditionally in human sexual selection research, however, the immunocompetence handicap hypothesis has attracted the most attention as an explanation of how masculine traits evolved in men. Most research based on this hypothesis has focused particularly on masculinity in men's facial structure as an indicator of heritable immunocompetence (i.e. good genes), which should then be associated with greater mating and reproductive success. While we find that the effect of facial masculinity on mating was similar in size to that of other traits (r = .08), it was not significantly different from zero. Furthermore, the effect of facial masculinity on mating was largely driven by mating attitudes and was close to zero for mating behaviors, suggesting that men's facial masculinity exerts virtually no influence on mating when moderated by female choice. Similarly, the influence of facial masculinity on fertility in high fertility samples was non-existent (r = .00). Although the relationship with reproductive success appeared stronger, this was based on only two samples. Overall, these findings contradict a large body of literature claiming that women's preferences for masculinity in men's faces are adaptive, and rather indicate that such preferences (to the extent that they exist at all) are a modern anomaly only found in industrialized populations, as suggested by Scott and colleagues (43).

A limitation of our analysis is that we only assessed linear relationships, ignoring possible curvilinear associations. There is evidence suggesting that moderate levels of masculinity might be associated with increased reproductive success (see e.g. 64, for offspring survival rates) and perceived attractiveness (45, 161, but see 48), with a decrease for very high levels of masculinity. However, if such results indicate that greater-than-average levels of masculinity are associated with peak fitness/attractiveness, we would still expect to see positive, albeit weak, linear relationships.

Another caveat for interpreting our results is that testosterone is reactive. Testosterone decreases, for example, when men enter a relationship or get married (162, 163), when they become fathers (162, 164), or when they engage in childcare (162). Thus, men whose circulating testosterone was previously high may show declining testosterone levels because their fatherhood status has changed, meaning that we cannot determine with certainty whether there really is no relationship between testosterone levels and reproductive outcomes. The sample size for reproduction is also small. Furthermore, in our analysis, men with high testosterone levels have more favorable attitudes towards and engage in more casual sex, but we cannot determine whether high testosterone men pursue more mating opportunities which leads to more mating encounters, or whether high testosterone results from having many mating encounters.

Our findings raise important concerns for the human sexual selection field, particularly with respect to whether (and which) mating measures can be used as reliable indicators of likely ancestral fitness. Since reproductive outcomes – for good reason – are not considered meaningful fitness measures outside of naturally fertile populations, we typically test fitness outcomes in industrialized populations using mating measures such as sociosexual attitudes and casual sexual encounters, under the assumption that such measures index mating strategies that ancestrally would have increased men's offspring numbers. However, if mating

outcomes (be it attitudinal or behavioral) measured in low fertility populations truly index reproductive outcomes in naturally fertile contexts, we would expect traits that predict mating to also reliably and consistently predict reproduction across samples; we do not have compelling evidence that this is always the case. Our findings therefore raise the question of whether these widely used measurements are truly valid proxies of what we purport to be measuring. Our findings illustrate that when we attempt to test the same underlying research questions using different measurements in different populations, this may yield conclusions that are erroneous or misleading when applied outside of the studied population. Wherever possible, we thus need to use the same measurements across populations, or at least resist the temptation of applying our findings universally.

In summary, we used a large-scale meta-analysis of six masculine traits and their relationships with mating and reproductive outcomes to test whether such traits are under present selection in humans. We found that all masculine traits except facial masculinity were associated with significantly greater mating success. However, only body masculinity and height predicted higher fertility. It should be noted that we are constrained by a lack of data from natural fertility samples. We argue that our findings illustrate that when we test hypotheses about human evolution largely in industrialized populations, we risk drawing conclusions that are not supported outside of evolutionary novel, highly niche mating contexts. We therefore call for greater sample diversity and more homogenous measurements in future research.

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