Does masculinity really matter?
A meta-analysis of the relationships between sexually dimorphic traits in men and mating/reproduction

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Abstract

Humans are sexually dimorphic: on average men significantly differ from women in body build and composition, craniofacial structure, and voice pitch, likely mediated in part by developmental testosterone exposure. Hypotheses which attempt to explain the evolution of dimorphism in humans assume that more masculine men have historically achieved greater biological fitness. This may be because: more masculine men out-compete other men for mates; women preferentially select masculine men (e.g. due to their greater competitiveness and/or heritable immunocompetence); masculine men expend more energy on mating effort; and/or masculine men father more viable offspring. Thus far, however, evidence for an association between masculinity and mating/reproductive outcomes is unclear. We conducted the most comprehensive meta-analysis to date on the relationship between six types of masculine traits and mating/reproductive outcomes, comprising 474 effect sizes from 96 studies (total *N* = 177,044). Body masculinity, i.e. strength/muscularity, was the strongest and only consistent predictor of both mating and reproduction. Voice pitch, height, digit ratios, and testosterone levels all predicted mating; height and digit ratios also predicted some reproductive measures in some samples. Facial masculinity did not significantly predict either mating or reproduction. There was insufficient evidence for any effects on offspring mortality. Our findings support arguments that strength/muscularity can be considered sexually selected in humans, but raise concerns over other forms of masculinity. We are also constrained by lack of reproductive data, particularly from naturally fertile populations. Our data thus 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 e.g. 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 compared to women, showing a greater shoulder-to-hip ratio (9, 10). A closely related measure, also contributing to the impression of a V-shaped torso, is the waist-to-chest ratio (11, 12). Second-to-fourth finger (digit) length ratios are sexually dimorphic, with men showing a lower 2D:4D than women (13; but see also 14), particularly in the right hand (15). 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.

The evolution of sexual dimorphism in the human lineage is, to date, not well understood (1). We are often forced to test hypotheses about human evolution in current industrialized populations, but data from other sources are imperative. Fossil records provide clues to the evolution of skeletal dimorphism, but are less informative in terms of dimorphism in soft tissues (24). Comparative evidence from our primate relatives can provide further clues, as can data from contemporary small-scale, naturally fertile societies. If a trait which is proposed to be sexually selected increases mating/reproductive success in such populations, that bolsters claims the trait may also have increased mating/reproductive success ancestrally (25).

Two main hypotheses have been proposed to explain how and why masculine traits evolved in men. According to the immunocompetence handicap hypothesis (26), male sexually dimorphic 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 reproductive success, 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. However, there is inconsistent evidence for two key predictions of the hypothesis, namely the putative associations between testosterone/testosterone-dependent traits and health outcomes, and the extent to which such traits are actually 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).

An alternative hypothesis that has been gaining increasing support, the male-male competition hypothesis, is that 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 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). In this case, even though competitiveness and formidability are correlated, it is not necessarily the physical traits (i.e. the cues) that need be attractive to women, but demonstrations of competitiveness. In support of this, formidable men typically report greater mating success, and this relationship appears to be mediated by male-rated dominance rather than female-rated attractiveness (44, 45). Thus, it is not necessarily because they are perceived by women to be more physically attractive that formidable men achieve more partners, but rather because they are perceived by other men to be more competitive and this in turn creates circumstances under which women may select them as partners. In a study by Slatcher and colleagues (46), men high in testosterone behaved in a more dominant manner towards a competitor; those men were also given higher ratings by a female experimental confederate of how much they ‘clicked’.

The mechanisms outlined above are not an exhaustive list of ways in which masculine men might increase fitness. Another possibility is that such men expend more energy on mating efforts (rather than, e.g. investment in one relationship). This suggestion relies on the assumption that masculine men have higher levels of circulating testosterone, which in turn motivates sexual behavior (47, 48). 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 (49). Second, masculine trait expression in adulthood is not consistently correlated with adult testosterone (e.g. 50, 51).

As already alluded to, men can increase biological fitness either by producing better quality offspring or a greater quantity of offspring; the latter may be achieved by mating with a greater number of partners. 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 (52). Previous studies testing the relationships between masculine traits and such fitness outcomes have produced a mixture of positive, negative, and null results (e.g. 53-55), 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 (56) 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 (57) 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 (58) 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. (47) 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 sexually dimorphic 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.

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).

Both the immunocompetence hypothesis and the male-male competition hypothesis predict that masculine men should have greater mating and reproductive success, although the mechanism by how this is achieved differs between hypotheses. While our aim was not to evaluate the two hypotheses against each other, we note that the male-male competition hypothesis predicts that it is primarily physically formidable traits, such as body masculinity and height, that should be associated with a greater number of partners and thereby also greater fertility. The immunocompetence hypothesis, on the other hand, has primarily been applied to facial masculinity, and predicts that more masculine men should not only acquire more partners and more offspring, but also more surviving offspring and lower offspring mortality.

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: 59, 60) 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 where participants were at least 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 effect sizes from the analyses only affected the results for 2D:4D and mating, presented below, and will not be discussed otherwise). In total, 96 studies were selected (8, 9, 12, 15, 44, 45, 51, 53-56, 61-145), 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 (47, 56-58). 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 (146) 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, 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. For predictor traits, all six masculine traits were first 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.

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), or 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. We would therefore only expect masculine men to produce more viable offspring, with lower mortality, if masculinity is associated with heritable good genes. 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 meta-regressions to test for potential moderator variables. For all traits, these 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 type, peer-review status, sexual orientation, transformation of variables, conversion of effect sizes, age control, and other control variables. For trait-specific moderators, refer to the SI, section 1.4.; overall, no trait-specific moderators significantly affected the results, with the exception of type of body masculinity on mating (presented below). We therefore only 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 below. For complete moderation analysis results, 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

Overall analyses

The overall association between global masculinity and total fitness was positive and significant: r = 0.080 (95% CI: [0.061, 0.101]). Dividing outcomes into the three domains, the associations with mating and reproduction were significant, but not with 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]). The difference between these effects was not significant, but we note that sample sizes differed considerably between domains.

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 will therefore not be reported further in the Results.

Mating

Main analyses. The following set of analyses tested the prediction that masculine traits are positively associated with mating. As can be seen in Tables 1 and 2, for all traits bar facial masculinity, greater masculinity predicted significantly higher mating success. 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 were also significant predictors of mating, but 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 not significant (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 behaviours 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 behaviours 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 behaviours 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 behaviours 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 behaviours 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	Voice pitch	Height	T levels
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 behaviours 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 behaviours 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 behaviours 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 1) shows availability bias rather than publication bias. With the exception of 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.

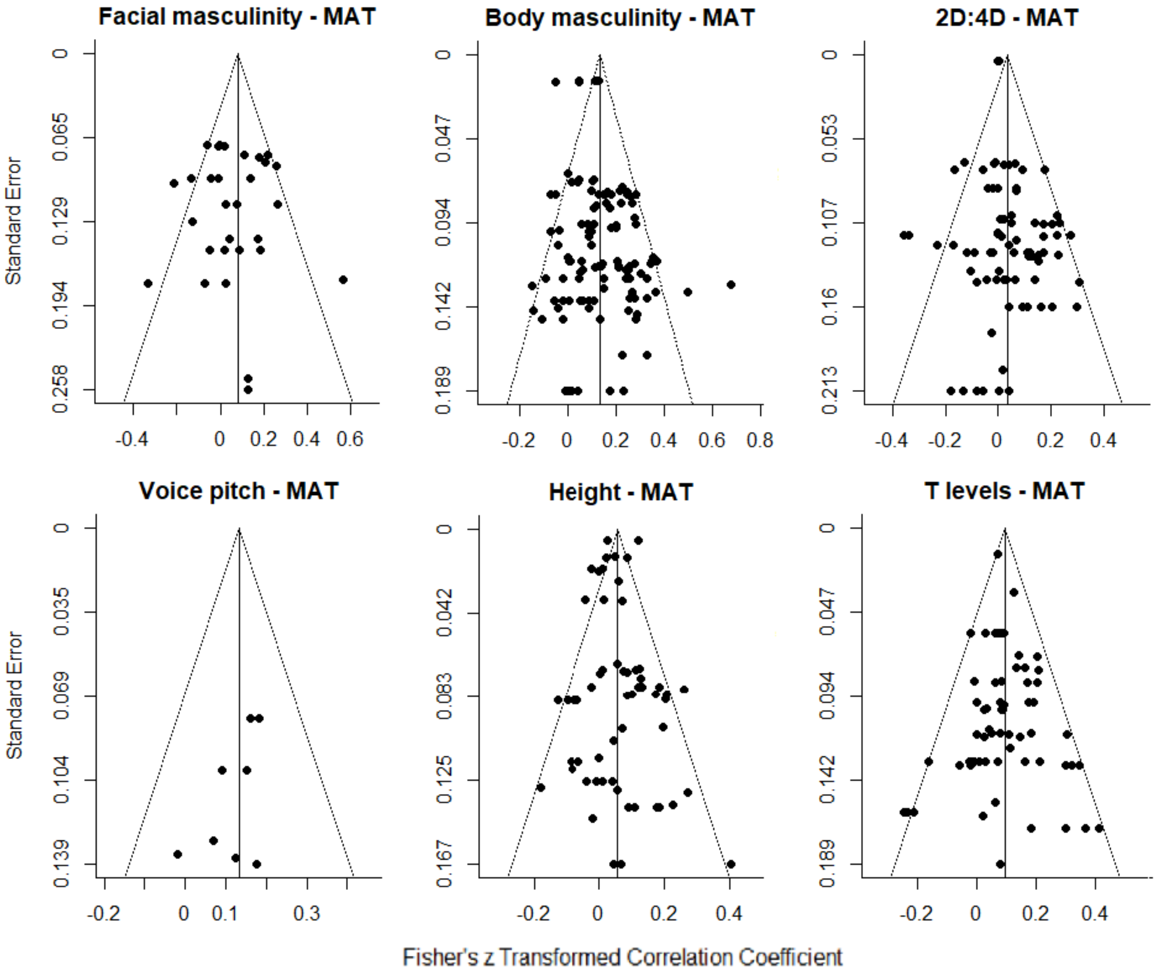

Figure 1. Funnel plots of effect sizes for mating measures (MAT). T = testosterone.

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 outcome 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, the majority of 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 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 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. All effects came from studies measuring mating domain and/or mating behaviors. All associations were significant and of equal strength ($r \sim .125$).

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. In this set of analyses, we tested the hypothesis that masculine traits positively predict reproduction. As Tables 3 and 4 show, relationships were generally in the predicted direction, but body masculinity was the 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* = .049 (-0.041, 0.138) *k* = 15, *s* = 6, *n* = 84175 Q(df = 14) = 20.296, *p* = .121
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 (0.075, 0.278)** *k* = 4, *s* = 4, *n* = 383 Q(df = 3) = 0.883, *p* = .830
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	*r* = .044 (-0.134, 0.222) *k* = 8, *s* = 3, *n* = 330 Q(df = 7) = 9.957, *p* = .191

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_ = .169 (0.027, 0.315)** *k* = 3, *s* = 3, *n* = 194 Q(df = 2) = 0.871, *p* = .647

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**	*r* = .039 (-0.067, 0.145) *k* = 3, *s* = 3, *n* = 351 Q(df = 2) = 0.387, *p* = .824
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* = 0
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 = 1
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 = 0

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.

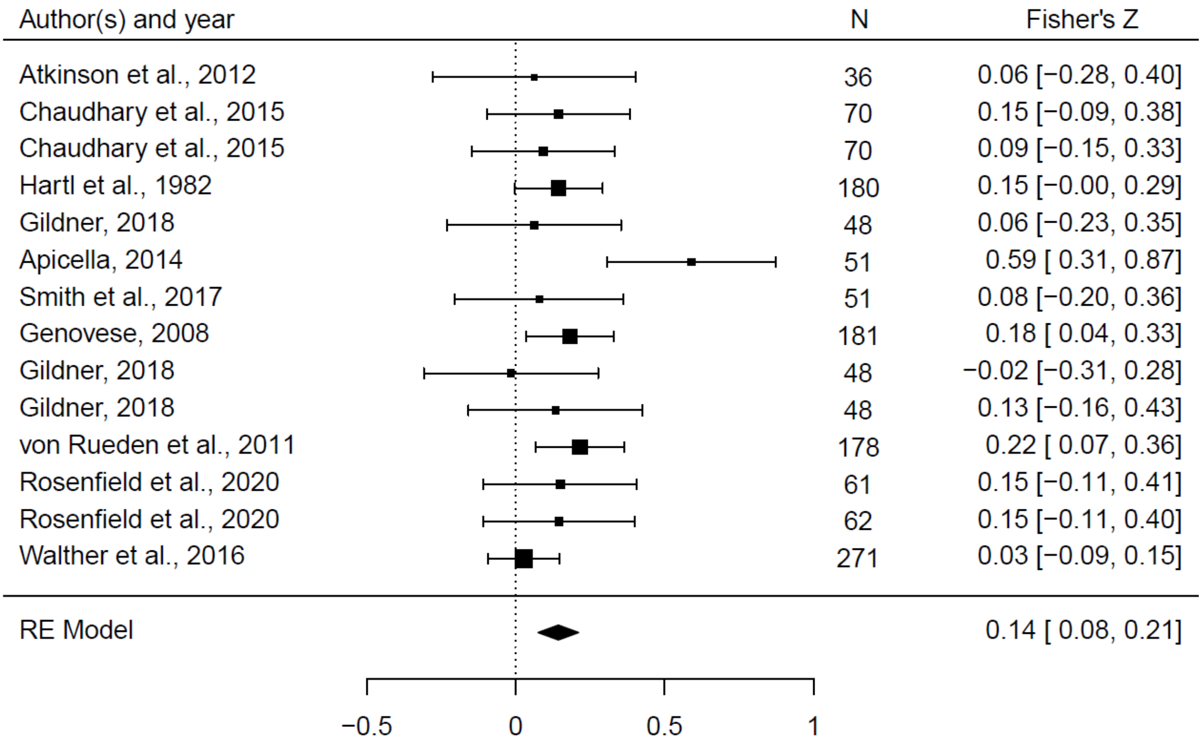

Figure 2. Forest plot of the association between body masculinity and reproductive domain. Effect sizes are shown as Z-transformed r, with 95% confidence intervals in brackets. The width of the diamond corresponds to the confidence interval for the overall effect.

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.

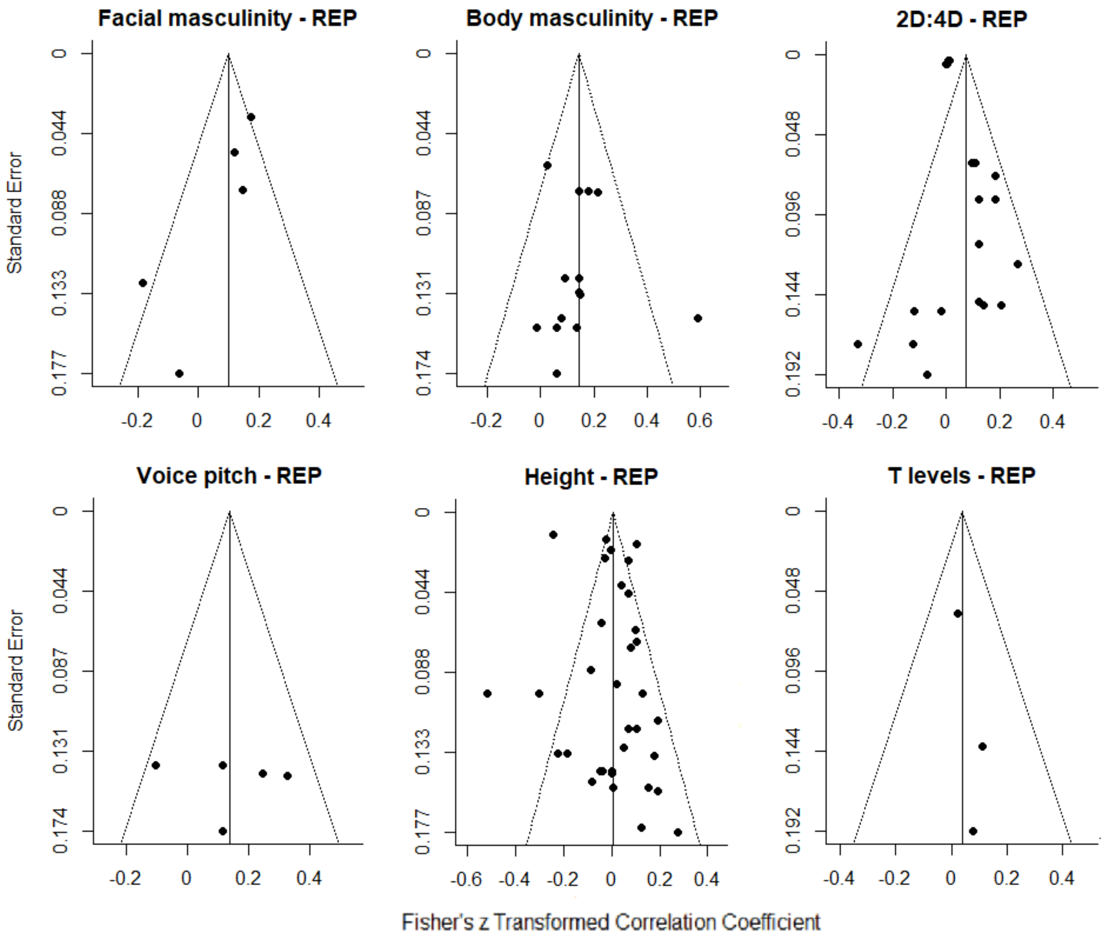

Figure 3. Funnel plots of effect sizes for reproductive measures (REP). T = testosterone levels.

Subgroup and moderator analyses. In this step of the analyses, we tested the hypothesis that masculine traits positively predict the reproductive 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 but not reproductive success was significant (r = .130, 95% CI: [0.060, 0.201]) 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 (three out of four samples from high fertility populations: r = .174, 95% CI: [0.075, 0.278]); although a considerably 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 exclusively in terms of fertility, and two of three samples were low fertility samples. 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.

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 of 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, measured primarily as a function of height, showed no effect, but we note that this measure severely lacked data from which to draw conclusions.

The effects mentioned above are potentially meaningful in an evolutionary context. As benchmarks for interpreting correlations, (148) suggest that a correlation of .10, while being a small effect that is unlikely to be meaningful in terms of single events, 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 (56), height/strength and reproductive outcomes (57, 58), and testosterone levels and mating effort (47), our analysis benefits from more comprehensive measures of masculinity, larger sample sizes, and inclusion of more unpublished effects. With the exception of (58), we observe smaller effect sizes, suggesting that previous meta-analyses overestimated the association between masculinity and fitness outcomes.

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 discrepant 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 lend 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, 149), and male intergroup aggression increases mating/reproductive success in both non-industrialised human societies and in non-human primates (150, 151). For example, in the Yanomamö Indians, killing increases men’s reproductive success (152). The relationship between formidable traits and fitness outcomes is not necessarily 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);

(126) 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). 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 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 and more data is thus needed. 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 (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. 54, for offspring survival rates) and perceived attractiveness (77, 153, but see 154), 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 is that testosterone is reactive. Testosterone decreases, for example, when men enter a relationship or get married (155, 156), when they become fathers (155, 157), or when they engage in childcare (155). 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 the partially overlapping predictions of two hypotheses explaining how and why masculine traits may have evolved in human males: *i.* that masculinity – particularly in men's faces - signals heritable immunocompetence and is thus favored by female choice in addition to being associated with greater offspring viability, and *ii.* that masculinity – with emphasis on formidable traits in the body, such as strength and muscularity – increases men's intrasexual competitiveness for mates. 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. While our aim in this analysis was not to evaluate the immunocompetence and male-male competition hypotheses against each other, our findings lend stronger support to the male-male competition hypothesis. We also note 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, and we call for greater sample diversity and more homogenous measurements in future research.

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