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Masculinity matters (but mostly if you're muscular): A meta-analysis of the relationships between sexually dimorphic traits in men and mating/reproductive success

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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, such as the immunocompetence handicap hypothesis and the male-male competition hypothesis, assume that more dimorphic (i.e. masculine) men have historically achieved greater mating success, resulting in greater reproductive success. This is either because women select more masculine men due to their greater immune function, because more masculine men expend more energy on mating effort, or because more masculine men out-compete their rivals for other routes to mating success. Thus far, however, evidence for an association between masculinity and reproductive success is unclear. We conducted the most comprehensive meta-analysis to date, on the relationship between masculinity in six domains (faces, bodies, voices, height, digit ratios, and testosterone levels) and mating/reproductive success, comprising 434 effect sizes from 91 studies (total N = 155,348). Body masculinity, i.e. muscularity and strength, predicted both mating and

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reproductive success. Voice pitch, height, digit ratios and testosterone levels all predicted mating but not reproductive outcomes. Facial masculinity did not significantly predict either. Our findings support arguments that muscularity/strength can be considered sexually selected in humans, but raise concerns over other forms of masculinity, most especially facial 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 industrialised populations.

Introduction

Sexual dimorphism refers to sex differences in morphological and behavioural traits, excluding reproductive organs (Plavcan, 2001), with particular emphasis on traits thought to have evolved through sexual selection (Crook, 1972). Humans are a sexually dimorphic species (albeit moderately so compared to our closest primate relatives: Plavcan, 2001). Sexual selection is commonly argued to have acted more strongly on male traits, as a consequence of greater variance in males' reproductive output (Hammer et al., 2008) and a male-biased operational sex ratio, i.e. a surplus of reproductively available men relative to fertile females.

Dimorphic traits that are exaggerated amongst males are typically referred to as masculinity. In humans, masculine faces are characterised by features such as a pronounced brow ridge, a longer lower face, and wide mandibles, cheekbones and chins (Swaddle & Reierson, 2002). Men are, on average, 7-8% taller than women (Gray & Wolfe, 1980) and weigh approximately 15% more (Smith & Jungers, 1997). 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, 78% more muscle mass in the upper arms, and 90% greater upper body strength (Lassek & Gaulin, 2009). Men's bodies

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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 (Hughes & Gallup, 2003; Singh, 1993). A closely related measure, also contributing to the impression of a V-shaped torso, is the waist-to-chest ratio (Tovée et al., 1999; Weeden & Sabini, 2007). Second-to-fourth finger (digit) length ratios are sexually dimorphic, with men showing a lower 2D:4D than women (Apicella et al., 2016; Manning, 2002), particularly in the right hand (Hönekopp et al., 2006). Fundamental frequency, commonly referred to as voice pitch (Atkinson et al., 2012), is produced by vibration of the vocal folds and is influenced by the vocal tract's size and shape (Evans et al., 2008). Under the influence of androgen production in puberty the vocal fold length in boys increases, thus deepening the voice (Harries et al., 1998) and resulting in an adult male voice pitch approximately six standard deviations lower than women's (Puts et al., 2014). The development of these dimorphic traits in men is influenced by prenatal and pubertal 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 (Galis et al., 2010; Richards et al., 2019), masculine traits generally develop or become exaggerated following a surge in T production at sexual maturity (Butterfield et al., 2009; Fechner, 2003; Weston et al., 2007) – 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 (Plavcan, 2001). We are often forced to test hypotheses about human evolution in modern, industrialised populations, but data from other sources are imperative. Fossil records provide clues to the evolution of skeletal dimorphism; however, fossil evidence can also potentially be misleading and is not informative in terms of soft tissue dimorphism (Plavcan, 2012). 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

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sexually selected increases mating/reproductive success in such populations, that indicates that the trait may also have increased mating/reproductive success ancestrally (Hill et al., 2016).

Two main hypotheses have been proposed to explain how and why masculine traits evolved in men. According to the immunocompetence handicap hypothesis (Folstad & Karter, 1992), male sexually dimorphic traits across species index heritable immunocompetence, i.e. good genetic quality. This hypothesis rests upon the notion that testosterone has immunosuppressive properties, increasing vulnerability to pathogens (Muehlenbein & Bribiescas, 2005). Hence, amongst humans, 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 offspring, and thereby also be able to attract a greater number of partners. This suggests that masculinity in men is intersexually selected and evolved or was maintained through female choice.

The immunocompetence hypothesis has been widely applied to facial masculinity in particular. However, this hypothesis is also increasingly criticised, with respect to inconsistent findings regarding both the putative associations between testosterone/testosterone-dependent traits and health outcomes as well as the extent to which such traits are actually attractive to women - both of which are key predictions of the hypothesis. For example, recent evidence suggests that testosterone may have a modulating rather than suppressive effect on immune functioning (Nowak et al., 2018), and facial masculinity is not consistently linked to better health (Boothroyd et al., 2013; Foo et al., 2020; Zaidi et al., 2019). Evidence is similarly mixed regarding the claim that women are attracted to masculinity in men's faces (Little, 2015; Scott et al., 2013).

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An alternative hypothesis, 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, either through direct physical contests or by deterring rivals (Hill et al., 2016; Sell et al., 2012). Greater stature and increased physical strength, especially in the upper body, is arguably advantageous in direct contests, and strength cues such as increased musculature are likely to intimidate competitors. Indeed, people treat physical strength as a proxy of fighting prowess (Sell et al., 2009) and, in assessing overall strength, favour cues found in the upper body (Durkee et al., 2018). Other traits, such as facial masculinity and voice pitch, do not directly impact fighting prowess, but may have an indirect relationship with formidability (Butovskaya et al., 2018; Haselhuhn et al., 2015; Jordan et al., 2018; Little et al., 2015; Puts & Aung, 2019; Scott et al., 2014). Furthermore, perceived dominance appears to mediate the relationship between formidability and mating success (Hill et al., 2013; Kordsmeyer et al., 2018). Thus, being formidable may increase masculine men's reproductive success by enabling them to accrue a greater number of partners through the benefits of dominance (e.g. social capital and/or resources). This proposal has garnered increasing support in recent years (Hill et al., 2016; Puts, 2016). While this hypothesis suggests that masculinity in men is intrasexually selected, this type of selection may also work in conjunction with female choice if women preferentially mate with formidable/dominant men (Kordsmeyer et al., 2018; Slatcher et al., 2011).

Reproductive success can be achieved either by producing better quality offspring and/or a greater quantity of offspring; the latter may (in men) be mediated by mating with a greater number of partners. Previous studies testing the relationships between masculine traits and fitness outcomes have produced a mixture of positive, negative and null results, highlighting the need for meta-analytic evidence. To date, however, such analyses are rare, and typically exclude many aspects of masculinity in addition to focussing exclusively on

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mating *or* reproductive outcomes. Van Dongen and Sprengers (2012) meta-analysed the relationships between men's handgrip strength (HGS) and sexual behaviour in only three industrialised populations (showing a weak, positive association [r = .24]). Across 33 non-industrial societies, von Rueden and Jaeggi (2016) 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, Norton and Rahman (2018) reported no significant association between men's height and offspring numbers across 16 studies. Lastly, a meta-analysis of 16 effects by Grebe, Sarafin, Strenth and Zilioli (2019) 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-analysed in relation to mating/reproduction.

The present article is the first to meta-analyse the relationships between five sexually dimorphic traits in humans (facial masculinity, body masculinity, 2D:4D, voice pitch, and height) and both mating and reproductive success. According to the immunocompetence handicap hypothesis, the association between masculine traits and mating/reproductive outcomes rests upon the notion that masculine traits index testosterone levels. We therefore also included testosterone levels as a predictor. We focussed on fertility outcomes (offspring numbers and age of reproductive onset) as indices of reproductive success, and mating success/mating strategies as a proxy thereof. Both the immunocompetence hypothesis and the male-male competition hypothesis predict that masculine men should enjoy greater reproductive and mating success, although the mechanism by how this is achieved differs. 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 increased

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reproductive/mating success. The immunocompetence hypothesis, on the other hand, has primarily been applied to facial masculinity.

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. Studies were also retrieved through cross-referencing, citation searches, citation alerts, and by asking researchers directly for data on social media and through personal communications. Studies submitted for analysis up to 1 September 2019 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. Outcome measures included reproductive and mating outcomes; in traditional populations without access to modern medicine and contraception, reproductive success can be measured directly. In industrialised populations, on the other hand, mating-based proxies of reproductive success must be used instead, such as number of spouses and number of sexual partners, as these should have correlated with reproductive success in men under ancestral conditions (Pérusse, 1993). Thus, the outcome measures were:

- Reproductive success, i.e. fertility: number of offspring and grand-offspring, and reproductive onset (early reproduction increases potential reproductive output in traditional populations, since that allows for a greater lifetime number of offspring; this variable was thus reverse coded).
- Mating success: global sociosexuality (Penke & Asendorpf, 2008; Simpson & Gangestad, 1991) and specific measures of mating attitudes and mating behaviours where:

    i. Mating attitudes included: preferences for short-term mating/short-term mating

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orientation, and sociosexual attitudes and desires.

ii. Mating behaviours included: number of sexual partners (NSPs; during one's lifetime or within a specified time period), number of one-night-stands/short-term relationships, number of potential conceptions (Pérusse, 1993), sociosexual orientation behaviour subscale, extra-pair copulations/partners, age at first sexual intercourse/encounter (early sexual activity is associated with increased mating success since it allows for a greater lifetime number of sexual partners; this variable was therefore reverse coded), and number of spouses.

Both published and unpublished studies were eligible, but 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 conducted or not reported, authors were asked to provide effect sizes or raw data. If data were reported in more than one study, we selected the analysis with the larger sample size or greater inclusion of appropriate control variables. 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 analysing 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; where the relevant relationships had been analysed but effect sizes were not convertible and/or not possible to obtain from the authors, the study was excluded. Where 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 made no difference to the results, so will not be discussed further). In total, 91 studies were selected, comprising 434 effect sizes from 92 samples and 155,348 unique participants. This exceeds the number of studies for each of the meta-analyses published previously (Grebe et al., 2019; Van Dongen & Sprengers, 2012; Von Rueden & Jaeggi, 2016; Xu et al., 2018). Please see SI for full details

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about the literature search, study/measure selection decisions, effect size conversions, and the study list.

Results

Statistical analyses

We used the *metafor* package (Viechtbauer, 2010) in R 3.6.2 (R core team, 2019). *metafor* transforms Pearson's *r* to Fisher's *z* for analysis; effect sizes were converted back to *r* for presentation of results. Analyses were conducted using random-effects models. Twelve main analyses were carried out assessing the relationships between each masculine trait and mating/reproductive success, respectively. For mating success, we also conducted separate subgroup analyses for mating attitudes and mating behaviours. Subgroup analyses were also conducted for low versus high fertility samples (with a cut-off of three or more children/woman on average within that population at the time of sampling). To test for the impact of study characteristics, we also performed a series of moderation analyses on factors linked to study quality (e.g. controls for age where relevant, objective vs subjective measures, repeat measurements) or generalisability (e.g. sexual orientation of participants). Full lists of moderators are given in SI; significant moderators are reported below. In all analyses, effect sizes were clustered by sample and by study. Only relationships with a minimum of three independent samples from a minimum of two separate studies were analysed. 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. Thus, for all traits, the predicted relationships with mating/reproductive success were positive. Additional details and full results, including R code, can be found in SI.

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Mating success

Main analyses. The first set of analyses tested the prediction that masculine traits and testosterone levels are associated with increased mating success. As can be seen in Tables 1 and 2, for all traits bar facial masculinity, greater masculinity/testosterone levels predicted significantly higher mating success. The strongest associations with mating outcomes 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 = .097, 95% CI: [0.070, 0.125]); 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 success, but showed significantly smaller effect sizes than body, voice or testosterone levels (height: r = .057, CI: [0.027, 0.087]; 2D:4D: r = .034, CI: [0.000, 0.069]). The relationship between facial masculinity and mating success was not significant (r = 0.080, 95% CI: [-0.003, 0.164]).

Table 1

Facial masculinity, body masculinity and 2D:4D predicting mating success: main analyses and subgroup analyses of mating success type and sample type

Mating success (MS)			
Outcome Sample	Facial masculinity	Body masculinity	2D:4D
MS (all) Full sample	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 = 22, n = 66807 Q(df = 83) = 101.994, p = .077
MS att. Full sample	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
MS beh. Full sample	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

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MS (all) 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* = 0.038 (-0.002-0.073) *k* = 82, *s* = 21, *n* = 66751 Q(df = 81) = 101.369, *p* = .063
MS (all) 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. MS att. = Mating success attitudes; MS beh. = Mating success behaviours; fert. = fertility; k = number of observations; s = number of samples; n = number of unique participants. Statistically significant associations are bolded.

Table 2

Voice pitch, height and testosterone levels predicting mating success: main analyses and subgroup analyses of mating success type and sample type

Mating success (MS)

Outcome Sample	Voice pitch	Height	T levels
MS (all) Full sample	***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* = .097 (0.070-0.125)** *k* = 62, *s* = 20, *n* = 7022 Q(df = 61) = 63.732, *p* = .381
MS att. Full sample	*s* = 0	*r* = .028 (-0.013-0.068) *k* = 9, *s* = 6, *n* = 4232 Q(df = 8) = 5.137, *p* = .743	***r* = .110 (0.032-0.188)** *k* = 19, *s* = 10, *n* = 978 Q(df = 18) = 24.197, *p* = .149
MS beh. Full sample	***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* = .085 (0.059-0.112)** *k* = 31, *s* = 16, *n* = 6704 Q(df = 30) = 27.928, *p* = .574
MS (all) 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* = .103 (0.074-0.133)** *k* = 54, *s* = 19, *n* = 6734 Q(df = 53) = 58.777, *p* = .272
MS (all) 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. MS att. = Mating success attitudes; MS beh. = Mating success behaviours; fert. = fertility; T = testosterone; k = number of observations; s = number of samples; n = number of unique participants. Statistically significant associations are bolded.

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Subgroup and moderator analyses. For all predictors, the majority of effect sizes (94 %) came from low fertility samples.

The nonsignificant relationship between facial masculinity and mating success was not moderated by measurement type. Effect sizes were larger for mating attitudes than for mating behaviours, but the difference was not statistically significant. All samples bar one were from low fertility populations.

Body masculinity predicted both mating behaviours and mating attitudes in the full sample, and moderator analysis showed no difference in the strength of these two relationships. While the positive relationship between body masculinity and mating success was significant in the 28 low fertility samples and nonsignificant in the 4 high fertility samples, moderator analysis did not show the strength of relationship to differ between these two population types. Furthermore, moderation analyses of type of body masculinity showed that muscularity and strength did not predict mating success differently, but that body shape was a significantly weaker predictor of mating success than strength (B = -0.089, p = .003). For muscularity and body shape, which can be assessed either through subjective ratings or objective measurements, effect sizes were larger for subjectively rated masculinity (B = 0.178, p = .007). For objectively measured masculinity, there was a significant effect of number of measurements, with a stronger effect for studies with three measurements compared to studies with an unspecified number of measurements (B = 0.128, p = .045). Additionally, effect sizes were larger in studies that had controlled (vs not controlled) for participant age (B = 0.096, p = .031), smaller in non-student than student populations (B = -0.118, p = .020), smaller in non-published than published results (B = -0.086, p = .029), and smaller in samples that were not exclusively heterosexual (B = -0.085, p = .035).

For 2D:4D, effect sizes did not differ between mating attitudes and mating behaviours. All samples except one were from low fertility populations. Effect sizes were larger in studies

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where 2D:4D had been measured through hand scans instead of directly from hands (B = 0.091, *p* = .032), when 2D:4D had been measured three times compared to an unspecified number of times (B = 0.102, *p* = .006), and in studies where non-normally distributed variables had been transformed to normality (B = 0.094, *p* = .010). Ethnicity was also a significant moderator, with weaker effects in samples that were not predominantly white (B = -0.080, *p* = .014). There was no difference between left and right 2D:4D.

No moderation analyses could be carried out for voice pitch due to an insufficient number of studies.

Height had a significant effect on mating behaviours but not mating attitudes, but the difference between them was not significant. The association between height and mating success was significant in low fertility samples and not in high fertility samples, but there was no significant difference between these two associations. There were no other significant moderators of relationships between height and mating success.

Testosterone levels significantly predicted mating attitudes and mating behaviours to a similar degree. Only one sample was from a high fertility population. Effect sizes were significantly weaker in non-exclusively heterosexual samples (B = -0.057, *p* = .004), and larger in studies where variables had been transformed to normality (B = 0.055, *p* = .019).

Inclusion bias/heterogeneity. Since the analysis included unpublished data, the funnel plots in this case indicate 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. There was significant heterogeneity of effect sizes for facial masculinity, body masculinity, and height.

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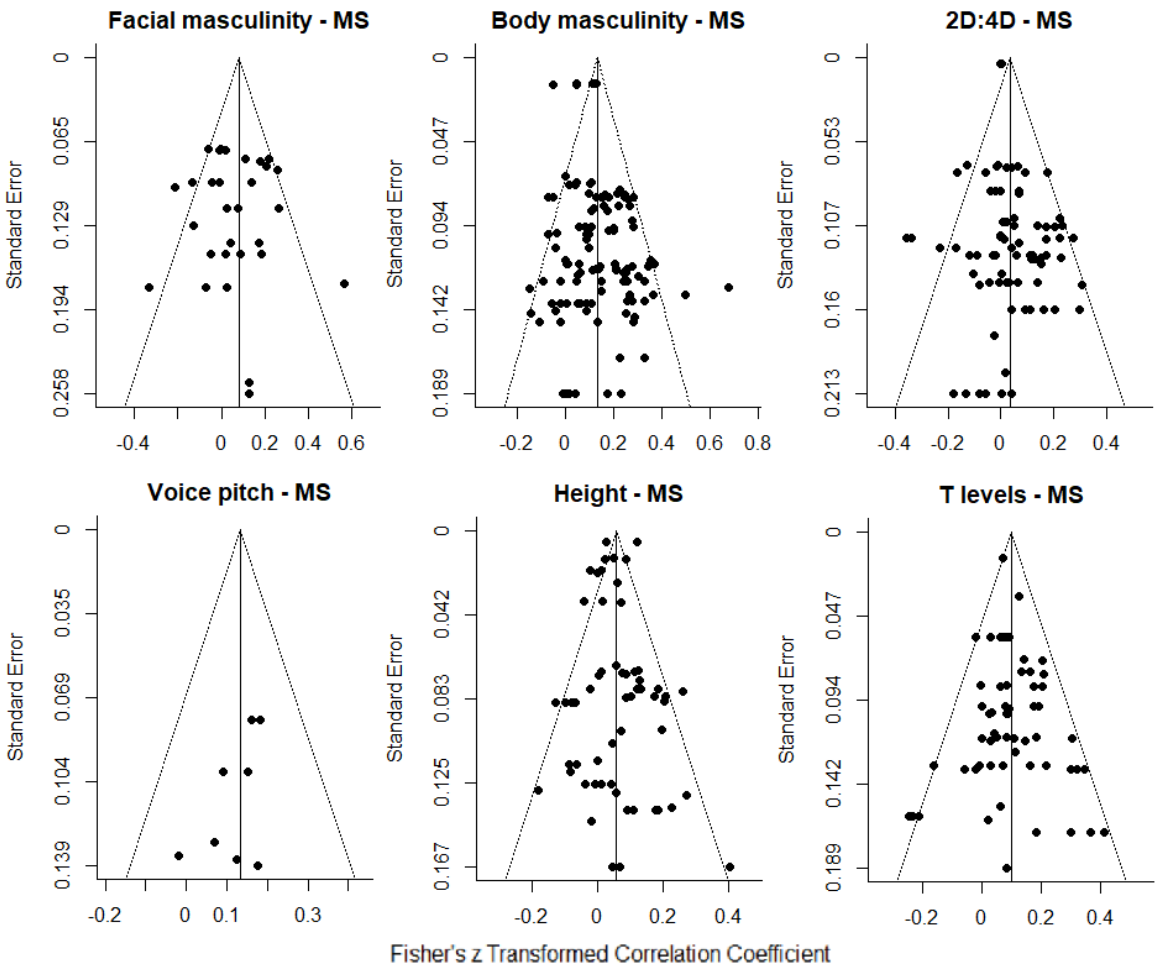

Figure 1. Funnel plots of effect sizes for mating success (MS).

Reproductive success

In the second set of analyses, we tested the hypothesis that masculine traits and testosterone levels positively predict reproductive success. As Tables 3 and 4 show, relationships were in the predicted direction, but body masculinity was the only significant predictor (r = .119, 95% CI: [0.058, 0.182]). The only trait with an effect size significantly different from body masculinity was height (B = -0.093, p = .017); the other traits did not significantly differ.

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Table 3

Facial masculinity, body masculinity and 2D:4D predicting reproductive success: main analyses and subgroup analyses of sample type

Reproductive success (RS)			
Outcome Sample	Facial masculinity	Body masculinity	2D:4D
RS Full sample	*r* = .072 (-0.097-0.242) *k* = 4, *s* = 4, *n* = 1232 **Q(df = 3) = 8.776,** ***p* = .032**	***r* = .119 (0.058-0.182)** *k* = 12, *s* = 8, *n* = 897 Q(df = 11) = 6.036, *p* = .871	*r* = .053 (-0.029-0.136) *k* = 16, *s* = 7, *n* = 84223 Q(df = 15) = 20.889, *p* = .140
RS Low fert. samples	*s* = 1	*s* = 1	*r* = .052 (-0.065-0.169) *k* = 7, *s* = 3, *n* = 83845 Q(df = 6) = 8.335, *p* = .215
RS High fert. samples	*r* = .030 (-0.278-0.338) *k* = 3, *s* = 3, *n* = 895 **Q(df = 2) = 8.692,** ***p* = .013**	***r* = .146 (0.083-0.212)** *k* = 11, *s* = 7, *n* = 626 Q(df = 10) = 3.026, *p* = .981	*r* = .056 (-0.088-0.199) *k* = 9, *s* = 4, *n* = 378 Q(df = 8) = 10.118, *p* = .257

Note. Fert. = fertility; k = number of observations; s = number of samples; n = number of unique participants. Statistically significant associations are bolded.

Table 4

Voice pitch, height and testosterone levels predicting reproductive success: main analyses and subgroup analyses of sample type

Reproductive success (RS)			
Outcome Sample	Voice pitch	Height	T levels
RS Full sample	*r* = .093 (-0.064-0.251) *k* = 4, *s* = 3, *n* = 143 Q(df = 3) = 3.190, *p* = .363	*r* = .011 (-0.038-0.060) *k* = 28, *s* = 25, *n* = 22326 **Q(df = 27) = 401.101,** ***p* < .001**	*r* = .039 (-0.067-0.145) *k* = 3, *s* = 3, *n* = 351 Q(df = 2) = 0.387, *p* = .824
RS Low fert. samples	*s* = 0	*r* = -.028 (-0.097-0.041) *k* = 9, *s* = 9, *n* = 17741 **Q(df = 8) = 256.064,** ***p* < .001**	*s* = 2
RS High fert. samples	*r* = .093 (-0.064-0.251) *k* = 4, *s* = 3, *n* = 143 Q(df = 3) = 3.190, *p* = .363	*r* = .055 (-0.005-0.115) *k* = 19, *s* = 16, *n* = 4585 Q(df = 18) = 26.606, *p* = .087	*s* = 1

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Note. Fert. = fertility; T = testosterone, k = number of observations; s = number of samples; n = number of unique participants. Statistically significant associations are bolded.

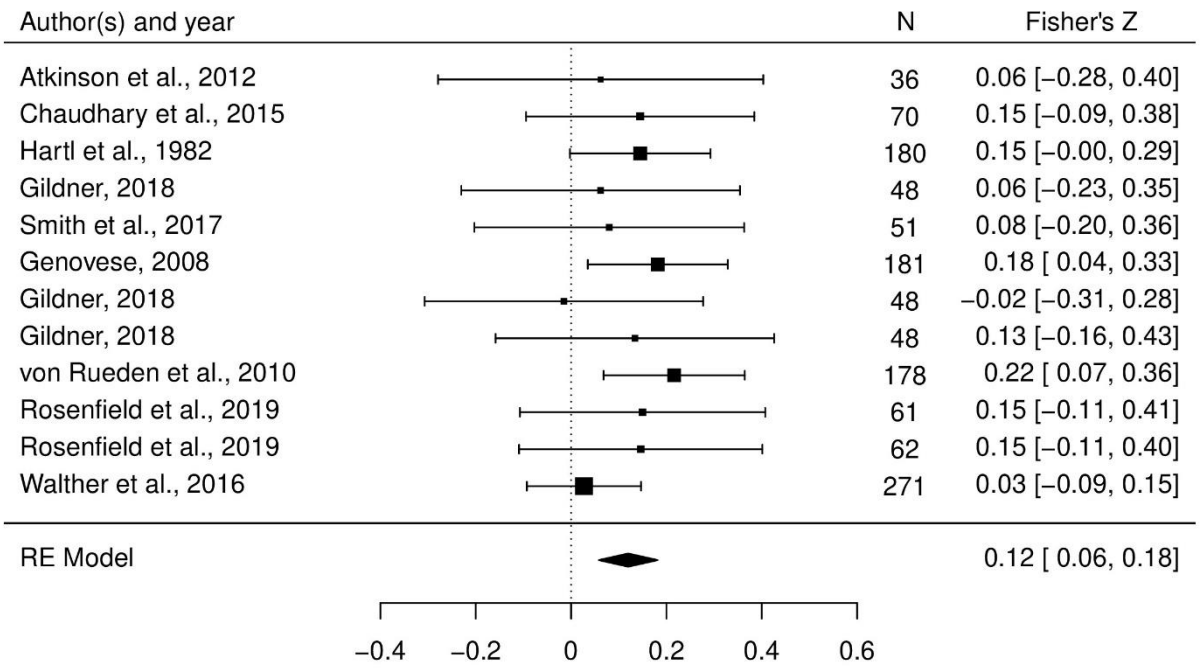

Figure 2. Forest plot of the association between body masculinity and reproductive success. Effect sizes are shown as *Z*-transformed *r*, with 95% confidence intervals in brackets. The width of the diamond corresponds to the confidence interval for the overall effect.

Subgroup and moderator analyses. The majority (70 %) of observations were from high fertility samples (see Tables 3 and 4). Subgroup analyses/moderation analyses of low versus high fertility samples could only be conducted for 2D:4D and height; effect sizes did not differ significantly between high and low fertility samples. Due to too few observations, no moderation analyses could be performed for facial masculinity, voice pitch, or testosterone levels. There were no significant moderators of the relationship between body masculinity and reproductive success. Effect sizes were significantly smaller for 2D:4D studies that had not controlled for finger injuries (B = -0.128, p = .003) than ones that had. For height, the relationship with RS was significantly stronger in non-exclusively heterosexual samples (B = 0.115, p = .019).

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

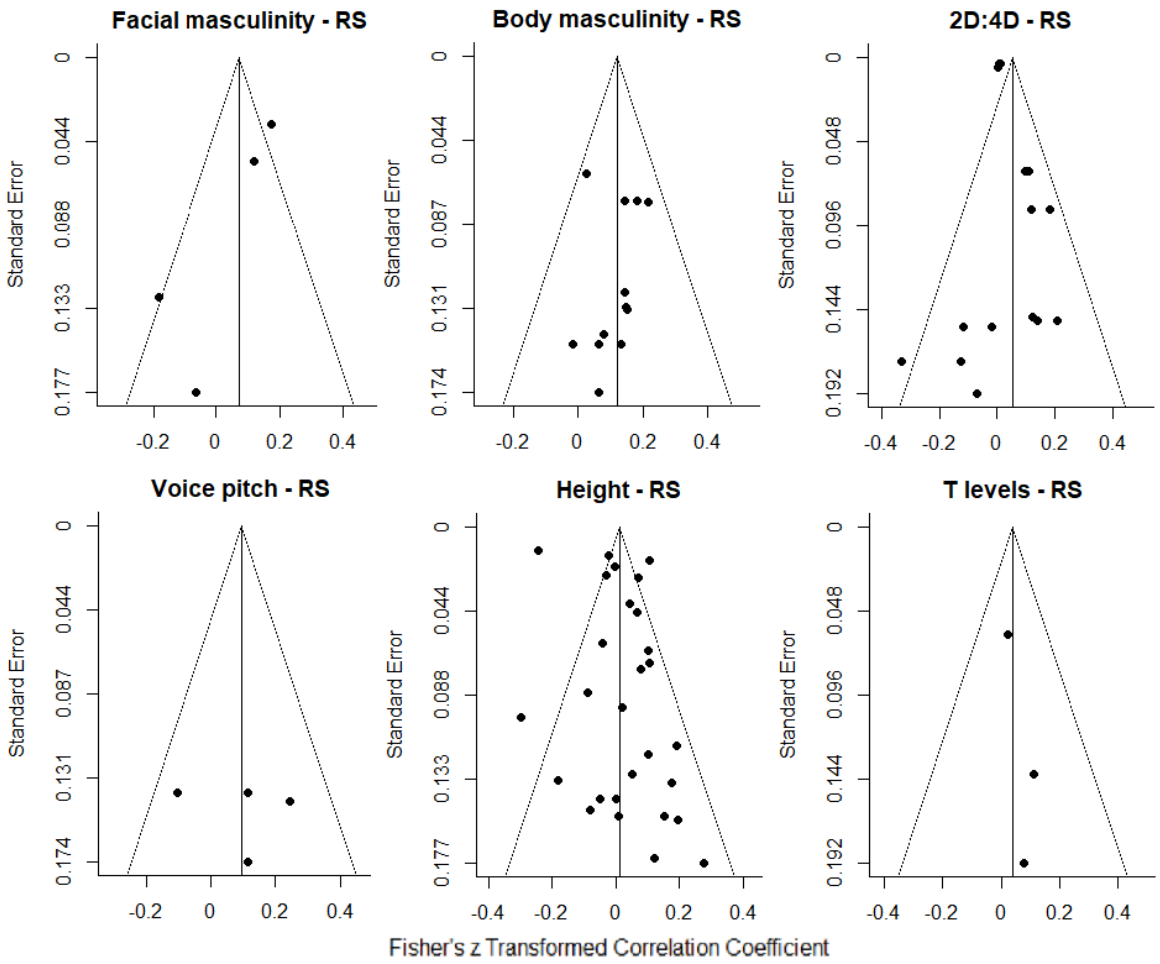

Figure 3. Funnel plots of effect sizes for reproductive success (RS).

Overall findings

Combining all types of masculinity, the overall association with mating success was r = .092 (95% CI: [0.072, 0.112]) and with reproductive success r = .037 (95% CI: [-0.003, 0.076]); the difference between these two effects was not significant. Moderation analyses of outcome type (mating versus reproductive success) for each trait showed that facial masculinity, voice

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pitch, height, and testosterone levels had weaker associations with reproductive than mating success, but the differences were not significant. However, we had far fewer observations for reproductive success, so this might reflect lack of power. For body masculinity and 2D:4D, there was no difference between outcome types.

Discussion

In this first comprehensive meta-analysis of the relationships between masculine traits/testosterone levels and mating/reproductive success in men, mating success – which was predominantly measured in low fertility samples – was positively associated with all of the masculine traits we assessed, apart from facial masculinity. In contrast, reproductive success was measured mainly in high fertility samples and was correlated only with body masculinity. The strongest correlations with mating success were r = .13 (for both body masculinity and voice pitch), and body masculinity predicted reproductive success with r = .12. These three effects are potentially meaningful in an evolutionary context. As benchmarks for interpreting correlations, Funder and Ozer (2019) 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 the long run and in large populations.

Compared to previous meta-analyses, assessing associations between handgrip strength and mating outcomes (Van Dongen & Sprengers, 2012), height/strength and reproductive outcomes (von Rueden & Jaeggi, 2016; Xu et al., 2018), and testosterone levels and mating effort (Grebe et al., 2019), our analysis benefits from more comprehensive measures of dimorphism, larger sample sizes, and inclusion of more unpublished effects. With the

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exception of Xu et al. (2018), we observe smaller effect sizes, suggesting that other meta-analyses overestimated the association between masculinity and fitness outcomes.

As the only trait in our analysis that is consistently (and most strongly) correlated with fitness outcomes across populations, body masculinity is the only trait we can conclude appears to be under present selection in naturally fertile populations. Regardless of how other traits may influence or be linked to men's mating strategies in low fertility populations, these strategies show no evidence of translating into higher fertility, either because these traits operate differently in high fertility populations, or because these mating strategies are insufficient to achieve higher reproductive success without body masculinity. Since traits such as strength and muscularity are associated with formidability, this finding lends support to the male-male competition hypothesis. In species with male-male competition, males tend to evolve to become larger, stronger and more formidable than females, as they are in humans. There is reason to suspect that male-male violence has influenced human evolution (Gat, 2015; Hill et al., 2016): male intergroup aggression increases mating/reproductive success in both non-industrialised human societies and non-human primates (Glowacki & Wrangham, 2015; Manson et al., 1991). The relationship between formidable traits and fitness outcomes might, however, be mediated by other factors that are important in mate choice. For example, features that are advantageous in intraspecies conflicts may also be advantageous when hunting game (Sell et al., 2012); Smith et al. (2017) 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 sexually dimorphic traits. Male-male competition for resources and mates, female choice, and intergroup violence are all plausible, non-mutually exclusive explanations (Plavcan, 2012). Traditionally in human sexual selection research, however, the

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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 focussed particularly on masculinity in men's facial structure as an indicator of heritable immunocompetence (i.e. good genes), which should then be associated with heritable mating/reproductive success. While we find that the effect of facial dimorphism on mating success is similar in strength to that of other traits (r = .08), this association is not significant. Furthermore, the effect of facial masculinity on global mating success is largely driven by mating attitudes and is close to zero for mating behaviours, suggesting that men's facial masculinity exerts virtually no influence on female choice. Additionally, the influence of facial masculinity on reproductive success in high fertility samples is extremely weak (r = .03). 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 industrialised populations, as suggested by Scott et al. (2014).

While 2D:4D, voice pitch, height, and testosterone levels significantly predict mating success in our analysis, none of these traits are significantly associated with reproductive outcomes. The latter was primarily measured in high fertility populations, where offspring numbers are not constrained by widespread use of contraception. It is thus mainly in these naturally fertile contexts present selection may take place. Our findings mean that for none of these traits do we have evidence suggesting that greater mating success translates into greater reproductive success; we therefore have no evidence that these traits are currently under selection, but we also note that we are constrained by a lack of data from these populations.

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. Boothroyd et

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al., 2017 for offspring survival rates) and perceived attractiveness (Frederick & Haselton, 2007; Johnston et al., 2001; Sell et al., 2017), with a decrease for very high levels of masculinity. However, given that such results typically 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 and decreases for example when men enter a relationship or get married (Archer, 2006; Holmboe et al., 2017), when they become fathers (Archer, 2006; Lee et al., 2011) or engage in childcare (Archer, 2006); thus, men whose circulating testosterone was previously high may show declining testosterone levels because their fatherhood status has changed, meaning we cannot determine with certainty whether there really is no relationship between testosterone levels and reproductive outcomes. In our analysis, men with high testosterone levels also have higher mating success, but since T also motivates sexual behaviour (Roney & Gettler, 2015), this raises the possibility that high T men pursue more mating opportunities which increases their mating success, or conversely that high T results from many mating encounters.

Our findings raise important concerns for the human sexual selection field, particularly with respect to whether mating success 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 industrialised populations using mating measures such as number of sex partners and one-night-stands, under the assumption that such measures index mating strategies that ancestrally would have increased men's reproductive success. However, if mating outcomes measured in low fertility populations truly indexed reproductive success in naturally fertile contexts, we would expect traits that predict mating success to also predict reproductive success across samples; we do not have evidence that this is the case. Our findings therefore

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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 resist the temptation of applying our findings universally.

In summary, we used a large-scale meta-analysis of several masculine traits and both mating and reproductive outcomes to test partially overlapping predictions of two hypotheses explaining how and why such traits may have evolved in human males: *i.* that masculinity – particularly in men's faces - signals heritable immunocompetence and is thus favoured by female choice, and *ii*. that masculinity – with emphasis on formidable traits in the body, such as strength and muscle mass – increases men's intrasexual competitiveness for mates. We found that masculinity in all traits except facial morphology is associated with significantly greater mating success. However, this increased mating success does not appear to translate into greater reproductive success for any other trait than masculinity in men's bodies. While our aim in this analysis was not to evaluate the two hypotheses against each other, our findings thus contradict the immunocompetence hypothesis and 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 industrialised 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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