

Review

Does Human Ejaculate Quality Relate to Phenotypic Traits?

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ABSTRACT: A given man's phenotype embodies cues of his ancestral ability to effectively defend himself and his kin from harm, to survive adverse conditions, and to acquire status and mating opportunities. In this review, we explore the hypothesis that a man's phenotype also embodies cues to fertility or the probability that an ejaculate will fertilize ova. Female mate choice depends on the ability to discern the quality of a male reproductive partner through his phenotype, and male fertility may be among the traits that females have evolved to detect. A female who selects as mates males that deliver higher quality ejaculates will, on average, be more fecund than her competitors. Data on several non-human species demonstrate correlations between ejaculate quality and secondary sexual characteristics that inform female mate choice, suggesting that females may select mates in part on the basis of fertility. While the non-human literature on this topic has advanced, the human literature remains limited in scope and there is no clear consensus on appropriate methodologies or theoretical positions. We provide a comprehensive review and meta-analysis of this literature, and conclude by proposing solutions to the many issues that impede progress in the field. In the process, we hope to encourage interest and insight from investigators in other areas of human mating and reproductive biology. *Am. J. Hum. Biol.* 28:318–329, 2016. © 2015 Wiley Periodicals, Inc.

INTRODUCTION

Sexual selection produces adaptations in males that function to increase the likelihood of securing copulations (pre-copulatory selection) and to increase the likelihood that those copulations result in fertilizations (post-copulatory selection; Andersson and Simmons, 2006). In pre-copulatory selection, males (typically) compete against other males (intrasexual competition) to secure copulations from choosy females (intersexual competition; Parker et al., 2013). Females favor mating with high-quality males and make these discriminations by attending to variations in male morphology and behavior (for reviews, see Mays and Hill, 2004; Price et al., 1993).

A growing literature highlights the significance of post-copulatory sexual selection in human evolution (Baker and Bellis, 1995; reviewed in Pham and Shackelford, 2014). Women's reproductive tracts are generally inhospitable for parasites and pathogens (e.g., low pH, heightened immune responses; Ravel et al., 2011), but also for sperm (Birkhead et al., 1993; Moyer et al., 1970; Suarez and Pacey, 2006). Thus, this environment selects for higher quality sperm that are better able to fertilize ova by virtue of abundance, durability, motility, etc. (for a review, see Wira et al., 2010). Additionally, sperm competition may influence ejaculate quality by generating selection pressures to outcompete rival ejaculates in the female reproductive tract (Baker and Bellis, 1989, 1993a, b, 1995; Shackelford and Pound, 2006; Shackelford et al., 2005). However, the competitiveness of an ejaculate is not identical to its fertility. A competitive ejaculate may be competitive not because it can fertilize ova, but because it reduces the probability that rival sperm fertilize ova (e.g., toxins in semen that harm a female, but dissuade her from mating with other males; Johnstone and Keller, 2000). That said, recurrent ancestral exposure to sperm competition is expected to promote fertility in male lineages.

Studies have documented relationships between men's ejaculate quality and phenotypic traits that women find attractive, including facial attractiveness, body symmetry,

and intelligence (see Table 1). One explanation for such relationships is a *general fitness factor*, which predicts positive correlations among traits that contribute to survival and reproduction—including ejaculate quality (Houle, 2000). In this view, correlations between ejaculate quality and the phenotypic traits that women find attractive are byproducts of their shared correlation with a third, underlying variable (e.g., developmental stability, parasite load, mutation load; see Pierce et al., 2009). Another explanation is that a preexisting correlation between phenotypic traits and ejaculate quality may have selected for adaptations in human female mating psychology to detect and capitalize on the reproductive benefits afforded by a high-quality ejaculate. Thus, a correlation with ejaculate quality may represent one of many reasons that particular phenotypic traits are found attractive. A woman seeking reproductive opportunities could benefit from attending to any phenotypic traits that reliably cue a man's ejaculate quality. Ancestral women who found more fertile men more sexually attractive would have out-reproduced women with different preferences. It could also benefit men who are capable of producing high-quality ejaculates to signal this ejaculate quality to women. Such a signal would facilitate matings with women who discriminate for effective ejaculates, allowing the couple to produce sons with competitive sperm and daughters who discriminate on the basis of fertility. However, because there is no evidence of adaptations in men designed to advertise ejaculate quality, we use the (passive) term “cue” rather than the (active) term “signal” with reference to humans.

Ten percent of sexually active heterosexual couples are infertile (Mosher, 1985) in both developed and developing

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countries (Boivin et al., 2007). Low-quality ejaculate is independently responsible for about 20% of these cases, and contributes to another 27% of cases in which male and female factors interact (World Health Organization, 1987). Modern factors contribute to reduced male fertility (e.g., exposure to chemicals and modern dietary habits; Mendiola et al., 2009; Povey et al., 2012; Tielemans et al., 1999) and it will remain unknown what percentage of men across our ancestral history experienced difficulty fertilizing ova. However, research demonstrates that male infertility is largely attributable to genetic differences (Ferlin et al., 2007; O'Flynn O'Brien et al., 2010), suggesting that there have long existed polymorphisms vulnerable to disruptions in spermatogenesis. To be clear, we will review evidence for and against the hypothesis that phenotypic traits provide information about ejaculate quality in fertile men and not that phenotypic traits distinguish fertile men from infertile men.

Ejaculate quality is not detectable directly (without a microscope), but may be assessed indirectly from other observable traits. The phenotype-linked fertility hypothesis (PLFH) proposes that females assess male fertility through secondary sexual characteristics (SSCs) that provide honest cues of a male's probability of fertilizing ova (Sheldon, 1994). The PLFH thus links pre-copulatory selection with post-copulatory selection, with females making pre-copulatory mate choices based on phenotypic markers of post-copulatory fitness (see Mautz et al., 2013, for review). When the PLFH was originally advanced, Sheldon (1994) suggested that females acquire extra-pair partners who display cues of fertility as insurance against the infertility of their regular partner. In humans, women typically seek extra-pair copulations with men who display more desirable traits (e.g., health, attractiveness, dominance) than their regular partner (Pillsworth and Haselton, 2006). Although the PLFH aligns with the "good genes" hypothesis of female infidelity (i.e., seeking a mate that will produce reproductively successful offspring), it does not exclude the possibility that women also select extra-pair partners who (incidentally) produce higher quality ejaculates. A broad interpretation of the PLFH predicts that females conduct a phenotypic estimation of ejaculate quality in all or some mate choice calculations, rather than strictly securing insurance against regular partner infertility by pursuing extra-pair copulations.

The literature exploring the relationship between male phenotype and fertility provides mixed results depending on the species and methodology (see section on non-human studies; Mautz et al., 2013), and only a small collection of disparate studies has investigated this relationship in humans. To render this human literature easier to navigate and understand, we review every study that addresses correlations between men's phenotypic traits and ejaculate quality, interpret these findings in the context of female mate choice, and conduct and present the results of a series of meta-analyses. Our review includes studies linking ontogenetically stable phenotypic traits to ejaculate quality and excludes studies linking evolutionarily novel or ontogenetically unstable traits (smoking, diet, exercise, weight, etc.) to ejaculate quality. All studies on this topic have investigated adults in modern industrialized societies, many of whom are affiliated with universities in East Asia, Western Europe, the United States, and Australia. Table 1 details the studies found in prepa-

ration of this review. Throughout, we explore the possibility that human female mating psychology is attentive to cues of ejaculate quality displayed in men's observable traits. These studies test the hypothesis that trait attractiveness *positively* correlates with ejaculate quality. As we will argue, there are theoretical and empirical reasons to doubt positive relationships between human ejaculate quality and many traits. The direction of the relationship between phenotype and ejaculate quality is irrelevant to the hypothesis that women use phenotype to infer ejaculate quality, as long as there is some consistent relationship with ejaculate quality for any given phenotypic trait. After addressing the state of the human literature and reporting the results of the meta-analyses, we turn briefly to the non-human literature, and close with a discussion of how to improve future research in this area. The body of this review underlines problems that exist in the literature, leaving it until the conclusion to propose solutions to those problems.

HUMAN STUDIES

Facial attractiveness

Facial attractiveness may honestly advertise good health and, thus, mate value (for a review, see Thornhill and Gangestad, 1999). Women's attraction to particular male facial traits may motivate them to mate with males that produce high-quality ejaculates. In a Spanish sample, men's facial attractiveness—as rated by women—correlated positively with sperm motility, sperm morphology, and sperm concentration (Soler et al., 2003). These findings were replicated in research that secured Spanish and Colombian women's assessments of Spanish men's facial attractiveness (Soler et al., 2014). Soler et al. (2014) also found that measurements of men's cheekbone width—a trait linked with testosterone, aggressiveness, dominance, and status (Lefevre et al., 2013)—correlated negatively with ejaculate quality. In an Australian sample, the same three semen parameters were not correlated with women's ratings of men's facial and body attractiveness, or with women's ratings of facial and body masculinity, averageness, or symmetry (Peters et al., 2008). However, whereas women's ratings of traits such as symmetry and masculinity can be compared to objective measurements, facial attractiveness is a subjective trait in these studies and is not objectively verifiable. One result of this is that a woman can be inaccurate in her report of facial symmetry, but still rate more symmetrical men to be more attractive. This kind of report bias may explain why the objective measure of facial masculinity (e.g., cheekbone width), but not the subjective reports of facial masculinity, correlated with ejaculate quality (Peters et al., 2007; Soler et al., 2014).

The different results among these studies may be attributable to methodological differences. Soler et al. (2003, 2014) asked women to report their interest in a *long-term* relationship with the photographed male, whereas Peters et al. (2007) asked women to report their *short-term* sexual interest in the photographed male. These different contexts influence the traits that women find attractive, with a priority on masculinity in short-term contexts but not in long-term contexts (Li and Kenrick, 2006; Little et al., 2002; Soler et al., 2012). No a priori hypotheses provide a clear prediction for the mating context in which a woman's sensitivity to fertility should

TABLE 1. Published research on the relationship between human male phenotypic traits and ejaculate quality

Author(s)	Participants and Equipment	Phenotype	Semen Parameter(s)	Results	Notes
Arden, Gottfredson, Miller, and Pierce (2009)	425 US veterans aged 37.6 (2.6) years	Intelligence: Composite score derived from 5 different spatial, quantitative, and verbal scores	Sperm concentration	$r = 0.15^{**}$	
Auger and Eustache (2010)	Cellsoft CASA 193 French men, 122 with pregnant partners, 71 infertile testicular cancer patients, aged 32.8 (4.6) and 30.4 (5.1) years, respectively	2D:4D ratio: Right hand, fingers measured with caliper while bent over the edge of a table	Sperm count Percentage of motile sperm Sperm concentration Sperm count	$r = 0.19^{**}$ $r = 0.14^{**}$ $r = -0.15$ $r = -0.18^*$	Data from men with pregnant partners shown
Baker (1997)	Unspecified analysis equipment 34 British students aged 19–22 years Neubauer haemocytometer	FA: Composite score derived from bilateral caliper measurements of index fingers, ears, wrists, and ankles 2D:4D ratio: Right hand traced on paper and measured	Percentage of living sperm Percentage of motile sperm Percentage of morphologically normal sperm Sperm count	$r = -0.02$ $r = 0.03$ $r = -0.09$ $F = 5.599^*$	Among cancer patients, no relationships between 2D:4D and semen parameters approached significance Bilateral symmetry was strongly correlated with rated attractiveness
Bang, Charlsen, Holm, Petersen, Skakkebaek, and Jorgensen (2005)	360 Danish men aged 19.5 (1.1) years	2D:4D ratio: Right hand traced on paper and measured	Sperm concentration	$r = -0.004$	For men with 2D:4D ≤ 1 , positive correlation between 2D:4D and sperm count, $B = 8.1^*$
Firman, Simmons, Cummins, and Matson (2003)	Bürker-Türk haemocytometer 50 Australian students, 18–35 years	FA: Composite score derived from bilateral caliper measurements of ears, wrists, elbows, ankles, feet, and digits	Sperm count Percentage of motile sperm Ejaculate volume	$r = -0.004$ $r = -0.007$ $r = 0.053$	Univariate tests shown
Leivers, Rhodes, and Simmons (2014)	Neubauer haemocytometer 81 Australian students, 22.2 (4.5) years	Mate value: Composite score derived from men's self-rated mate value and women's ratings of those men's attractiveness and dominance	Sperm count Percentage of motile sperm Sperm head length	$t = 2.28^*$ $t = 2.03^*$ $t = 2.18^*$	Only body FA was positively associated with semen parameters
Lu, Huo, Liu, Shi, and Zhao (2012)	Hamilton-Thorne CASA 268 Chinese men, 72 controls aged 29.8 (5.6) years and 196 diagnosed infertile aged 31.5 (6.7) years	2D:4D ratio: Left hand photocopied and images measured	Sperm tail length Semen quality: Composite score derived from sperm concentration, motile sperm percentage, and several measures of sperm velocity Percentage of motile sperm	$t = 0.71$ Attractive stimuli: $\beta = 0.377^*$ Unattractive stimuli: $\beta = -0.127$ Among controls: $r = 0.051$ Among infertile: $r = .341^{**}$	Men masturbated to stimuli rated for high or low attractiveness Women rated short-term sexual attractiveness Infertile men had significantly larger 2D:4D than controls, $t = 3.43^{**}$
Manning, Scutt, and Lewis-Jones (1998a)	WLJY-9000 CASA 61 British men attending a fertility clinic aged 33.5 (6.2) years	FA: Composite score derived from differences between caliper measurements of digit lengths on right and left hands, measured from crease to tip of finger	Sperm count Sperm speed Sperm migration test	$B = -17.04^*$ $B = -17.95^*$ $B = -10.05^*$	2D:4D on the left hand showed the strongest effect of all finger pairs Relationships nonsignificant when azoospermic men removed
Manning, Scutt, and Lewis-Jones (1998b)	Makler haemocytometer 58 British men attending a fertility clinic aged 34.1 (6.1) years	2D:4D ratio: Right hand, calipers measure from crease to tip of finger	Sperm count	$B = -44.97^{**}$	2D:4D on left hand showed no significant association with any semen parameter

TABLE 1. Continued

Author(s)	Participants and Equipment	Phenotype	Semen Parameter(s)	Results	Notes
Peters, Rhodes, and Simmons (2007)	Makler haemocytometer 118 Australian students aged 22.5 (4.9) years	Attractiveness: Composite score derived from women's ratings of photographs of face and body attractiveness, masculinity, symmetry, and averageness	Percentage of motile sperm Sperm speed Percentage of progressive sperm	$B = -8.57$ $B = -19.64$ $B = -24.12$	Raters at low risk of conception produce first r , raters at high risk produce second r
	Neubauer haemocytometer		Sperm migration test Sperm concentration	$B = -20.27$ $r = -0.052$	Women rated short-term sexual attractiveness
			Percentage of motile sperm	$r = -0.020$	
			Percentage of morphologically normal sperm	$r = -0.091$	
			Composite index of semen quality	$r = -0.058$ $r = -0.054$ $r = -0.075$ $r = -0.029$ $r = -0.026$	
Seo, Kim, and Rho (2010)	26 Korean students with 2D:4D ≥ 1 and 33 students with 2D:4D < 1 , aged 23.9 years	2D:4D ratio: Right hand traced on paper and measured	Sperm count	$r = 0.042$	
	Unspecified semen analysis equipment		Percentage of motile sperm	$r = 0.129$	
			Ejaculate volume	$r = -0.051$	
Simmons, Peters, and Rhodes (2011)	54 Australian students aged 22.0 (3.67) years	Attractiveness: Women gave attractiveness ratings of vocal recordings of English vowels	Sperm concentration	$r = -0.370^{**}$	No prompting for short- or long-term attractiveness
			Composite score derived from 7 sperm motility parameters	$r = -0.088$	
Soler et al. (2014)	Hamilton-Thorne CASA 50 Spanish students aged 22.7 (3.0) years	Attractiveness: Women gave attractiveness ratings of frontal and lateral facial photographs	Composite sperm index derived from sperm concentration, percentage of motile sperm, and percentage of normal morphology	$F = 30.7^{**}$	No association between voice pitch and sperm motility parameters Women rated long-term sexual attraction
	Neubauer haemocytometer		Sperm concentration	$r = 0.026$	Facial width, a measure of facial masculinity, negatively correlated with the sperm quality index
Soler et al. (2003)	66 Spanish students aged 23.4 (2.7) years	Attractiveness: Women gave attractiveness ratings of frontal and lateral facial photographs	Percentage of motile sperm	$r = 0.275^*$	Women rated men's attractiveness as a permanent partner
	Neubauer haemocytometer		Percentage of morphologically normal sperm	$r = 0.325^{**}$	
			Composite index of semen quality	$r = 0.298^*$	

Sample age is shown as mean age (standard deviation) where available. Results column shows relationship between noted semen parameters and the phenotypic trait in bold. Equipment noted was used to assess sperm count and concentration. Where CASA was not used, sperm smears and sperm in culture medium were viewed under magnification to assess morphology and motility, respectively. Baker (1997) assessed copulatory samples. All other studies assessed masturbatory samples. CASA, Computer-assisted semen analysis; FA, Fluctuating asymmetry; 2D:4D, Ratio acquired after dividing the length of the second digit from the length of the fourth.

* $P < 0.05$, ** $P < 0.01$.

be more acute. In short-term sexual relationships, there may be greater pressure to achieve fertilization from fewer copulations (e.g., during a one-night stand). Because the woman might only gain indirect benefits from short-term relationships (e.g., high-quality genes), she may seek short-term partners who produce higher quality ejaculates (for lack of direct benefits like resources and protection that are more often acquired in long-term relationships; Gangestad and Simpson, 2000). The opposite hypothesis is also defensible, because a woman in a *long-term* relationship with a man who produces lower quality ejaculates will incur reproductive costs, particularly if the man effectively guards against her infidelity. If women prefer fertility-linked traits in long-term contexts more than in short-term contexts, then the risk of low-fertility long-term partners may have had greater relevance in human evolutionary history. That is, women may incur more costs when mating with a man who produces lower quality ejaculates in long-term contexts than in short-term contexts and, therefore, women find facial traits that are positive correlates of ejaculate quality more attractive in long-term than in short-term partners. In these scenarios, a *negative* correlation between phenotype and fertility (i.e., more attractive men produce lower-quality ejaculates) would generate the same competing considerations in female mate choice, because it is only the relative difference in men's fertility, as signaled by their phenotype that is relevant.

Leivers et al. (2014) found that an aggregate of men's attractiveness, dominance (both rated by women), and self-perceived mate value correlated positively with their masturbatory ejaculate quality, but only when they produced the ejaculate while viewing images of highly attractive women. There was no correlation between men's mate value and their ejaculate quality when the ejaculate was produced while viewing low attractiveness women. Thus, men with attractive phenotypic traits may produce higher quality ejaculates when copulating with an attractive woman and, potentially, when at greater sperm competition risk (Goetz et al., 2005; Pham and Shackelford, 2013; Pham et al., 2014; Shackelford et al., 2002, 2007). Leivers et al. (2014) argue that future studies in this area must account for the context in which men ejaculate because the perceived mate value of both men and women influences the quality of the ejaculate. The researchers also noted that if they ignored female attractiveness in their study, then they would have produced inconsistent results depending on the use of masturbatory stimulus.

Fluctuating asymmetry

Developmental perturbations in utero and in early life can produce fluctuating asymmetries (FA) in bilateral traits and indicate poor developmental conditions, poor health, and perhaps poor heritable immunocompetence (Van Dongen and Gangestad, 2011). Thus, FA may provide information about male genetic quality (Gangestad et al., 1994). For example, women are more attracted to men with more symmetrical faces (Grammer and Thornhill, 1994; Scheib et al., 1999), and women rate men with lower body FA as having more attractive faces (Gangestad et al., 1994). Sperm motility, morphology, and concentration are not correlated with subjective measures of men's facial symmetry (Peters et al., 2007), but are correlated with objective measures of symmetry. Manning et al.

(1998a) found that FA across the second, third, fourth, and fifth fingers correlates negatively with sperm number, average sperm speed, and sperm speed migration performance (i.e., more symmetrical hands are associated with higher-quality ejaculates). Firman et al. (2003) constructed a composite measure of body FA from measurements of ear length, wrist diameter, elbow diameter, ankle diameter, foot length, foot width, and the lengths of the second and fourth fingers, and found that body FA correlates negatively with sperm number, sperm motility, and sperm head length. Finally, Baker (1997) found that a composite measure of body FA (second finger length, ear length, wrist width, and ankle width) correlates negatively with sperm number.

Baker (1997) argued that men with lower FA—relative to men with higher FA—produce more competitive ejaculates because they have more sexual partners and, therefore, consistently experience higher levels of sperm competition (Simmons et al., 2004; Thornhill and Gangestad, 1994). This is consistent with the prediction that ejaculate quality is reflected in male phenotype, and suggests that an evolutionary history of sperm competition may account, in part, for the correlations between FA, sexual attractiveness, and ejaculate quality. In fact, it has been suggested that women have historically encouraged sperm competition by mating multiply, increasing the chance that their ova are fertilized by the man with the most competitive ejaculate (Bellis and Baker, 1990; Nummi and Pellikka, 2012).

2D:4D Ratio

The ratio of the length of the second finger (index finger) to the fourth finger (ring finger), 2D:4D is a sexually dimorphic trait with men having lower 2D:4D than women, on average (Manning, 2002). Prenatal hormones influence 2D:4D (Zheng and Cohn, 2011), and finger growth and testes development are both prenatally influenced by Hox genes (*Hoxa* and *Hoxd* groups; Herault et al., 1997; Peichel et al., 1997). Disruption at these loci could be responsible for associations between ejaculate quality and digit ratio. Although research has shown that hand features are relevant to female perceptions of male attractiveness and mate value (Kościński, 2011, 2012; Saino et al., 2006), when 2D:4D is independently assessed in digitally manipulated images, no relationship is found with perceived hand attractiveness (Kosciński, 2011). Thus, 2D:4D is not likely to be a phenotypic cue that women attend to directly, and our discussion of 2D:4D is limited to the sense in which it provides a widely measured proxy for developmental androgenization (i.e., testosterone exposure; Lutchmaya et al., 2004; Manning and Taylor, 2001). Naturally occurring testosterone is not only necessary for spermatogenesis (Walker, 2009), but higher circulating testosterone is associated with improved spermatogenesis (Parapanov et al., 2009) and with increased sexual attractiveness in humans (Sadalla et al., 1987). Indeed, exogenously administered testosterone—which reduces natural testosterone levels—has been linked with impaired sperm production (Sjögren and Gottlieb, 2001). Women's ovulatory cycle status moderates their attraction to testosterone-linked traits (Roney and Simmons, 2008). Women at high fertility are more attracted to testosterone-linked traits than are women at low fertility (Gildersleeve et al., 2014; Penton-Voak and Perrett, 2000). Women also

find men with lower 2D:4D to have more attractive faces and husbands and wives have positively correlated 2D:4D ratios, suggesting that 2D:4D correlates with phenotypic traits that inform assortative mate choices (Ferdenzi et al., 2011; Voracek et al., 2007). If women attend to cues of ejaculate quality to inform mate choices, then low 2D:4D may be associated with rated attractiveness because of a shared association with ejaculate quality.

Data on the relationship between 2D:4D and ejaculate quality are equivocal and may depend on ethnicity. In a Danish sample, 2D:4D was positively correlated with total sperm count (contrary to the prediction that more masculine 2D:4D would correlate with higher quality ejaculate), but only among men who had a 2D:4D less than or equal to 1.0 (Bang et al., 2005). In a Chinese sample, 2D:4D was negatively correlated with sperm motility among infertile men, but not among fertile men (Lu et al., 2012). Conversely, in a French sample, 2D:4D was negatively correlated with sperm number among fertile men, but not among infertile men (Auger and Eustache, 2010). Auger and Eustache (2010) also measured testes volume among fertile men and found it to be negatively correlated with 2D:4D. Manning et al. (1998b) found that testosterone level, sperm number, ejaculate size, and average sperm swimming speed correlated negatively with 2D:4D ratio, but only for the right hand. Firman et al. (2003) did not find a correlation between 2D:4D and sperm number, sperm motility, sperm head length, or sperm tail length. Finally, in a South Korean student sample, no significant correlations were identified between 2D:4D and ejaculate volume, sperm number, or percentage of motile sperm (Seo et al., 2010). The regionally scattered evidence for a relationship between 2D:4D and fertility may be related to the finding that 2D:4D ratios vary by ethnicity, with differences between men from different populations being greater than sex differences within populations (Manning, 2002). This may be related to ethnic differences in circulating testosterone (Lynn, 1990).

Intelligence. Intelligence is important in assessments of human mate value (Prokosch et al., 2009) because it represents an ability to solve adaptive problems (Cosmides and Tooby, 2002). Women highly value intelligence in potential long-term mates (Feingold, 1992; Li et al., 2002) and short-term mates (Haselton and Miller, 2006). If men's intelligence is linked with ejaculate quality, then women who select intelligent men as mates are thereby selecting men who produce high-quality ejaculates. Arden et al. (2009) found that men with higher general intelligence produced ejaculates with greater sperm numbers, greater sperm concentration, and a greater percentage of motile sperm. Pierce et al. (2009) suggested that polyunsaturated fatty acids could simultaneously influence cognitive ability and ejaculate quality. Polyunsaturated fatty acids are critical to both neurodevelopmental function and spermatogenesis (Barcelo-Coblijn et al., 2003; Lenzi et al., 2000). Mutations in genes that influence the production of these fatty acids may explain the correlation between intelligence and ejaculate quality. Other studies have found negative correlations between intelligence and FA (i.e., more intelligent men are more symmetrical; Furlow et al., 1997; Luxen and Buunk, 2006; Prokosch et al., 2005), and positive correlations between intelligence and longevity (Batty et al., 2007). These findings support the

hypothesis of an underlying general fitness factor (see Haselton and Miller, 2006).

Voice pitch. Low voice pitch in men is rated as more masculine and attractive by women (Collins, 2000; Feinberg et al., 2005), and men with lower voice pitch report more sexual partners and more offspring (Apicella et al., 2007; Hodges-Simeon et al., 2011; Hughes et al., 2004). Women may have evolved to prefer lower voice pitch because it correlates with larger body size, higher level of circulating testosterone, greater upper body strength, and perceived social dominance (Evans et al., 2006; Jenkins, 1998; Puts et al., 2012). However, direct evidence indicates that men's voice pitch does not correlate with sperm motility or sperm concentration (Simmons et al., 2011). Simmons et al. (2011) also found that men with more attractive (but not necessarily lower pitch) voices have *lower* sperm concentrations, suggesting a tradeoff between investment in attractive phenotypic traits (e.g., lower voice pitch) and investment in ejaculate quality. In several species, sexually dominant males produce ejaculates with lower sperm concentrations, both across the lifespan and conditionally, when dominance is acquired (cockroaches: Tamara Montrose et al., 2008; salmon: Pitcher et al., 2009; bustard bird: Preston et al., 2011; crickets: Simmons et al., 2010). The correlation between social dominance and attractiveness (von Rueden et al., 2011) suggests that males who are highly attractive experience less pressure to fertilize ova during any given copulation because they have more opportunities to copulate with any given female. Attractive men may thus be able to afford to invest less in each ejaculate, whereas unattractive men make each copulation count. Furthermore, highly attractive men may experience lower sperm competition risk than less attractive men and, therefore, can invest fewer resources into producing higher quality ejaculates. Indeed, women who perceive their regular partner to be unattractive also report greater interest in copulating with other men (Gangestad et al., 2005) and report that their regular partner performs more mate guarding behaviors (Pillsworth and Haselton, 2006).

META-ANALYSIS

We performed a series of meta-analyses to characterize the distribution of effects produced by the studies described above (and listed in Table 1). For each set of analyses, we used the random effects model described by Hedges and Olkin (1985). This technique begins by converting effect sizes into *z*-scores (Fisher transformation), calculating an appropriate weight for each *z*-score based on within-study and between-study variability, calculating the mean and standard error of these weighted scores (denoted \bar{Z} and *SE*), and computing the probability of observing that mean given the null hypotheses that the mean effect size is zero (to produce a *P* value). We use the random effects model rather than the fixed effects model due to the expectation of heterogeneity in each set. Heterogeneity is here reported in the form of the I^2 statistic, which indicates the percentage of total variance in a set of effect sizes that is attributable to between-study variance, as defined by Higgins and Thompson (2002). The full set of 14 studies included three samples of infertile men drawn from fertility clinics. We excluded

data from clinical samples from our analyses because we wanted to assess the hypothesis that subclinical variance in male fertility is predicted by variance in phenotypic traits.

Our first two analyses explored the relationship between the percentage of motile sperm and two sets of distinct phenotypic traits: 2D:4D and attractiveness/fluctuating asymmetry. Studies of attractiveness and fluctuating asymmetry were combined into one analysis because attractiveness and symmetry are strongly correlated (as factors related to mate choice; Peters et al., 2007; Scheib et al., 1999) and because separate meta-analyses would only include two and three studies. For the same reasons, we included two studies that assessed correlations between attractiveness and *composite* measures of ejaculate quality (in both studies reporting composite measures of ejaculate quality, sperm motility was among the traits with the largest factor loadings; Leivers et al., 2014; Soler et al., 2014). Sperm motility was selected because it is the one ejaculate parameter that is common across each study and because it is strongly linked with fertilization success (Donnelly et al., 1998; Hirano et al., 2001). The mean weighted effect size of the relationship between 2D:4D and percentage of motile sperm across four studies was $\bar{Z} = 0.019$, $SE = 0.041$, $P > 0.05$, $I^2 = 0\%$. The mean weighted effect size of the relationship between attractiveness/fluctuating asymmetry and percentage of motile sperm (including two studies with composite measures) across five studies was $\bar{Z} = 0.241$, $SE = 0.107$, $P = 0.012$, $I^2 = 74\%$. The set of 2D:4D studies demonstrated homogeneity, indicating that there was no significant contribution of between-study variance to the calculation of the mean effect; however, the mean effect was nonsignificant. In contrast, the set of attractiveness/fluctuating asymmetry studies demonstrated significant between-study variance and produced a significant mean effect. These findings indicate that the relationship between 2D:4D and sperm motility is consistently measured but nonsignificant, whereas the relationship between factors related to mate choice and sperm motility is inconsistently measured, but significant.

To further probe the relationship between phenotype and individual ejaculate parameters, we performed three further meta-analyses investigating the mean effect of all measured phenotypic traits on the percentage of motile sperm (eight studies), sperm concentration (six studies), and sperm count (five studies). Collapsing across phenotypes is consistent with the concept of a general fitness factor that influences phenotypes broadly (e.g., androgenization reduces 2D:4D, increases attractiveness, and improves ejaculate quality). To limit our analyses to individual ejaculate parameters in healthy men, we excluded data from studies that only reported composite scores (Leivers et al., 2014; Soler et al., 2014) and we excluded data from studies of clinical samples, leaving nine studies. Additionally, we reversed the sign (i.e., multiplied by -1) of each of the 2D:4D effects to account for the predicted negative relationship between ejaculate quality and 2D:4D that conflicts with the predicted positive relationship with factors related to attractiveness (in effect, we converted to 4D:2D). The mean weighted effect size of the relationship between all measured phenotypes (intelligence, attractiveness, symmetry, and 2D:4D) and percentage of motile sperm across eight studies was $\bar{Z} = 0.045$, $SE = 0.048$, $P > 0.05$, $I^2 = 56\%$. For sperm concentration,

across six available studies (intelligence, attractiveness, symmetry, and 2D:4D), the mean weighted effect size was $\bar{Z} = 0.011$, $SE = 0.062$, $P > 0.05$, $I^2 = 71\%$. For sperm count, across five available studies (intelligence, symmetry, and 2D:4D), the mean weighted effect size was $\bar{Z} = 0.125$, $SE = 0.076$, $P = 0.0503$, $I^2 = 78\%$. Only the relationship between the listed phenotypes and sperm count approached significance ($P = 0.0503$), suggesting that if a general fitness factor accounts for variation in ejaculate quality, it may do so via sperm number. Finally, we thought it prudent to report these analyses with the study of intelligence (Arden et al., 2009) removed, as its larger effects and sample may have moved the results closer to significance without resembling the weaker effects of the other, morphological phenotypes included in the analyses. Removing this study did indeed attenuate each of the mean effects (motility: $\bar{Z} = 0.021$, $SE = 0.052$, $P > 0.05$, $I^2 = 46\%$; concentration: $\bar{Z} = -0.028$, $SE = 0.069$, $P > 0.05$, $I^2 = 63\%$; count: $\bar{Z} = 0.087$, $SE = 0.069$, $P > 0.05$, $I^2 = 62\%$), even reversing the relationship between phenotype and sperm concentration.

The literature summarized here indicates that the percentage of motile sperm is not correlated with 2D:4D, although it appears to be correlated with factors related to mate choice (attractiveness and symmetry). However, when taken together, morphological phenotypes do not cumulatively correlate with any one of the three most commonly measured ejaculate parameters. From such a small number of studies ($k = 8$ in the largest set, $k = 4$ in the smallest set), we can conclude little with confidence, except to suggest that future work will need to refine the set of human phenotypes and ejaculate parameters that are theoretically relevant. In the meantime, we encourage an examination of the measurement strategies employed in this area.

MEASURING EJACULATE QUALITY

The quality of a man's ejaculate can be defined as the probability that it will produce viable offspring following copulation in a natural environment. However, in the study of human reproduction, ejaculate quality is often assessed in terms of sperm concentration, morphology, and motility, which are proxies for fertility (Bonde et al., 1998). "High-quality ejaculates" differ from "high-quality genes." High-quality ejaculate refers to the semen parameters, and not to the genetic contents of sperm. That said, men's fertility is among the many traits encoded in "good genes" that women may have evolved to detect for their own benefit and for the benefit of their offspring. Various semen parameters comprise ejaculate quality, including ejaculate volume, total sperm number, sperm concentration, agglutination, semen viscosity (coagulation and liquefaction), semen pH, sperm morphology, sperm vitality (cellular integrity), and the presence of cellular elements other than spermatozoa, such as genitourinary epithelial cells and leukocytes (Johanisson et al., 2000; World Health Organization, 2010). Principle components analyses consistently extract clusters of traits that covary (e.g., measures of motility, morphology, and concentration form a single principle component; Auger and Eustache, 2010; Leivers et al., 2014), suggesting an underlying ejaculate quality component.

The human semen parameters reported in the literature vary across studies, but typically include the

percentage of motile sperm, sperm concentration, and sperm count. Although these three parameters influence the likelihood of fertilization, other parameters also influence the likelihood of fertilization (World Health Organization, 2010). Sperm number and concentration are less predictive of fertility than individual assessment of sperm kinematics (e.g., flagellar and head movement; Mortimer, 1997) and morphology (Bonde et al., 1998). Additionally, the differences in semen analysis techniques across time and place, and the difficulty in acquiring adequate numbers of ejaculates, complicates the cross-examination of the associations between phenotypic traits and ejaculate quality, even when the same semen parameters are assessed. For example, the study of 2D:4D ratio and semen quality conducted in China compared sperm motility in 196 infertile men and 72 healthy controls with computer-aided semen analysis, identifying the proportion of sperm in each ejaculate that displayed “class A or B” motility (moving faster than 5 $\mu\text{m/s}$; Lu et al., 2012; World Health Organization, 2010). Another study of 2D:4D measured the percentage of motile sperm in 58 healthy American men, using a manual count of motile sperm in a Makler counting chamber under magnification (motility criteria were not specified; Manning et al., 1998a,b). A third study of 2D:4D in 50 healthy Australian men generated motility classifications with a manual count of class A or B sperm at 10 different microscopic fields in a Neubauer counting chamber (Firman et al., 2003). It is difficult to know if the extant research correlating ejaculate quality with phenotypic traits can be defensibly integrated, given that the procedures, equipment, and samples are so varied (see Table 1).

The different techniques for semen assessment sometimes produce varying levels of agreement (Christensen et al., 2005; Mahmoud et al., 1997). In fact, retrospective reports of widespread declines in sperm concentration over the past 50 years might be accounted for by shifts in semen assessment technology and techniques (Pacey, 2013). Additionally, most studies that have investigated the correlation between human phenotypic traits and ejaculate quality have assessed masturbatory ejaculates, which are known to be lower in quality than copulatory ejaculates (Zavos and Goodpasture, 1989). Semen parameters vary under sociosexual circumstances such as the risk of sperm competition, but these effects are sometimes specific to copulatory samples (Baker and Bellis, 1993a,b,1995). Studies using masturbatory samples do not fully account for ejaculate adjustments made in copulation (Baker and Bellis, 1993a,b). We wish to explore how mate preferences evolved with respect to reproductively successful ejaculates, and because it is copulatory (and not masturbatory) ejaculate quality that influences reproductive success, assessing copulatory ejaculate quality is more appropriate in this line of research.

NON-HUMAN STUDIES

In the non-human literature, the correlation between phenotypic traits and ejaculate quality varies by population, strain, species, and phenotypic trait, with attention limited to male secondary sexual characteristics (SSCs). Researchers have identified positive correlations between SSC development and ejaculate quality in several species. For example, the attractiveness of the courtship displays in wild Trinidadian guppies (*Poecilia reticulata*) varies

from male to male by virtue of differences in swimming strength, coloration, and size, each of which is positively correlated with the number of sperm reserved in the reproductive tract and the number of sperm deposited in solicited copulations (controlling for sperm reserves; Matthews et al., 1997; Pilastro et al., 2002). Larger, more colorful male guppies, who are preferred as mating partners, also have larger, more abundant, and more motile sperm than their smaller rivals (Locatello et al., 2006; Skinner and Watt, 2006; see also, red deer, Malo et al., 2005; pied flycatchers, Calhim et al., 2009; houbara bustard, Chargé et al., 2010; fly, Hosken et al., 2008; dung beetle, Simmons and Kotiaho, 2002).

Other studies have found negative correlations between features of male SSCs and ejaculate quality. Female cod (*Gadus morhua* L.) assess mate quality through the sounds produced by males during courtship. Males with larger “drumming muscles” produce more attractive sounds, and drumming muscle size is negatively correlated with spermatocrit level (concentration of sperm in the ejaculate; Engen and Folstad, 1999; see also, red junglefowl, Parker et al., 2006; guppy, Evans, 2010). Researchers usually interpret such negative correlations as indicative of a developmental tradeoff between investment in male SSCs and investment in ejaculate quality (Mautz et al., 2013). In other cases, the relationship is interpreted as the result of attractive males either producing more frequent ejaculates and experiencing diminishing returns due to sperm depletion (Dewsbury, 1982; Preston et al., 2001), diverting sperm production resources to mate guarding and courtship behavior (Warner et al., 1995), downregulating their ejaculate size in contexts of abundant non-competitive matings (Wedell et al., 2002), or all of the above. In several studies, there are no correlations found between features of male SSCs and ejaculate quality. For example, among Sedge warblers (*Acrocephalus schoenobaenus*), larger song repertoires are more attractive to females, but the size of the repertoire is not correlated with sperm numbers or with the percentage of morphologically normal sperm (Birkhead et al., 1997; see also, cricket: Klaus et al., 2011; pied flycatcher: Lifjeld et al., 2012; zebra finch: Birkhead and Fletcher, 1995). Evidence for the relevant associations is mixed in other studies. For example, in the domestic rooster (*Gallus gallus domesticus*), females are attracted to males that display larger and redder combs and sperm viability correlates positively with comb color but negatively with comb size (Navara et al., 2012; see also, fairy wren: Rowe et al., 2010).

In a meta-analysis of 38 studies of 21 non-human species, Mautz et al. (2013) parsed 228 effect sizes for the correlations between behavioral and morphological male SSCs and various measures of ejaculate quality. The analyses yielded small but significant correlations between behavioral and morphological SSCs and sperm viability ($r = 0.07$, $P < 0.05$), but these correlations failed to reach significance for sperm number, size, or swimming speed. The researchers conclude that although male phenotype accounted for less than 1% of the variance in sperm quality, small effect sizes can produce significant evolutionary trends (see Marczyk and Shackelford, 2010). They also warn that the varied methods of ejaculate extraction, the captive environment, and the operational definition of sperm quality are likely sources of error. As in the human literature, the method of collecting ejaculates varies by study. Of the studies included, some stimulate ejaculation

manually, or with the use of mock female receptacles, other studies extract semen surgically or by mechanical pressure (*post mortem*), and still others extract the ejaculate from the female reproductive tract after copulation. Data on different sperm parameters from different species (e.g., sperm length in dung beetles and sperm number in guppies) are difficult to integrate because different parameters may be more or less relevant to fertility in different species. Moreover, semen parameters serve as proxies for fertility, and very few studies establish fertility by identifying paternity. Similar to human ejaculate quality, non-human ejaculate quality varies as a function of naturally occurring contexts, and only one of the studies referenced here (Calhim et al., 2009) assessed phenotype and fertility in a wild population.

CONCLUSION

The selection pressures that influence men's fertility are many and varied. A woman's preference for early fertilization, the clustering of fitness-enhancing traits in men of high genetic quality and developmental stability, and the selection of men who succeed in sperm competition are all predicted to produce correlations between male attractiveness and ejaculate quality. However, because there are nontrivial costs to producing high-quality ejaculates, men of high genetic quality more often benefit from prudently allocating investment in each ejaculate (e.g., Leivers et al., 2014): Although they may be most capable of producing viable ejaculates, these ejaculates are also in greatest demand. Moreover, men of higher phenotypic quality incur the costs of producing and maintaining those phenotypes, including the developmental costs of an elaborate morphology and the time and energy costs of dominance posturing and mate guarding. These costs weigh upon an attractive male's ability to manufacture high-quality ejaculates, driving down the correlation between phenotype and fertility. Thus, there may be a tug-of-war between these selection pressures, simultaneously pulling attractive males towards fertility and pushing them away from fertility. Depending on the species and the trait measured, the correlation between male phenotype and fertility can move in either direction.

Currently, the evidence for phenotypic traits as cues for male fertility in humans is mixed. Research has documented positive, negative, and no correlations between phenotypic traits and ejaculate quality. Unfortunately, the results across species do not align with any obvious life-history commonalities (degree of paternal investment, mating strategy, method of fertilization, etc.). The between-species differences in findings do not show patterns that help in identifying confounding factors. Therefore, we do not identify any a priori reason to expect one pattern or another across all human traits, and conclude that theory lags behind the data, creating a situation in which each finding (positive or negative) generates its own theoretical position of unknown generalizability. It is possible that the pattern of both positive and negative results indicates the lack of any consistent relationship between phenotype and fertility, but many of these studies produce effect sizes that are larger than this null hypothesis would predict, and most studies measure different traits or measure the same traits in different contexts. If evidence of adaptation can be extracted from this literature, it will require a more nuanced interpretation of

the conditions under which a given phenotype, as assessed by a given female, corresponds with a given ejaculatory parameter as it relates to fertility. Each of these considerations must be made with explicit reference to human biology, ecology, and evolutionary history.

For researchers interested in developing and testing well-defined predictions on whether and how the relationship between men's phenotype and fertility may guide women's mate choice, we offer six methodological considerations. First, women's assessments of men's attractiveness should be carefully defined, with sensitivity to mating context and ovulatory cycle status. An ideal operational definition for male attractiveness will be open to objective validation, i.e., attractiveness should be established using both women's reports and direct measurement of men's traits so that we may refer more directly to phenotypes, rather than to the perception of phenotypes. We recommend that researchers secure measurements of male traits whose degree and context of attractiveness are established elsewhere (e.g., face shape, muscle mass, etc.) to identify traits that may be used as cues of ejaculate quality. When measurements are made, they should be made with image analysis software (e.g., ImageJ; Schneider et al., 2012) for greater measurement accuracy, consistency, and efficiency.

Second, researchers might benefit from novel thinking with respect to the traits that may correlate with ejaculate quality. Female mate choices may be informed by a wide array of morphological, behavioral, and psychological traits, any of which may be heavily weighted for associations with ejaculate quality. We recommend that researchers begin by scanning for traits that correlate with ejaculate quality and explore how these traits relate to mate value (e.g., heritable psychopathologies, sexual preferences, personality measures, life histories, etc.). Third, investigators will benefit from the use of methods that rule out alternative explanations for the attractiveness of precisely defined male traits. For example, if wrist width were correlated with ejaculate quality, but was otherwise linked with physiological costs, then female attraction to wrist width would constitute strong evidence for female adaptations to secure high-quality ejaculates. Fourth, we recommend making the measurement of phenotypic traits and ejaculate quality more naturalistic and context-sensitive. Acquiring copulatory ejaculates from men in relationships, providing women with video stimuli or brief meetings rather than still images for ratings of attractiveness, and retrospective assessments of men's lifetime sexual behavior are methods that might help to approximate more natural mating contexts. Following Leivers et al. (2014), future researchers should account for the relative mate value of the men producing ejaculates and the women that stimulate their arousal. Additionally, the finding that women's long-term mate preferences differ from their short-term mate preferences and that these preferences change across the ovulatory cycle also raises questions that have yet to be explored. Although most studies exclude women using hormonal contraceptives, few studies account for the ovulatory phase of the raters. This is most likely to complicate findings from studies using small numbers of female raters, as in Peters et al. (2008; 12 women), who also did not exclude women using hormonal contraceptives. Fifth, due to ethnic, economic, and cultural differences in phenotype, attractiveness, and ejaculate quality, researchers must

limit the scope of their findings to their study population. All the results we cite are drawn from developed nations, and most participants are college educated. Research will need to assess non-industrialized, non-Western populations to explore whether the proposed relationships between male phenotype and fertility are universal. That said, unless there is theoretical reason to expect industrialized life to fundamentally alter female mating psychology, greater diversity may not be necessary in identifying female adaptations.

Finally, a proper assessment of the proposed relationships in humans requires developing consensus on the measurement of ejaculates and the traits that may correlate with ejaculate quality in men. Without consistent adherence to ejaculate measurement guidelines and consistent measurement of male traits, the literature will continue to be difficult to integrate. For example, in a meta-analysis of 94 studies investigating the correlations between FA and health outcomes in humans, Van Dongen and Gangestad (2011) identified hundreds of traits under study. Most studies aggregated bodily features or facial features, overlapping with or excluding measures from other studies, creating a situation in which the effect size of the correlation between FA and health outcomes was impossible to specify (but estimated to be between .08 and .67), despite a total sample of nearly 50,000 participants. In FA research, we recommend assessing traits that are influenced primarily by developmental instability, as opposed to lateralized behavior (handedness and footedness), and only those visible traits that ancestral women could have used to assess mate value. Because evolutionary research on human ejaculate quality is relatively new, we recommend that future studies assess many trait indicators of ejaculate quality, as described by the World Health Organization (2010), using computer-aided semen analysis equipment. From here, it is essential that investigators are familiar with the evolving literature on how ejaculate characteristics interact to facilitate or decrease the likelihood of fertilization in humans, so that there can be agreement on which characteristics are relevant. In providing these recommendations we hope to encourage constructive conversation between researchers studying human mate choice, human reproductive biology, and related evolutionary forces, knowing that better methods and theoretical considerations will continue to emerge as these fields progress.

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