Perceived physical strength in men is attractive to women but may come at a cost to ejaculate quality

Yong Zhi Foo^{a, b, *}, Leigh W. Simmons^{a, b}, Marianne Peters^a, Gillian Rhodes^a

^a *ARC Centre of Excellence in Cognition and its Disorders, School of Psychological Sciences, University of Western Australia, Crawley, WA, Australia*

^b *Centre for Evolutionary Biology & School of Biological Sciences, University of Western Australia, Crawley, WA, Australia*

Article history:

Received 12 January 2018

Initial acceptance 22 February 2018

Final acceptance 8 June 2018

Available online xxx

MS. number: 18-00035R

* Correspondence: Y- Z Foo, *ARC Centre of Excellence in Cognition and its Disorders, School of Psychological Sciences, University of Western Australia, 35 Stirling Hwy, Crawley, 6009, WA, Australia.*

E-mail address: yong.foo@uwa.edu.au (Y-Z Foo)

Studies of sexual selection acting on physical strength in humans have focused mostly on its role in premating male–male competition. Recent theoretical frameworks suggest that male strength could be subject to trade-offs with postmating sperm competitiveness. Here, we

examined whether male strength is linked to ejaculate quality. We also asked whether strength is attractive to women and affects male self-reported mating success. Perceived strength was negatively associated with ejaculate quality as predicted by the trade-off hypothesis. Perceived strength positively predicted attractiveness and both perceived strength and attractiveness shared similar variance in predicting self-reported mating success. Our findings indicate that despite the benefits to premating sexual selection, having greater strength may come at a cost to sperm competitiveness.

Keywords:

female choice

physical strength

sexual selection

sperm competition

Male physical strength plays a significant role in human sexual selection. Men have substantially greater upper body size and strength than women (Lassek & Gaulin, 2009) and stronger men enjoy greater self-reported mating success (Gallup, White, & Gallup, 2007; Lassek & Gaulin, 2009). A very recent study using data from a large-scale U.K. prospective study data set ($N > 500\,000$) showed that male strength continues to be under directional selection in contemporary populations (Sanjak, Sidorenko, Robinson, Thornton, & Visscher, 2017). But what are the aspects of sexual selection that drive the evolution of male strength? The two main sexual selection processes are male–male competition and female choice (Darwin, 1871). Each of them can occur both premating and postmating. During premating sexual selection, in order to gain access to females, males develop traits such as weapons, body size and physical strength to compete with same-sex rivals (male–male competition) and ornaments to attract females (female choice). Because females often mate with multiple

males, male–male competition and female choice continues postmating in the form of sperm competition (Parker, 1970) and cryptic female choice (Eberhard, 1996), respectively. To fully understand the evolution of sexually selected traits, it is therefore necessary to study the influence of each of these processes on these traits.

Studies on male strength in humans have focused mainly on its role in premating male–male competition. For instance, stronger men are more likely to win physical contests (see review by Sell, Hone, & Pound, 2012). One important function of strength in male–male competition is to signal one’s fighting ability to deter potential rivals. Given the potential costs of losing a physical fight (e.g. life-threatening injuries), game theory suggests that individuals should evolve the ability to accurately assess a potential rival’s fighting ability so that they can decide whether to fight or flee (Parker, 1974). Indeed, in many species, conflicts are often resolved after the visual assessment of relative fighting ability and before they escalate to actual physical trials of strength (Hardy & Briffa, 2013). Some of the common visual cues to fighting ability across species include body size, perceived strength and the size of weapons (Archer, 1988). In humans, there is good evidence for perceived strength as a cue to fighting ability. Individuals are highly accurate in judging others’ strength, particularly men’s upper body strength, from full-body images (Sell et al., 2009). In Sell et al.’s (2009) study, perceived strength from full-body images shared 50% of its variance with upper body strength, which was quantified using a composite score based on four upper body exercises, including arm curl (biceps), abdominal crunch (abdominal muscles), chest press (pectorals), and super long pull (deltoids). In contrast, the same study found that handgrip strength, a measure that is commonly used in the literature, shared only 24% of variance with upper body strength (see electronic supplementary material in Sell et al., 2009). Furthermore, stronger men are also perceived as more masculine and dominant (Fink, Neave, & Seydel, 2007) and to have superior fighting ability (Little, Třebický, Havlíček, Roberts, & Kleisner,

K., 2015; Sell et al., 2009). Importantly, perceived strength is positively associated with winning a fight in mixed martial arts competitions, indicating that perceived strength is a valid cue to fight outcome (Little et al., 2015).

While these findings highlight the role that strength plays in premating male–male competition, a growing literature indicates that the evolution of male strength is also influenced by other aspects of sexual selection. For instance, recent theoretical developments suggest that male expenditure on physical strength for premating male–male competition might be limited by trade-offs with postmating sperm competitiveness (Parker, Lessells, & Simmons, 2013; Simmons, Lüpold, & Fitzpatrick, 2017). From a life history perspective, resource allocation trade-offs occur between life history traits such as growth, health and reproduction (Stearns, 1977). Expenditure on competitive traits and ejaculate production are both resource-costly activities (Elia, 1992; Gage & Cook, 1994; Hardy & Briffa, 2013; Kvarnemo & Simmons, 2013). Therefore, not all males can possess highly developed competitive traits because they negatively impact male fertility by diverting limited resources away from ejaculate production (Parker et al., 2013; Simmons et al., 2017). Such trade-offs have been demonstrated in various nonhuman animal species (Fry, 2006; Joseph, Sasson, Emberts, & Miller, 2018; Moczek & Nijhout, 2004; Simmons & Emlen, 2006; Somjee, Miller, Tatarnic, & Simmons, 2018). For instance, in the crusader bug, *Mictis profana*, males use their enlarged hindlegs to fight off rival males. When males are experimentally induced to lose their hindlegs through the process of autotomy, a defensive mechanism for getting away from the grasp of predators and/or distract predators in order to escape, they grow bigger testes (Somjee et al., 2018).

In humans, recent studies suggest that ejaculate quality might be traded off against competitive and/or attractive traits, including facial and vocal masculinity and mate-guarding behaviour (Leivers, Rhodes, & Simmons, 2014; Simmons, Peters, & Rhodes, 2011; Soler et

al., 2014). No studies, however, have examined whether this trade-off also applies to strength. Experimental evidence to suggest that it might comes from a study in which increased expenditure on physical training involving treadmill exercises was found to result in reduced ejaculate quality and this effect may have been due to adjustments to the hypothalamus-pituitary-testis axis (Safarinejad, Azma, & Kolahi, 2009). This finding suggests that ejaculate quality in humans is susceptible to down-regulation due to increased expenditure on physical training. However, this experiment does not allow us to separate the impact of strength building from other potential physical effects of treadmill exercises such as endurance. Nevertheless, given that muscle tissues are energetically costly, accounting for approximately 20% of metabolic rate (Elia, 1992), there is good reason for us to expect that expenditure on building superior strength may come at a cost to other fitness-enhancing traits such as ejaculate production.

Besides pre- and postmating male–male competition, female choice, particularly premating attractiveness, can also influence the evolution of male strength. In many nonhuman animal species, traits used to signal fighting ability and male–male competitiveness are also used to attract females (Andersson, 1994; Berglund, Bisazza, & Pilastro, 1996). Likewise, strength can be positively related to attractiveness in men (Fink et al., 2007; Sell, Lukazsweski, & Townsley, 2017). These results suggest that at least part of the relationship between strength and mating success is accounted for by attractiveness. Indeed, in humans, one study found that the relationship between men’s physical fitness and self-reported mating success was fully accounted for by attractiveness, which suggests that physically fit men enjoy greater mating success because they are preferred by women (Hönekopp, Rudolph, Beier, Liebert, & Müller, 2007). However, the physical fitness measure used by Hönekopp et al. (2007) included components other than strength, such as endurance and cardiovascular health. Therefore, it is unclear whether the findings were due to physical

strength per se, indicating the need for further work on the relationship between strength, attractiveness and mating success.

A related question is whether strength predicts mating success independently after controlling for attractiveness. Some researchers have argued that male–male competition may be more important than female choice in determining men’s mating success (Puts, 2010). Puts (2010) predicted that, if so, traits that facilitate male–male competition, such as strength, should predict mating success independent of attractiveness and their independent contributions to mating success should be greater than that of attractiveness. One supporting study (Hill et al., 2013) showed that when attractiveness and a composite masculinity score comprising a variety of face, body and voice measures, some of which are related to strength (e.g. bicep circumference), were entered together to predict men’s self-reported mating success, only masculine traits, and not attractiveness, showed independent contributions. However, no studies have specifically examined the independent contributions of strength, an important determinant and visual signal of male–male competitiveness, and attractiveness to male mating success.

Here, we examined how male strength relates to ejaculate quality and female choice. We used third-party ratings of the participants’ physical strength as a valid index of strength (Sell et al., 2009). First, we examined whether strength is negatively associated with ejaculate quality, as predicted if males trade off expenditure between premating and postmating traits (Parker et al., 2013; Simmons et al., 2017). Second, we examined whether strength predicts attractiveness and self-reported mating success and the extent to which the relationship between strength and mating success is accounted for by attractiveness.

<H1>METHODS

<H2>*Ethical Note*

This research was approved by the Human Ethics Committee at the University of Western Australia (ref. no. RA/4/1/2323). All participants provided informed consent prior to participation.

<H2>*Participants*

This study was conducted using data from a previous data set that examined the relationship between physical appearance and ejaculate quality in 118 self-reported heterosexual Caucasian men (mean age $\pm$ SD = 22.5 $\pm$ 4.9 years; Peters, Rhodes, & Simmons, 2008; Peters, Simmons, & Rhodes, 2008).

<H2>*Participant Procedure*

Full-length and close-up face-only photographs of each participant wearing a fitted white singlet and dark-coloured shorts were taken. Participants were told to adopt a neutral expression with their mouth closed, and to stand with their feet slightly apart and their arms by their sides.

Following the photography, participants completed a lifestyle questionnaire that is commonly used to control for potential lifestyle-related confounds on ejaculate quality (Kilgallon & Simmons, 2005). The questionnaire included items on dietary and exercise habits, weekly sexual activities, location of childhood upbringing, whether the participants kept their mobile phones close to their testes (i.e. in the hip pocket or on the belt), exposure to various toxins, medication usage and consumption of alcohol, caffeine and illicit drugs.

Participants were also asked to report their lifetime number of sex partners (i.e. self-reported mating success).

<H2>Ejaculate Collection and Assessment

Participants were provided with detailed instructions on the ejaculate collection and were instructed to deliver the sample within 1 h of collection to avoid decline in sperm motility. Participants also reported the time of collection, time taken to collect the sample and time since last ejaculation.

The ejaculate quality assessment was conducted according to World Health Organization (1999) guidelines by one of our experimenters (Marianne Peters), who was trained by a qualified seminologist at a local fertility clinic. The experimenter's proficiency was verified to be in line with standards of professional fertility clinics. The samples were assessed immediately upon delivery for sperm concentration, motility and morphology. Sperm concentration (number of sperm $\times 10^6$ /ml ejaculate) was determined by the average number of spermatozoa present in $5 \times 1 \text{ mm}^2$ cells in each of two chambers of a Neubauer haemocytometer. To assess sperm motility, 10 μl aliquot of each sample was placed on a slide and examined under 400 $\times$ magnification using bright-field illumination. One hundred and thirty spermatozoa per sample were observed and motility was expressed as the percentage of progressive motile sperm out of the 130 spermatozoa. To assess morphology, smears were prepared from a 5 μl drop of ejaculate, air dried, and then stained using the Diff- Quik stain (Baxter Diagnostics, Inc., McGraw Park, IL, U.S.A.). Two hundred sperm cells were examined under oil immersion at 1000 $\times$ magnification. A morphology score was calculated based on the percentage of sperm cells with normal morphology using the classification guidelines from the World Health Organization (1999).

<H2>*Ratings of Photographs*

The original data set contained composite scores of female ratings of attractiveness and masculinity (hereinafter referred to as attractiveness and masculinity, respectively). Twelve women rated the attractiveness of the body-only and face-only photographs and another 12 women rated the masculinity. The composite scores were computed by calculating an average attractiveness and masculinity score for each face and body and then combining the face and body ratings of each individual using principal component analysis. The composite scores of female ratings of attractiveness were used as a measure of female preference. The masculinity composite score was used to test whether the relationship between strength and attractiveness was distinct from that of the broader trait, masculinity.

<H3>*Additional physical strength ratings*

An additional 202 participants were recruited online from Amazon Mechanical Turk to rate the physical strength of the male participants from their photographs. Of these, 111 responses were excluded because of at least one of the following a priori exclusion criteria: did not complete the ratings study, button-bashing (e.g. choosing only one score for all the faces), age above 50, non-Caucasians, nonheterosexuals. We included only ratings from heterosexual individuals because we were interested in male–male competition and female preference. We included only Caucasian raters because our male participants were all Caucasian. We excluded raters above age 50 in accordance with previous studies on human sexual selection that have utilized ratings from Internet participants (e.g. Foo, Simmons, & Rhodes, 2017). The nature of Internet testing makes it tricky to recruit specific populations because it is difficult to ensure honest reporting on prescreening eligibility questions

(Chandler and Paolacci, 2017). Therefore, we chose to collect data from the entire Amazon Mechanical Turk sample pool and use only the eligible participants based on our a priori exclusion criteria. The remaining 91 self-reported heterosexual Caucasian participants consisted of 37 women (mean age $\pm$ SD = 35.2 ± 7.7 years, range 22–48) and 54 men (mean age $\pm$ SD = 33.9 ± 7.8 years, range 23–50). Raters were randomly assigned to rate the full-length (12 women, 16 men), body-only (13 women, 21 men) or face-only photos (12 women, 17 men) for physical strength on a seven-point Likert scale (1 = very weak, 7 = very strong). Previous research has shown that there are valid cues to physical strength in both the face and body (Sell et al., 2009). Here, we collected ratings of physical strength not only from the full-length images, but also from the face-only and body-only images in order to verify that the ratings from the three image types converge into a single physical strength component, which is what we would expect if rated physical strength is a valid measure of actual physical strength.

<H1>RESULTS

There was good consensus on judgements of physical strength within male and female raters and within each image condition (Table 1). There was also high agreement between average male and female ratings in each image condition (full length: Pearson $r = 0.86$, $P < 0.001$; body only: Pearson $r = 0.92$, $P < 0.001$; face only: Pearson $r = 0.79$, $P < 0.001$; all $dfs = 116$). Therefore, we computed averages across male and female raters for each image condition. The conclusions of our results did not change when we used the ratings of physical strength from only the female or male raters. The average ratings were significantly correlated across image conditions (Pearson $r = 0.47$ – 0.92 , $Ps < 0.001$; all $dfs = 116$), and

reduced to a single overall physical strength principal component (hereinafter referred to as perceived strength) explaining 76.6% of the variance (eigenvalue = 2.3; Table 2).

Table 3 shows the descriptive statistics. One participant was excluded from ejaculate analysis due to an abnormally high concentration of sperm (626 million sperm/ml; 5.7 SD away from our sample mean and 2.4 times the 97.5 centile of reference values from the World Health Organization (1999) using the same ejaculate quality assessment method).

Because age was significantly correlated with perceived strength and number of sexual partners (Table 4), we ran all our multiple regression analyses controlling for age. To ensure that our multiple regression models were not subject to the problem of multicollinearity, we calculated the variance inflation factor (VIF) for each predictor in the multiple regression models. The VIFs ranged from 1.09 to 6.10, which were below the recommended maximum of 10 (Montgomery & Peck, 1992; Zuur, Ieno, & Elphick, 2010). Therefore, it was unlikely that our multiple regression models suffered from issues of multicollinearity.

<H2>Perceived Physical Strength and Ejaculate Quality

Ejaculate quality is sensitive to environmental and lifestyle factors (Aitken, Koopman, & Lewis, 2004). To identify such confounds in this data set, a previous study entered lifestyle, collection (time to produce the ejaculate, time since previous ejaculation and time from ejaculation to ejaculate analysis, as independent variables) and testes size variables into stepwise general linear models predicting each ejaculate quality parameter (Peters et al., 2008). A significant model was found only for sperm concentration. Variables that remained in the model were time since last ejaculation, exposure to toxins, use of antibiotics and/or medication, exposure to heat and time taken to produce the ejaculate. None of the potential confounds were related to sperm motility or morphology. Therefore, in this study we ran our

analyses using the raw motility and morphology data and the sperm concentration residuals after controlling for the potential confounds identified by the stepwise linear regression model.

After controlling for age, perceived strength negatively predicted sperm concentration ($B(SE) = -0.60(0.28)$, $P = 0.03$, 95% confidence interval, CI $[-1.15, -0.05]$), but not sperm motility ($B(SE) = -1.21(1.77)$, $P = 0.50$, 95% CI $[-4.72, 2.31]$) or sperm morphology ($B(SE) = -0.32(0.85)$, $P = 0.71$, 95% CI $[-2.01, 1.37]$). As reported previously, there was no relationship between either attractiveness or masculinity and ejaculate quality in this data set (Peters et al., 2008; see also Table 4). However, given that perceived strength was related to both masculinity and attractiveness (Table 4) and previous findings have demonstrated potential links between ejaculate quality and masculine/attractive traits (e.g. Simmons et al., 2011; Soler et al., 2014), we wanted to confirm that the relationship between strength and ejaculate quality was distinct from that between masculinity/attractiveness and ejaculate quality. Hence, we tested the relationship between perceived strength and ejaculate quality controlling for masculinity and attractiveness to see if the results changed. Controlling for both masculinity and attractiveness did not change our results.

<H2>Perceived Physical Strength, Attractiveness and Self-reported Mating Success

Perceived strength positively predicted attractiveness after controlling for age (Table 5), supporting the role of female choice in selection for male strength. Because both perceived strength and attractiveness were positively related to masculinity (Table 4), we tested the extent to which their relationship was due to masculinity to examine whether strength's influence on attractiveness is distinct from that of the broader trait of masculinity. After entering both masculinity and perceived strength into the regression model, perceived

strength became nonsignificant while masculinity remained significant (Table 5, Model 3), suggesting that masculinity mediated the relationship between perceived strength and attractiveness. We formally tested the indirect effect using a Sobel's test, which confirmed masculinity as a significant mediator ($z = 6.54$, $P < 0.001$). The results indicate that the influence of strength on attractiveness was completely mediated by masculinity.

Next, we examined whether strength predicted self-reported mating success and the extent to which the relationship was accounted for by attractiveness. Because mating success is count data with a positively skewed, Poisson-like distribution, we ran our analyses using generalized linear regression models with a negative binomial distribution, which accounts for overdispersion in the data (O'Hara & Kotze, 2010). As predicted, perceived strength positively predicted self-reported number of sex partners after controlling for age ($B(SE) = 0.26(0.09)$, $P = 0.004$, 95% CI [0.07,0.44]). However, neither perceived strength ($B(SE) = 0.15(0.11)$, $P = 0.16$, 95% CI [-0.07,0.38]) nor attractiveness ($B(SE) = 0.16(0.10)$, $P = 0.12$, 95% CI [-0.05,0.38]) remained significant after controlling for the other variable, suggesting that both shared similar variance in predicting mating success.

<H1>DISCUSSION

Consistent with the trade-off hypothesis (Parker et al., 2013; Simmons et al., 2017), we found that strength was negatively related to sperm concentration in men. The influence of strength on ejaculate quality was independent of its relationships with masculinity and attractiveness, suggesting that the relationship found was indeed due to strength per se, and not other potential variables associated with attractiveness and/or masculinity. Therefore, our results suggest that despite the benefits of increased strength to male success in premating male–male competition and/or premating female choice, the development of strength may be

limited by its negative impacts on ejaculate quality. Such constraints would provide an explanation for why we continue to observe variation in strength across men despite directional selection for increased male strength, which is expected to deplete variation in the trait (the lek paradox; Borgia, 1979; Kirkpatrick & Ryan, 1991; Taylor & Williams, 1982). Our finding contributes to a growing list of male competitive and/or attractive traits that associate negatively with ejaculate quality, including facial and vocal masculinity and mate-guarding behaviour (Leivers et al., 2014; Simmons et al., 2011; Soler et al., 2014). One potential physiological mechanism for the relationship between strength and ejaculate quality is the effect of testosterone. Testosterone increases muscle mass and strength (Herbst & Bhasin, 2004) but can impair ejaculate production at high levels (World Health Organization, 1996).

We also showed that male strength is selected via female choice. Strength predicted attractiveness (rated by women) via masculinity, a known factor in male attractiveness (Rhodes, 2006), suggesting that strength is a component of masculinity, which in turn influences attractiveness. This result is in line with findings showing that male strength is attractive in humans (Fink et al., 2007; Sell et al., 2017). More importantly, strength shared similar variance with attractiveness in predicting self-reported mating success, thus confirming the role of premating female choice in the selection of male strength.

Contrary to recent suggestions that male–male competition may be more important than female choice in influencing mating success in humans (Puts, 2010), we did not find any evidence that strength predicted self-reported mating success independent of its association with attractiveness. Therefore, our results indicate that strength enhances mating success because women prefer stronger-looking men. Note that we are not suggesting that male–male competition has no effect on selection for male strength. In some cases, male–male competition and female choice may be highly associated such that the two aspects do not

contribute independently to mating success. For example, in many nonhuman species, competitive traits are preferred by females because they provide benefits including protection, resources and good genes that, for example, contribute to male–male competitiveness and/or health in the offspring (Andersson, 1994; Berglund et al., 1996). Similarly, in humans, stronger men have more resources and better health (Sell et al., 2012; von Rueden, Gurven, & Kaplan, 2008). Therefore, strength may be attractive to women because it is a signal of male quality.

There are two potential limitations to our study. First, our study is correlational, thus precluding conclusions concerning the causal relationship between strength and ejaculate quality. However, an experimental study has shown that increased expenditure on physical training can reduce ejaculate quality in men (Safarinejad et al., 2009), which is consistent with a causal effect of investment in strength on ejaculate quality. Second, our findings are based on perceived strength and not actual measures of strength. We have, however, good reasons to believe that our findings are biologically relevant. First, given that many species use visual displays of strength to settle disputes (Hardy & Briffa, 2013) and perceptions of strength and dominance are linked to real-life competitive ability (e.g. Little et al. 2015; Mueller & Mazur, 1997), the perception of strength represents a critical and intrinsic aspect of the sexual selection process in terms of male and female assessment of competitive ability. Furthermore, perceived strength from whole-body images is highly correlated with actual upper body lifting strength (Sell et al., 2009). This finding is consistent with game theory that individuals should evolve the ability to accurately assess a potential rival's fighting ability given the importance of the signalling of strength in conflict resolution (Parker, 1974). The percentage variance shared between perceived strength and actual upper body lifting strength is twice that of handgrip strength, a well-established measure of strength in the literature (50% versus 24%; Sell et al., 2009). Second, controlling for the potential influence of

masculinity and attractiveness did not alter our conclusions, suggesting that the relationship between perceived strength and ejaculate quality is unlikely to be due to effects from other masculine/attractive traits. It would, however, be interesting to replicate the negative relationship between strength and ejaculate quality using a gold standard, composite measure of actual upper body lifting strength (e.g. Sell et al., 2009) in future studies.

Collectively, our results show that despite the mating success accrued through female choice, the evolution of male strength in humans may be constrained by potential costs to postmating ejaculate performance. Future studies to identify the potential mechanisms (e.g. hormonal) and/or the nutritional resources involved in the trade-off between strength and ejaculate quality will be fruitful for furthering our understanding of the evolution of male strength.

Acknowledgments

The study is supported by the ARC Centre of Excellence in Cognition and its Disorders (CE110001021), ARC Professorial Fellowships to L.W.S. (DP110104594) and G.R. (DP0877379), and an ARC Discovery Outstanding Researcher Award to G.R. (DP130102300).

References

- Aitken, R. J., Koopman, P., & Lewis, S. E. M. (2004). Seeds of concern. *Nature*, 432, 48–52.
doi:10.1038/432048a
- Andersson, M. (1994). *Sexual Selection*. New Jersey, NJ: Princeton University Press.
- Archer, J. (1988). *The Behavioural Biology of Aggression*. Cambridge, U.K.: Cambridge University Press.

- Berglund, A., Bisazza, A., & Pilastro, A. (1996). Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society*, 58, 385–399. doi:10.1006/bijl.1996.0043
- Borgia, G. (1979). Sexual selection and the evolution of mating systems. In M. S. Blum & N. A. Blum (Eds.), *Sexual Selection and Reproductive Competition in Insects* (pp. 19–80). New York, NY: Academic Press.
- Chandler, J. J., & Paolacci, G. (2017). Lie for a dime: When most prescreening responses are honest but most study participants are impostors. *Social Psychological and Personality Science*, 8, 500–508. doi:10.1177/1948550617698203
- Darwin, C. R. (1871). *The Descent of Man and Selection in Relation to Sex*. London, U.K.: John Murray.
- Eberhard, W. G. (1996). *Female Control: Sexual Selection by Cryptic Female Choice*, Princeton, N.J.: Princeton University Press.
- Elia, M. (1992). Energy expenditure to metabolic rate. In J. M. McKinney & H. N. Tucker (Eds.), *Energy Metabolism: Tissue Determinants and Cellular Corollaries* (pp. 19–49). New York, NY: Raven Press.
- Fink, B., Neave, N., & Seydel, H. (2007). Male facial appearance signals physical strength to women. *American Journal of Human Biology*, 19, 82–87. doi:10.1002/ajhb.20583
- Foo, Y. Z., Simmons, L. W., & Rhodes, G. (2017). Predictors of facial attractiveness and health in humans. *Scientific Reports*, 7, 39731. doi:10.1038/srep39731
- Fry, C. L. (2006). Juvenile hormone mediates a trade-off between primary and secondary sexual traits in stalk-eyed flies. *Evolution and Development*, 8, 191–201. doi:10.1111/j.1525-142X.2006.00089.x
- Gage, M. J. G. & Cook, P. A. (1994). Sperm size or numbers? Effects of nutritional stress upon eupyrene and apyrene sperm production strategies in the moth *Plodia*

- interpunctella* (Lepidoptera: Pyralidae). *Functional Ecology*, 8, 594–599.
doi:10.2307/2389920
- Gallup, A. C., White, D. D., & Gallup, G. G. Jr. (2007). Handgrip strength predicts body morphology, aggression, and sexual behavior in male college students. *Evolution and Human Behavior*, 28, 423–429. doi:10.1016/j.evolhumbehav.2007.07.001
- Hardy, I. C. W. & Briffa, M. (Eds.) (2013). *Animal Contests*. Cambridge, U.K.: Cambridge University Press.
- Herbst, K. L. & Bhasin, S. (2004). Testosterone action on skeletal muscle. *Current Opinion in Clinical Nutrition & Metabolic Care*, 7, 271–277.
- Hill, A. K., Hunt, J., Welling, L. L. M., Cárdenas, R. A., Rotella, M. A., Wheatley, J. R., et al. (2013). Quantifying the strength and form of sexual selection on men's traits. *Evolution and Human Behavior*, 34, 334–341.
doi:10.1016/j.evolhumbehav.2013.05.004
- Hönekopp, J., Rudolph, U., Beier, L., Liebert, A., & Müller, C. (2007). Physical attractiveness of face and body as indicators of physical fitness in men. *Evolution and Human Behavior*, 28, 106–111. doi:10.1016/j.evolhumbehav.2006.09.001
- Joseph, P. J., Sasson, D. A., Emberts, Z. & Miller, C. W. (2018). Males that drop a sexually selected weapon grow larger testes. *Evolution*, 72, 113–122. doi:10.1111/evo.13387
- Kilgallon, S. J. & Simmons, L. W. (2005) Image content influences men's semen quality. *Biology Letters*, 1, 253–255. doi:10.1098/rsbl.2005.0324
- Kirkpatrick, M. & Ryan, M. J. (1991). The evolution of mating preferences and the paradox of the lek. *Nature*, 350, 33–38. doi:10.1038/350033a0
- Kvarnemo, C. & Simmons, L. W. (2013). Polyandry as a mediator of sexual selection before and after mating. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368, 20120042. doi:10.1098/rstb.2012.0042

- Lassek, W. & Gaulin, S. (2009). Costs and benefits of fat-free muscle mass in men: Relationship to mating success, dietary requirements and natural immunity. *Evolution and Human Behavior*, 30, 322–328. doi:10.1016/j.evolhumbehav.2009.04.002
- Leivers, S., Rhodes, G., & Simmons, L. W. (2014). Sperm competition in humans: Mate guarding behavior negatively correlates with ejaculate quality. *PLoS ONE*, 9, e108099. doi:10.1371/journal.pone.0108099
- Little, A. C., Třebický, V., Havlíček, J., Roberts, S. C., & Kleisner, K. (2015). Human perception of fighting ability: facial cues predict winners and losers in mixed martial arts fights. *Behavioral Ecology*, 26, 1470–1475. doi:10.1093/beheco/arv089
- Moczek, A. P. & Nijhout, H. F. (2004). Trade-offs during the development of primary and secondary sexual traits in a horned beetle. *American Naturalist*, 163, 184–191. doi:10.1086/381741
- Montgomery, D.C. & Peck, E.A. (1992) *Introduction to Linear Regression Analysis*. New York, NY: Wiley.
- Mueller, U. & Mazur, A. (1997). Facial dominance in *Homo sapiens* as honest signaling of male quality. *Behavioral Ecology*, 8, 569–579. doi:10.1093/beheco/8.5.569
- O’Hara, R. B. & Kotze, D. J. (2010). Do not log-transform count data. *Methods in Ecology and Evolution*, 1, 118–122. doi:10.1111/j.2041-210X.2010.00021.x
- Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biological Reviews*, 45, 525–567. doi:10.1111/j.1469-185X.1970.tb01176.x
- Parker, G. A. (1974). Assessment strategy and evolution of fighting behavior. *Journal of Theoretical Biology*, 47, 223–243. doi:10.1016/0022-5193(74)90111-8
- Parker, G. A., Lessells, C. M., & Simmons, L. W. (2013). Sperm competition games: A general model for pre-copulatory male-male competition. *Evolution*, 67, 95–109. doi:10.1111/j.1558-5646.2012.01741.x

- Peters, M., Rhodes, G., & Simmons, L. W. (2008). Does attractiveness in men provide clues to semen quality? *Journal of Evolutionary Biology*, 21, 572–579. doi:10.1111/j.1420-9101.2007.01477.x
- Peters, M., Simmons, L. W., & Rhodes, G. (2008). Testosterone is associated with mating success but not attractiveness or masculinity in human males. *Animal Behaviour*, 76, 297–303. doi:10.1016/j.anbehav.2008.02.008
- Puts, D. A. (2010). Beauty and the beast: Mechanisms of sexual selection in humans. *Evolution and Human Behavior*, 31, 157–175. doi:10.1016/j.evolhumbehav.2010.02.005
- Rhodes, G. (2006). The evolutionary psychology of facial beauty. *Annual Review of Psychology*, 57, 199–226. doi:10.1146/annurev.psych.57.102904.190208
- Safarinejad, M. R., Azma, K., & Kolahi, A. A. (2009). The effects of intensive, long-term treadmill running on reproductive hormones, hypothalamus-pituitary-testis axis, and semen quality: a randomized controlled study. *Journal of Endocrinology*, 200, 259–271. doi:10.1677/JOE-08-0477
- Sanjak, J. S., Sidorenko, J., Robinson, M. R., Thornton, K. R., & Visscher, P. M. (2017). Evidence of directional and stabilizing selection in contemporary humans. *Proceedings of the National Academy of Sciences*, 201707227. doi:10.1073/pnas.1707227114
- Sell, A., Cosmides, L., Tooby, J., Sznycer, D., von Rueden, C., & Gurven, M. (2009). Human adaptations for the visual assessment of strength and fighting ability from the body and face. *Proceedings of the Royal Society of London B: Biological Sciences*, 276, 575–584. doi:10.1098/rspb.2008.1177
- Sell, A., Hone, L. S. E., & Pound, N. (2012). The importance of physical strength to human males. *Human Nature*, 23, 30–44. doi:10.1007/s12110-012-9131-2

- Sell, A., Lukazsweski, A. W., & Townsley, M. (2017). Cues of upper body strength account for most of the variance in men's bodily attractiveness. *Proceedings of the Royal Society of London B: Biological Sciences*, 284, 20171819. doi:10.1098/rspb.2017.1819
- Simmons, L. W. & Emlen, D. J. (2006). Evolutionary trade-off between weapons and testes. *Proceedings of the National Academy of Sciences*, 103, 16346–16351. doi:10.1073/pnas.0603474103
- Simmons, L. W., Lüpold, L., & Fitzpatrick, J. L. (2017). Evolutionary trade-off between secondary sexual traits and ejaculates. *Trends in Ecology and Evolution*, 32, 964–976. doi:10.1016/j.tree.2017.09.011
- Simmons, L. W., Peters, M., & Rhodes, G. (2011). Low-pitched voices are perceived as masculine and attractive but do they predict semen quality in men? *PLoS ONE*, 6, e29271. doi:0.1371/journal.pone.0029271
- Soler, C., Kekäläinen, J., Núñez, M., Sancho, M., Álvarez, J. G., Núñez, J., et al. (2014). Male facial attractiveness and masculinity may provide sex- and culture-independent cues to semen quality. *Journal of Evolutionary Biology*, 27, 1930–1938. doi:10.1111/jeb.12446
- Somjee, U., Miller, C. W., Tatarnic, N. J., & Simmons, L. W. (2018). Experimental manipulation reveals a trade-off between weapons and testes. *Journal of Evolutionary Biology*, 31, 57–65. doi:10.1111/jeb.13193
- Stearns, S. C. (1977) The evolution of life history traits: A critique of the theory and a review of the data. *Annual Review of Ecology, Evolution, and Systematics*, 8, 145–171. doi:10.1146/annurev.es.08.110177.001045
- Taylor, P. D., & Williams, G. C. (1982). The lek paradox is not resolved. *Theoretical Population Biology*, 22, 392–409. doi:10.1016/0040-5809(82)90052-1

von Rueden, C., Gurven, M., & Kaplan, H. (2008). The multiple dimensions of male social status in an Amazonian society. *Evolution and Human Behavior*, 29, 402–415.

doi:10.1016/j.evolhumbehav.2008.05.001

World Health Organization, Task Force on Methods for the Regulation of Male Fertility.

(1996). Contraceptive efficacy of testosterone-induced azoospermia and oligozoospermia in normal men. *Fertility and Sterility*, 65, 821–829.

doi:10.1016/S0015-0282(16)58221-1

World Health Organization (1999). *WHO Laboratory Manual for the Examination of Human Semen and Sperm-Cervical Mucus Interaction*, 4th edn. Cambridge, U.K.: Cambridge University Press.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14.

doi:10.1111/j.2041-210X.2009.00001.x

Table 1

Cronbach's alpha for physical strength ratings by sex of rater and image type

Image type	Sex of raters	No. of raters	Cronbach's alpha
Full length	Female	12	0.87
	Male	16	0.79
Body only	Female	13	0.89
	Male	21	0.92
Face only	Female	12	0.71
	Male	17	0.69

Table 2

Means, SDs and factor loadings for perceived physical strength principal components

analyses

	Mean $\pm$ SD	<i>N</i>	PC1
Face-only ratings	4.39 $\pm$ 0.53	118	0.72
Body-only ratings	3.62 $\pm$ 0.72	118	0.93
Full-length ratings	3.99 $\pm$ 0.62	118	0.95
Eigenvalue			2.30
% Variance explained			76.57

Table 3

Descriptive statistics

	<i>N</i>	Mean	SD	Skewness	Kurtosis
Age	113	22.5	4.9	1.05	−0.20
Perceived strength	118	0.0	1.0	−0.45	0.12
Attractiveness	117	0.0	1.0	−0.18	−0.14
Masculinity	117	0.0	1.0	−0.27	−0.59
Self-reported no. of sex partners	113	5.8	6.3	1.81	3.18
Sperm concentration (10 ⁶ sperms/ml)	108	90.8	62.2	1.03	0.45
Sperm motility (%)	107	61.7	17.7	−0.96	1.37
Sperm morphology (%)	114	35.2	8.4	0.17	0.17

Table 4

Zero-order Pearson product-moment correlations, *P* values and *dfs*, between age, perceived strength, attractiveness, masculinity, mating success and ejaculate quality

	Age	Perceived strength	Attractiveness	Masculinity	No. of sex partners	Sperm concentration	Sperm motility	Sperm morphology
Age		0.28	−0.07	0.37	0.54	0.14	0.17	0.06
		0.003	0.441	0.000	0.000	0.148	0.089	0.537
		111	110	110	111	106	105	110
Perceived strength			0.56	0.86	0.29	−0.25	−0.02	−0.02
			0.000	0.000	0.002	0.010	0.841	0.830
			115	115	111	106	105	112
Attractiveness				0.67	0.12	−0.10	0.03	−0.03
				0.000	0.214	0.296	0.748	0.736
				115	110	105	104	111
Masculinity					0.34	−0.13	−0.01	0.02
					0.000	0.186	0.930	0.826
					110	105	104	111
No. sex partners						−0.08	0.14	0.04
						0.395	0.141	0.681
						106	105	110
Sperm concentration							0.23	0.13
							0.017	0.197
							101	105
Sperm motility								0.16
								0.095
								104
Sperm morphology								

Table 5

Multiple regression models testing masculinity as a mediator of the relationship between perceived strength and attractiveness

Outcome	Predictor	<i>B</i>	SE	<i>P</i>	95% CI lower bound	95% CI upper bound
Model 1						
Attractiveness	Perceived strength	0.64	0.08	0.000	0.48	0.80
	Age	−0.05	0.02	0.002	−0.08	−0.02
Model 2						
Masculinity	Perceived strength	0.81	0.05	0.000	0.71	0.91
	Age	0.03	0.01	0.004	0.01	0.05
Model 3						
Attractiveness	Masculinity	0.93	0.13	0.000	0.68	1.19
	Perceived strength	−0.12	0.13	0.356	−0.36	0.13
	Age	−0.08	0.01	0.000	−0.11	−0.05

CI: confidence interval.