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

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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.

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

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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; Somjee, Miller, Tatarnic, & Simmons, 2018; Simmons & Emlen, 2006). 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 autonomy, 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.

METHODS

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.

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).

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 &