Sperm Competition in Humans

Samantha Leivers
BSc Psychology, MSc Animal Behaviour

Centre for Evolutionary Biology
School of Animal Biology
The University of Western Australia

ARC Centre of Excellence in Cognition and its Disorders
School of Psychology
The University of Western Australia

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Summary

In species where females mate with multiple males, sperm competition may occur whereby the sperm of two or more males compete on a post copulatory level to fertilise the ova of a single female. Selection via sperm competition has given rise to the evolution of adaptations that affect a male’s chances of paternity when a female has mated, or is likely to mate, with another male. These adaptations improve a male's chances of paternity by i) avoiding or preventing sperm competition from occurring (defensive tactics) and ii) by engaging in sperm competition (offensive tactics). Adaptations to sperm competition can be morphological, behavioural or physiological. The aim of this thesis was to investigate the role that sperm competition has played in human evolution, particularly the evolution of defensive psychological adaptations and offensive physiological adaptations.

In Chapter 1, I examine the current evidence for morphological, behavioural and physiological adaptations for sperm competition in non-human animals and consider what this tells us about sperm competition in humans. The available evidence suggests that humans have primarily evolved defensive adaptations in response to the risk of sperm competition but that considerable further research investigating offensive adaptations to sperm competition in humans must be conducted before firm conclusions can be drawn.

In Chapter 2, I investigate the evolution of psychological adaptations in humans and provide the first known evidence that men can show accuracy in their judgements of faithfulness. This accuracy is dependent on the experimental task and stimuli used. Further investigation showed that priming men to an environment depicting sexual competition from rival males does not improve men’s accuracy in judgements of faithfulness.

In Chapters 3 and 4, I examine the evolution of physiological adaptations to sperm competition in men by investigating the factors that influence ejaculate quality and how these relate to sperm competition theory. Sperm competition theory predicts that males will increase ejaculate investment when mating with attractive females, although increasing evidence suggests that the quality of the male himself can also influence ejaculate quality (phenotype-linked fertility hypothesis). In Chapter 3, I show that ejaculate quality increases with a composite
measure of male mate value, but only when men view images of highly attractive women.

In Chapter 4, I investigate the extent to which men covary their performance of defensive and offensive sperm competition tactics. If a male's defensive tactics are highly successful at preventing or avoiding sperm competition, one would expect reduced investment in offensive adaptations for the engagement in sperm competition, and vice versa. In this study, I show that men in committed heterosexual relationships who perform more mate guarding behaviours produce ejaculates of poorer quality. These findings suggest that men covary their investment in defensive adaptations that function to avoid or prevent sperm competitions and offensive adaptations that function to engage in sperm competition.

Together, these studies examine the role that sperm competition has played through human evolution. I contribute to the literature that suggests that men have evolved psychological adaptations that function to avoid sperm competition by showing that men display some accuracy in their judgements of female faithfulness. Furthermore, I add to a growing literature that variation in men's ejaculate quality can, in part, be attributed to sperm competition risk.
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“There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.”

Charles Darwin, The Origin of Species

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Publications arising from this thesis

This thesis is submitted as a series of manuscripts, which have been submitted to or published in international journals.


All of these manuscripts have my supervisors Leigh Simmons and Gillian Rhodes as co-authors, except for Chapter 1 where Leigh Simmons acts as co-author. For the general introduction (Chapter 1), I was the first author and was responsible for the literature review and writing. Leigh Simmons helped plan the manuscript and contributed to the literature review and writing. For the manuscripts describing new experimental data (Chapters 2-4), I was the lead author, being responsible for experimental design, data collection, statistical analysis and writing. Leigh Simmons and Gillian Rhodes guided the experimental designs, contributed with ideas for the analysis of the data and reviewed the writing of these chapters. The contributions of each author to the manuscript are as follows: I SL= 75%, LWS= 25%. II SL= 75%, LWS= 10%, GR= 15%. III SL= 75%, LWS= 15%, GR= 10%. IV SL= 75%, LWS= 15%, GR= 10%.

All authors have given permission for all manuscripts to be included in this thesis.

Samantha Leivers
Candidate

Leigh W Simmons
Coordinating supervisor

Gillian Rhodes
Co-supervisor
In the 1871 publication, ‘The Descent of Man and Selection in Relation to Sex’, Charles Darwin introduced biologists to the concept of sexual selection whereby traits are selected for, not due to their ability to aid individual survival, but due to their ability to provide access to and result in matings. A century later, Geoffrey Parker’s research with yellow dung flies encouraged biologists to consider how sexual selection might act on a post-copulatory level. Parker (1970) recognised that sexual selection is unlikely to finish once copulation has occurred as females of many taxa often continue to mate with multiple males despite receiving enough sperm to fertilise all ova in one mating. This polyandrous mating provides the opportunity for sperm from multiple males to occupy the reproductive arena simultaneously, which may lead to ‘sperm competition’— the post-copulatory competition between the sperm of two or more males to fertilise the ova of a given female. Analogous to the evolution of traits designed to assist in pre-copulatory mating success, selection through sperm competition has given rise to the evolution of adaptations that affect a male’s chances of paternity when a female has mated, or is likely to mate, polyandrously. These adaptations improve a male’s chances of paternity in two ways— either in the avoidance or prevention of sperm competition altogether, or in the engagement in sperm competition by improving a male’s offensive or defensive sperm competitiveness. Adaptations to sperm competition can be morphological, behavioural or physiological.

Whether sperm competition has acted as a selective pressure in human evolution continues to be a hotly debated topic. The aim of this thesis was to investigate the role sperm competition might play in human evolution. More specifically, I have investigated the evolution of psychological tactics for the avoidance of sperm competition and physiological adaptations for the engagement in sperm competitions in humans. The thesis is composed of four distinct chapters that are introduced here.

In Chapter 1, I provide a thorough review of the current literature investigating sperm competition in humans. I examine evidence for morphological, behavioural and physiological adaptations to sperm competition in non-human animals and consider what this can and cannot tell us about sperm competition in humans. I highlight gaps in knowledge and directions for future research that
provide the basis of the experimental chapters that follow. Chapter 1 acts as the general introduction to the thesis.

Chapter 2 focuses on investigating psychological adaptations in men that are thought to act in the avoidance of sperm competition. One adaptation that men may have evolved is to avoid sperm competition by correctly identifying women who are likely to expose them to sperm competition threat. Trait judgement research has shown that men can make judgements of faithfulness from limited sensory information within short periods of time. However, the evidence that these judgements are accurate is mixed and direct comparisons between ratings of faithfulness and actual faithful behaviour are scarce. Furthermore, the visual cues that men may use to make these faithfulness judgements have not been well studied. In Chapter 2, I show that men are able to show accuracy in their judgements of faithfulness but that the type of experimental task— and the images used in this task— influence accuracy. Furthermore, I discuss the influence of attractiveness and trustworthiness judgements on the accuracy of faithfulness judgements. Finally, I show that men’s accuracy of faithfulness judgements are not influenced by being primed to alternative sexual environments, including environments depicting sperm competition. This chapter provides novel evidence that men can make accurate judgements of female faithfulness, which may aid them in avoiding and preventing sperm competition.

Chapters 3 and 4 focus on investigating men’s physiological adaptations for the engagement in sperm competition, specifically whether variation in men’s ejaculate quality can be attributed to sperm competition risk. Many non-human species show the ability to adjust their ejaculate based on the level of sperm competition during any one mating. Recent findings— particularly from in vitro fertilisation research— suggest that men have the ability to adjust the quality of their ejaculate, but what factors influence this adjustment, and how these factors relate to sperm competition, are not well studied.

In Chapter 3, I explore the influence of female attractiveness and male quality on ejaculate quality. The influence of female attractiveness on ejaculation in non-human species is well known, with the males of many species increasing their ejaculate quality when mating with attractive females. In addition, increasing evidence suggests that the quality of the male himself can also influence ejaculate quality (phenotype-linked fertility hypothesis), with some evidence that male
quality and female attractiveness may interact in determining ejaculate quality. In Chapter 3, I show an interaction between female attractiveness and male quality that predicts ejaculate quality in men, and that this effect is neither fully explained by the phenotype-linked fertility hypothesis or sperm competition theory. These results suggest that, although men’s ejaculate quality can— in part— be attributed to sperm competition risk, this relationship is influenced by intrinsic individual differences in the male.

In Chapter 4, I investigate the extent to which men’s engagement in and avoidance of sperm competition covary. Mate guarding functions in the avoidance of sperm competition while ejaculate quality functions in the engagement in sperm competition when a female has mated— or her mate perceives her to have mated— with a rival male. If a male’s avoidance tactics are highly successful at preventing sperm competition, one would expect reduced investment in adaptations for the engagement in sperm competition, and vice versa. This association between tactics that function to avoid and those that function to engage in sperm competition has not been well studied and those studies that have investigated the relationship often focus on the use of behavioural tactics alone, despite the fact that many tactics for the engagement in sperm competition are physiological. In Chapter 4, I show a negative association between investment in mate guarding behaviour and ejaculate quality in men, with those men who perform more mate guarding behaviours producing ejaculates of poorer quality. These results suggest that men’s investment for tactics for the avoidance of sperm competition covary with their investment in tactics for the engagement in sperm competition.

In the Epilogue, I collate findings from all four chapters, consider the extent to which they shed light on the debate over whether sperm competition has acted as a selective pressure through human evolution, and provide directions for future research.
CHAPTER ONE

Human sperm competition: Playing a defensive strategy
1.1. Abstract

Sperm competition is the competition between the sperm of two or more males to fertilise the ova of a single female. Over the past few decades, the extent to which sperm competition has acted as a selective pressure throughout human evolution has been hotly contested. This review aims to assess the current evidence for sperm competition in humans, the limitations of that evidence, and directions for future research. I conclude that humans have primarily evolved defensive adaptations in response to the risk of sperm competition. Thus men exhibit behaviours designed to anticipate and address their partner's infidelity, the success of which may have relaxed selection on physiological and morphological adaptations to tackle sperm competition offensively. However, the extent to which humans can perform offensive tactics has been sorely understudied and requires considerable further research before firm conclusions can be drawn.
1.2. Introduction

The females from many animal taxa, including mammals (Møller & Birkhead 1989), fish (Coleman & Jones 2011; Jones et al. 2001), insects (Simmons 2001) and birds (Birkhead & Møller 1992), have been shown to mate with multiple males during a single reproductive cycle. Even females of socially monogamous species frequently mate with males other than their pair-bonded partner, so called extra-pair copulations. Mating with two or more males within any one reproductive cycle can lead to sperm competition — the competition between the sperm of two or more males to fertilise the ova of a single female (Parker 1970). Sperm competition has favoured the evolution of behavioural, physiological and morphological adaptations that increase a male’s chances of obtaining paternity through either defensive or offensive mechanisms. As a socially monogamous species in which extra-pair copulations have been recorded (Baker & Bellis 1995; Johnson et al. 2001; Simmons et al. 2004), humans may also be subject to sperm competition, although the extent to which it has acted as a selective pressure during our evolutionary history remains controversial (Dixson 2009; Shackelford et al. 2002; Simmons et al. 2004). This review aims to assess the current state of research into adaptations to sperm competition in human populations. I begin with a brief overview of how sperm competition has influenced the evolution of reproductive behaviour, morphology and physiology in non-human animals, before considering these same categories of adaptation in humans. Limitations in the literature are identified and directions for future research discussed.

1.3. Adaptations to sperm competition in non-human animals

Adaptations to selection from sperm competition have been recognised in many animal taxa, including birds (Birkhead 1998a; Birkhead & Møller 1992, 1995), insects (Parker 1970; Simmons 2001), fish (Stockley et al. 1997; Taborsky 1998) and mammals (Dixson & Anderson 2004; Møller & Birkhead 1989; Stockley 2004). These adaptations can be defensive (functioning to prevent females remating with
rival males) or offensive (functioning to increase a male’s paternity success when females have mated with a rival male).

1.3.1. Defensive adaptations

Mate guarding

Mate guarding is the physical guarding of a female in order to deny rival males the opportunity to mate with her and is one of the mostly commonly used defensive strategies observed in mammals (Nichols et al. 2010), birds (Hoi et al. 2011), insects (Simmons 2001) and fish (Alonzo & Warner 2000). Mate guarding often involves the male staying in close proximity to the female, and can be achieved by prolonging copulation (Garcia-Gonzalez & Gomendio 2004) or by the use of post-copulatory mounting (Muse & Ono 1996; Sato & Kohama 2007). Mate guarding is generally performed when females are at their most fertile (Birkhead 1998b) and experimentally removing males from their mate during this period results in the female engaging in more extra-pair copulations with rival males, which in turn results in increased rates of extra-pair paternity (Chuang-Dobbs et al. 2001; Westneat & Webster 1994).

Copulatory plugs

Copulatory plugs are male-derived structures that are generally formed by substances secreted by the male reproductive accessory glands. Copulatory plugs can physically obstruct the reproductive tract of the female with whom the male has copulated (Parker 1970) and are present in a number of taxa including mammals (Dean 2013; Jia et al. 2002; Martan & Shepherd 1976; Michener 1984), reptiles (Moreira & Birkhead 2004; Shine et al. 2000), insects and spiders (Parker 1970; Simmons 2001; Uhl & Busch 2009). Nonetheless, the function of copulatory plugs remains somewhat inconclusive. Whilst some researchers argue that they may have evolved to reduce sperm leakage after insemination (Jia et al. 2002; Michener 1984), or to facilitate sperm survival within the female reproductive tract (Settlage & Hendrickx 1974), other evidence suggests that copulatory plugs may act as a defensive sperm competition tactic by preventing female re-mating (Martan & Shepherd 1976; Uhl & Busch 2009). Male guinea pigs, *Cavia porcellus*, are unable to mate with a previously mated female when a copulatory plug is
present in her reproductive tract (Martan & Shepherd 1976). Among species of butterfly, the size of the copulatory plug varies greatly, with the lowest female mating frequencies occurring among species with the largest copulatory plugs (Simmons 2001). As might be expected, in many species where copulatory plugs are used, males have evolved counter adaptations to remove the plugs of previous males (Fromhage 2012; Wallach & Hart 1983).

**Anti-aphrodisiac substances and seminal fluids**

Anti-aphrodisiac pheromones are commonly found among species of moth and butterfly and function either by repelling rival males (Lecomte et al. 1998) or by making the female less attractive to rival males after copulation (Andersson et al. 2003; Lecomte et al. 1998). In some species, anti-aphrodisiac pheromones are short lived, whilst other species produce pheromones that can last for the entire lifespan of the female, so that the female mates only once during her reproductive life, essentially eliminating sperm competition altogether (Simmons 2001).

Ejaculates are typically composed of both sperm and seminal fluid produced by the male reproductive accessory glands. It was traditionally believed that seminal fluids existed to provide a protective and nurturing environment for sperm (Mann & Lutwak-Mann 1981). However, it has now been widely accepted that proteins within the seminal fluid can manipulate female behaviour, physiology and longevity in a manner that reduces sperm competition from rival males and increases a male’s paternity assurance (Simmons & Fitzpatrick 2012). Seminal fluid proteins are particularly well researched in the fruit fly, *Drosophila melanogaster* (Wolfner 2002). Proteins are produced by the male accessory gland and are inseminated into the female within the seminal fluid. These seminal fluid proteins decrease the inseminated female’s attractiveness to rival males, reduce her receptivity to future matings, encourage the storage and use of sperm from the copulating male, and induce immediate oviposition. By decreasing a female’s attractiveness and reducing her receptivity to rival males, a male can avoid competition with rival sperm and ensure that his own sperm are used to fertilise the female’s eggs, thus increasing his chance of paternity (Scott 1986; Tram & Wolfner 1998). Seminal fluid proteins that enhance male fitness in these flies have been shown to impose significant costs on females by decreasing their lifespan (for a review, see Wolfner 1997).
1.3.2. Offensive adaptations

*In-pair copulations*

Whilst a male will regularly copulate with his mate, these in-pair copulations may increase in frequency as the risk of sperm competition increases. For example, male Montagu’s harriers, *Circus pygargus*, have been shown to increase the frequency with which they copulate with their mate upon the presentation of a decoy rival male (Mougeot et al. 2001), and male dung beetles, *Onthophagus taurus*, will increase their copulation frequency with their breeding partner after encountering a sneaker male in their breeding tunnel (Hunt & Simmons 2002). In-pair copulation frequency has also been found to increase after an expected or observed female infidelity in a number of socially monogamous bird species (e.g. Bailey et al. 1978; Barash 1977; McKinney et al. 1983). By increasing his number of copulations, the male can ensure that his sperm are consistently present or more abundant in his mate’s reproductive tract and therefore increase his chances of paternity when she fertilises her ova.

*Testes size, sperm quantity and sperm quality*

Theoretical modelling predicts evolutionary changes in male expenditure on the ejaculate in response to the strength of selection arising from sperm competition (Parker & Pizzari 2010). In accord with theoretical prediction, for many species of non-human animals the strength of selection from sperm competition is positively associated with male investment in the ejaculate. High sperm numbers are likely to be beneficial when sperm competition is intense; increasing the number and/or quality of sperm inseminated can increase paternity success, especially when males engage in sperm competition (Birkhead et al. 1999; Boschetto et al. 2011; Gage & Morrow 2003). Thus, polyandrous species, those species that regularly encounter sperm competition, tend to produce larger ejaculates with a greater concentration of sperm, greater sperm motility, and sperm with fewer morphological defects (Møller 1991; Simmons & Fitzpatrick 2012). Laboratory based studies have shown that ejaculate quality can evolve rapidly when selection from sperm competition is artificially increased, with house mice, *Mus domesticus*, evolving better quality ejaculates after only 12 generations of selection from sperm competition (Firman & Simmons 2011).
As the numbers of sperm per ejaculate increase, the amount of testicular tissue required to produce sperm must also increase. As such, one would expect testes size (relative to body size) of a species to be indicative of the strength of selection from sperm competition in their mating system, with polyandrous species evolving larger testes than monogamous species. There is strong evidence for this association across almost all animal taxa (Simmons & Fitzpatrick 2012), and field studies have shown that testes size can even differ within species according to variation in the strength of selection from sperm competition found among populations (Dziminski et al. 2010; Firman & Simmons 2008).

Strategic ejaculate adjustment to sperm competition cues

Adjusting the quality and quantity of sperm allocated during individual mating events is also a strategy that males implement in response to the anticipated level of sperm competition (Simmons & Fitzpatrick 2012; Wedell et al. 2002). Animals from a variety of taxa have been found to allocate a greater quantity of sperm (delBarco-Trillo 2011; Kelly & Jennions 2011) or better quality sperm (Pizzari et al. 2003; Simmons et al. 2007a; Snook 2005; Thomas & Simmons 2007) in response to cues indicating a high risk that their female will mate with a rival male. Recent meta-analyses of studies on so called "strategic ejaculation" by male insects, mammals, crustaceans, fish and birds have found a general effect of sperm competition risk on allocation to the ejaculate, and that this effect is homogeneous across taxonomic groups (delBarco-Trillo 2011; Kelly & Jennions 2011).

Males can assess the risk of a female mating with a rival male (and thus the probability that they will encounter sperm competition) based on a number of environmental cues. At high population densities females are more likely to remate, producing a greater risk of sperm competition compared with low-density populations (Gage 1995; Parker 1970), and males show an increased investment in ejaculate production as population density increases (Gage 1995; Hoi et al. 2011). Males have also been shown to invest more in their ejaculates when exposed to environmental cues of rival male presence, such as olfactory, visual, auditory and tactile cues (Bretman et al. 2011; delBarco-Trillo & Ferkin 2004).

Female attractiveness can also provide a cue to risk of sperm competition (Kelly & Jennions 2011; Reinhold et al. 2002). Although males were originally
thought to have an almost limitless supply of sperm (Dawkins 1976) and therefore to allocate as much sperm to as many females as possible, research has now shown that sperm can be energetically expensive to manufacture (Olsson et al. 1997). Due to the costs of sperm production, males must sometimes be choosy of their mates in order to gain the best fitness returns for their reproductive investment (Wedell et al. 2002). In a variety of taxa, males have been shown to increase their expenditure on the ejaculate when mating with attractive females (Cornwallis & Birkhead 2007b; Kelly & Jennions 2011; Wedell et al. 2002). This effect may be explained by males making a greater investment to sire the offspring of a female with greater reproductive value, as attractiveness can be an indicator of a female’s fecundity (Cornwallis & Birkhead 2007b; Lupold et al. 2011). However, increased ejaculate investment with attractive females could also arise because attractive females are more likely to attract additional male suitors and thereby represent a greater risk of sperm competition (Cornwallis & Birkhead 2007b; Kelly & Jennions 2011; Wedell et al. 2002).

Evidence is now emerging that a male’s own quality can also play a role in determining his ejaculate expenditure. Females generally invest more in producing offspring and, as such, they have evolved to be the choosier sex, mating with the highest quality males available in order to improve the quality of their offspring (Trivers 1972). Female mate choice has led to the evolution of attractive secondary sexual traits in males that provide honest indicators of male quality (Andersson, 1994). Male mate value can also be based on social factors within group-living species, such as dominance or status (Berglund et al. 1996; Pizzari et al. 2002). High status males are preferred as both short and long term sexual partners (Clutton-Brock & McAuliffe 2009; Fisher & Cockburn 2006; Huck & Banks 1982), providing them with a greater opportunity to mate with multiple females. Males who have access to multiple females due to their high value, allocate sperm prudently between females to ensure the best reproductive returns, investing more in attractive females (Cornwallis & Birkhead 2007b; Cornwallis & O’Connor 2009). Low value males are much less likely to be chosen as a mate and their mating opportunities are constrained by the presence of dominant males (Wilson et al. 2009). Subordinate males might therefore be expected to invest fully into each of their limited mating opportunities, regardless of female attractiveness. Feral fowl, *Gallus gallus*, have been found to show this response, with socially
dominant males investing better quality sperm in attractive females whilst subordinate males allocate the same quality of sperm, regardless of female attractiveness (Cornwallis & Birkhead 2007a).

**Male genital morphology**

Male genital morphology is highly variable across taxa (Eberhard 1985). Sperm competition theory argues that these differences have evolved as an adaptation to increase chances of paternity, with species that experience high levels of sperm competition tending to display particularly complex genital morphology (Hosken & Stockley 2004; Simmons 2014). In some species of insect, penis morphology is designed to remove rival sperm from the female’s reproductive tract, or to stimulate the female to use the copulating male's sperm to fertilise their ova (Simmons 2001; Waage 1979). In mammals the length of the baculum (penis bone) is positively correlated with sperm competition risk among rodents, carnivores, and pinnipeds, though not primates or bats (Fitzpatrick et al. 2012; Ramm 2007), and in house mice, baculum shape has been shown to diverge in direct response to experimentally imposed sperm competition (Simmons & Firman 2014). Primate penes, despite their diversity, are often piston-like in shape with the coronal glans wider than the shaft diameter (see Dixson 2009). It has been suggested that this morphology may have evolved to aid the removal of a rival male’s ejaculate by the ‘scooping out’ of rival semen by the coronal ridge (Simmons & Jones 2007). Moreover, penile spines, present in many mammalian species, have been suggested to play a stimulatory role in primates. Stockley (2002) suggests that penile spines may reduce female receptivity to further matings through altering neuroendocrine mechanisms mediating control of sexual behaviour and/or via effects of injury to the female genital tract, thus allowing males with penile spines to reduce the risk of sperm competition.

**Sperm morphology**

Mammalian sperm are typically uniform in structure and consist of a head (containing the genetic material), a mid-piece (containing mitochondria) and a flagellum (Dixson 2009). Despite this relative uniformity, structural differences are found across taxa. Sperm competition may favour the evolutionary divergence in sperm morphology, if sperm traits contribute to competitive fertilisation success.
(Simmons & Fitzpatrick 2012). For example, some rodents have evolved a hooked sperm head, which has been argued to contribute to sperm competitiveness by facilitating the formation of sperm "trains" that move more efficiently through the female's reproductive tract than single sperm (Moore et al. 2002). Sperm trains have been reported to move more efficiently than single sperm in both wood mice, *Apodemus sylvaticus*, and rats, *Rattus norvegicus* (Immler et al. 2007). However, in house mice there is no evidence of improved movement in sperm trains over single sperm and sperm hookedness does not appear to respond to selection from sperm competition (Firman et al. 2011; Immler et al. 2007).

The evidence that sperm competition has shaped other sperm morphological features is similarly mixed (Simmons & Fitzpatrick 2012). For example, there is no evidence of a relationship between relative testes size (a widely used proxy for the level of sperm competition) and sperm length characteristics among mammals (Anderson et al. 2005; Gage & Freckleton 2003). Gage and Freckleton (2003) also reported no association between relative testes size and sperm mid-piece volume although analysis with a larger data set of mammalian species suggests a positive evolutionary association between mid-piece volume and relative testes size (Anderson et al. 2005). This positive association has also been found specifically among primate species (Anderson & Dixson 2002). The mitochondria of the mid-piece is responsible for providing the sperm with the energy to move through the female's reproductive tract towards the ova (Piomboni et al. 2012). Selection from sperm competition may have resulted in species that experience high levels of sperm competition developing larger mid-piece volumes in order to house a greater number of mitochondria to power competitive sperm (Dixson 2009). A recent meta-analysis conducted on 226 mammalian species found that as selection from sperm competition increases, sperm components increase in length in an integrated manner. The increase in sperm length was found to be associated with enhanced swimming velocity, which is thought to be adaptive when competing with rival sperm (Tourmente et al. 2011).
1.3.3. Cryptic female choice

If sperm competition provides the opportunity for males to influence paternity at the post-copulatory level, we might also expect females to have evolved post-copulatory adaptations to bias paternity (Eberhard, 1996). During pre-copulatory sexual selection, females have the ability to influence paternity through actively choosing with whom they mate (Clutton-Brock & McAuliffe 2009). However, in some species, females may be subject to forced extra-pair copulations or may mate polyandrously to gain access to male controlled resources, resulting in a scenario where the female may find benefit from the ability to control paternity. Post-copulatory sexual selection imposed by females is termed cryptic female choice (Eberhard 1996; Thornhill 1983).

Similarly to sperm competition tactics in males, females can use behavioural, morphological and physiological mechanisms to bias paternity toward attractive, or for other reasons preferred males. In gryllid crickets for example, females can control entry of sperm into their sperm storage organs, and do so to bias paternity toward males that are attractive in pre-copulatory courtship (Hall et al. 2010), and against males that are closely related (Bretman et al. 2009; Tuni et al. 2013). In feral fowl, Gallus gallus domesticus, females expel from the cloaca sperm inseminated by subordinate males, thereby preventing those males from fertilizing their eggs (Pizzari & Birkhead 2000). These behaviours essentially afford the female some control over paternity, regardless of sperm competitiveness.

Morphological mechanisms of cryptic female choice can be found in species of waterfowl where females have evolved complex vaginal morphology that prevents males who subject them to forced extra-pair copulations from achieving paternity. In a study of 16 species of waterfowl in which males regularly perform forced extra-pair copulations, Brennan et al. (2007) found that females possessed a number of ‘dead-end’ pouches and spirals within the vaginal tract that are thought to act as anatomical barriers to prevent successful insemination, thus allowing the female some control over the paternity of her offspring.

A potential physiological mechanism of cryptic female choice has been identified in Chinook salmon, Oncorhynchus tshawytscha, whose ovarian fluids appear to influence the motility of sperm (Rosengrave et al. 2008; Rosengrave et
In addition to between-subject variability, individual male sperm-motility traits were also found to vary when exposed to different females’ ovarian fluids. Further research into this mechanism using the guppy, *Poecilia reticulata*, found that females are able to bias paternity of their offspring towards unrelated males because their ovarian fluid reduces the motility of sperm from genetically related males (Gasparini & Pilastro 2011). These findings suggest that ovarian fluid may act as a physiological filter to bias paternity by increasing or decreasing the competitiveness of sperm from different males.

1.4. Has sperm competition acted as a selective pressure in human evolution?

Whether sperm competition has been a selective pressure in human evolution has been a contentious topic within evolutionary biology and evolutionary psychology. Anthropological and paleontological evidence suggests that, whilst polygyny has occurred to a limited degree, social or serial monogamy is the dominant mating system observed in human populations (Brown et al. 2009; Labuda et al. 2010; Marlowe 2004). Mating systems are often correlated with anatomical traits, such as sexual dimorphism in body size, and evidence from hominids suggests that humans are mainly monogamous, with a shift away from polygyny possibly occurring up to 4.4 million years ago (Labuda et al. 2010; Lovejoy et al. 2009; Marlowe 2004; Nelson et al. 2011; Reno et al. 2003). In socially monogamous species, extra-pair copulations by females create the primary context for sperm competition, so the extent to which sperm competition occurred in our evolutionary past would have been dependent on the rates of female sexual infidelity (Shackelford et al. 2005b). Recent theoretical modelling of the evolutionary transition from promiscuity to social monogamy in humans predicts that, whilst women should generally be monogamous, complete sexual fidelity is not an evolutionary stable strategy, with faithfulness levels controlled by a balance between selection for good genes from short-term sexual partners and access to resources from long-term partners (Gavrilets 2012). Furthermore, extra-pair copulation behaviour may also evolve as a means by which females safeguard against male infertility (Hasson & Stone 2009). Both large and small scale surveys
of sexual behaviour generally find that approximately 20% of women report cases of sexual infidelities (Johnson et al. 2001; Simmons et al. 2004). Mate poaching (whereby an individual attempts to engage another individual, already in a committed relationship, into a relationship or brief sexual encounter) is a prevalent mating tactic. Schmitt and Buss (2001) reported that 60% of men admitted to attempting to poach woman for a brief sexual encounter whilst 31% of women admitted to being successfully poached from their committed relationship for a brief sexual encounter. These data show that extra-pair copulations are an integral component of the human mating system, although recorded rates of extra-pair paternity in contemporary societies are low.

Although extra-pair copulations appear relatively common in humans, they can only result in sperm competition if copulations between the in-pair male and rival male occur within a period of time where both male's sperm have the opportunity to fertilise the ova. Survey data suggests that women do have concurrent sexual partnerships, particularly in younger (and thus more reproductively viable) cohorts (Adimora et al. 2002; Howard et al. 1999; Rosenberg et al. 1999; Wellings et al. 1994). There is some evidence for sperm persistence within the female reproductive tract (Hunter 1987; Insler et al. 1980) with sperm believed to remain viable for approximately five days (Barrett & Marshall 1969; Gould et al. 1984; Wilcox et al. 1995). A survey of 2708 women who self-reported having a primary sexual partner found that of the 162 women who reported that their last copulation was an extra-pair copulation, 50 reported that this copulation was within five days of the previous copulation with their primary partner (Bellis & Baker 1990). Thus extra-pair copulations can generate competition among the sperm of different males. Interestingly, these ‘double matings’ show a significant association with probability of conception, suggesting that women may seek extra-pair copulations— and thus instigate sperm competition— when they are more fertile.

In contemporary western societies, pregnancies can be more easily controlled than in our evolutionary past through the use of contraception, so it is likely that our ancestors experienced higher rates of extra-pair paternity through extra-pair copulations than currently occurs. Indeed, evidence from a cross-temporal meta-analysis investigating rates of human extra-pair paternity reported from studies published between 1932 and 1999 suggests that extra-pair paternity
rates have been declining at a rate of between 0.83% and 0.91% per decade, most likely due to the introduction of the oral contraceptive pill in the early 1960s (Voracek et al. 2008). Current estimates have extra-pair paternity rates at a modest 2% (Voracek et al. 2008) and are believed to have been at this rate for at least 400 years in one Western European population (Larmuseau et al. 2013).

Although on average, rates of extra-pair paternity are low, some researchers argue that even relatively infrequent events can act as a strong selective pressure when they occur with some predictability and result in fitness cost (Marczyk & Shackelford 2010). Humans invest in their offspring for a prolonged period so a man who has been cuckolded is likely to suffer significant fitness costs. In addition to the loss of current paternity, a man may have his future mating prospects affected if he has been cuckolded. In a number of human societies, cuckolded men are chastised and lose status and reputation within the community, which can result in further reproductive losses as it hinders a man's future ascension in the social hierarchy and his ability to attract future mates (Buss 2005). Men have been found to display sensitivity to the risk of cuckoldry by showing some accuracy in predicting the paternity of their putative offspring. A survey of 67 paternity studies found that men who have high confidence of paternity have an actual non-paternity rate of approximately 1.7% (close to the average extra-pair paternity rates reported by Voracek et al. 2008). However, men with low confidence of paternity were found to have a non-paternity rate of 29.8% (Anderson 2006). Confidence of paternity can also predict paternal investment, with men having low confidence investing less in their offspring than men secure in their paternity (Anderson et al. 2007a). Such results suggest that sperm competition in human populations has been sufficient to have favoured mechanisms by which men recognize and respond to the risk of cuckoldry.

Shackelford (2003) proposes three separate adaptive problems for human males associated with sperm competition: anticipating, preventing and correcting female infidelity. Anticipating and preventing infidelity can be tackled through defensive sperm competition strategies whilst infidelity is corrected via offensive strategies. I will now examine current evidence for the existence of sperm competition strategies in humans designed to address these three adaptive problems.
1.4.1. Defensive sperm competition strategies in humans

*Anticipating female infidelity*

Research on sexual faithfulness judgements in humans has often overlooked person perception research that has focused specifically on how individuals make judgements about personality traits, such as trustworthiness. People have been shown to make personality judgements from minimal sensory information, such as physical appearance alone (Zebrowitz et al. 1996), and these judgements show high consensus, with observers generally agreeing on the levels of the trait held by the individual being judged (Blackman & Funder 1998). Whether people’s judgements of personality are accurate may have important evolutionary consequences. For example, it would be adaptive to make an accurate judgement of someone’s trustworthiness if misplacing trust in that individual could result in significant fitness costs. The real life accuracy of many personality judgements shows mixed results however. People have been reported to accurately predict male sexual orientation beyond chance when presented with a facial picture for only 50ms (Rule & Ambady 2008), and there is some evidence that those judged as more trustworthy actually are more trustworthy (Wilson & Eckel 2006). However, other research has failed to find predictive relationships between perceived and actual personality traits, including trustworthiness (Efferson & Vogt 2013; Rule et al. 2013).

As a socially monogamous species, extra-pair copulations provide the main context in which sperm competition can occur in humans so having the ability to accurately judge female faithfulness should be adaptive. Men make judgements of faithfulness by analysing their partner’s behaviour (Shackelford & Buss 1997) but they have also been shown to make judgements of faithfulness from limited sensory information (e.g. voice, O’Connor et al., 2011; waist-to-hip ratio, Singh, 2004). Men show high consensus on which women they consider likely to be unfaithful and, as has been found in non-human animals, men appear to judge partner extra-pair copulation risk based on female attractiveness, with a consistent positive correlation found between ratings of attractiveness and judgements of unfaithfulness (O’Connor et al. 2011; Singh 2004). Whilst men show high consensus, judgements of unfaithfulness are only advantageous if they are predictive of actual extra-pair copulation risk. Yet evidence of a relationship
between attractiveness and actual unfaithfulness is mixed: women possessing attractive secondary sexual features, such as low waist-to-hip ratios (WHR) and feminine voices, have been reported to have a greater number of sexual partners, including a greater number of extra-pair copulations (Hughes et al. 2004; Shackelford & Buss 1997), although other research has failed to find a predictive relationship between attractiveness and extra-pair copulation activity (Rhodes et al. 2005). Andrews et al. (2008) asked committed couples to rate the likelihood that their partner had engaged in unfaithful behaviour and found that men were relatively accurate at predicting the likelihood that their partner had engaged in extra-pair sex, whereas women were not. As mentioned previously, men also show some accuracy when predicting their probability of paternity, with men who have high confidence of paternity having a much lower rate of non-paternity compared to men with low confidence of paternity (Anderson 2006). However, in these studies it is likely that men’s perceptions of unfaithfulness were formed through interactions with their partner and not from initial impressions. Although men can make judgements of faithfulness quickly and from limited information (O’Connor et al. 2011; Singh 2004), whether these initial impressions show any validity has rarely been studied.

Recent research by Rhodes et al. (2013) aimed to test the accuracy of first impressions of faithfulness by having men make judgements of faithfulness from facial photographs of women for which the researchers held self-reported extra-pair copulation behaviour. Replicating previous findings, men rated attractive women as more likely to be unfaithful but these faithfulness judgements showed no accuracy based on the women’s self reported extra-pair copulation behaviour. It is interesting to note that Rhodes et al. (2013) also tested women’s ability to accurately judge men’s faithfulness and found that women’s ratings of faithfulness showed a small to moderate correlation with men’s self-reported extra-pair copulation behaviour.

One possible explanation for men’s lack of accuracy in Rhodes et al. (2013) could be that the face alone does not provide enough information for them to make an accurate judgement. The female body provides a wealth of information to prospective partners and recent studies indicate that the body may also hold important information when making judgements of traits related to mate choice (Dixson et al. 2011; Peters et al. 2007). Alternatively, using a simpler task might
improve men’s accuracy by reducing the range of prospective responses (‘faithful’ or ‘unfaithful’ as opposed to degree of faithfulness) or by allowing men a more direct comparison of experimental stimuli. For example, employing a forced choice paradigm whereby men are instructed to choose the most faithful of two presented women might reveal greater accuracy by allowing direct comparison of women who differ in their extra-pair copulation behaviour.

Allowing men to view dynamic movement of women might also facilitate accuracy in faithfulness judgements. In natural social situations, men are able to observe the dynamic movement of prospective partners and much of the information we glean from bodies especially comes from dynamic movement (Barrett et al. 2005; Fink et al. 2012; Thoresen et al. 2012). Most research comparing judgements between static and dynamic stimuli has focused on judgements of attractiveness, with some findings suggesting no correlation between judgements made from static versus dynamic stimuli (Lander 2008; Penton-Voak & Chang 2008; Rubenstein 2005) whilst others indicate a strong positive correlation (Rhodes et al. 2011; Roberts et al. 2009). The use of dynamic stimuli may well provide more ecologically valid and accurate results on men’s judgements of female fidelity. Tentative evidence that dynamic stimuli may result in more accurate judgements about sexual behaviour comes from Stillman and Maner (2009) who reported a significant positive correlation between men’s judgements of women’s sexual attitudes and women’s self-reported sexual attitudes when viewing dynamic images of women. Clearly, more work on the cognitive abilities of men to make accurate judgements of women’s fidelity, and the cues they use in making such judgements, is warranted.

**Preventing female infidelity**

Anthropological research on pre-industrial societies has identified strategies adopted by men that reduce the risk of sperm competition arising from female infidelity. Recent research has shown differences in extra-pair paternity rates between men of the Dogon people of Mali, West Africa, that is dependent upon their religion. The Dogon follow a number of alternative religions including Islam, Catholicism and other branches of Christianity, and their own indigenous religion. Those who follow the indigenous religion have an average extra-pair paternity rate of 1.8%, which is significantly lower than the 2.9% extra-pair
paternity rates among the Dogon population that follows Catholicism (see Figure 1.1) (Strassmann et al. 2012). These religious groups show a number of differences that may account for variation in extra-pair paternity rates, such as wealth (wealthier individuals tend to be Muslim whilst poorer individuals tend to be Christian) and mating system (polygyny is still allowed by the Dogon Catholics). However, analysis suggests that these factors are not predictors of extra-pair paternity rates. Time spent apart from one’s partner might also explain extra-pair paternity rates as the inability to physically guard one’s mate may theoretically lead to increased rates of female infidelity as men are unable to prevent rival males approaching their partner for extra-pair copulations. However, time spent apart did not predict extra-pair paternity rates. One plausible explanation for the reduced levels of extra-pair paternity in the indigenous population may be the use of ‘menstrual huts’. Dogon women who follow the indigenous religion are obligated to sleep in menstrual huts during menses, forcing them to signal their menstrual cycle to the men within the tribe (Strassmann 1996). This information can then be used to make paternity assessments in relation to the timing of copulation and thus help the woman’s partner avoid cuckoldry. Cuckoldry is detrimental in the Dogon as land is inherited patrilineally, meaning that resources can be misdirected into genetically unrelated linages. By forcing women to signal their menses, male relatives who may be affected by a woman’s infidelities are able to assist her husband with paternity assessments. Such collective policing of women’s fertility may reduce opportunities for women to engage in extra-pair copulations. Further evidence that signalling menses may be a successful anti-cuckoldry mechanism comes from the finding that there is no significant difference in extra-pair paternity rates between the Dogon following the indigenous religion and those following Islam. Although women following Islam are not required to use separate huts during menses, they are required to notify their husbands of menses and are prevented from praying during menses. This may compensate for the absence of menstrual hut use and similarly protect paternity. These results suggest that the use of menstrual huts or practices designed to make women indicate their time of menses act as successful measures to reduce the risk of cuckoldry.
Figure 1.1. Religion and menstrual hut use as a means to assure paternity in the Dogan. (A) The prevalence of father–son Y DNA mismatches by menstrual hut use. (B) Exact odds ratio (±95% confidence limits) for cuckoldry by religion (the Dogon religion which enforces menstrual hut use is the reference point which by definition has an odds ratio of 1.0). Redrawn from Strassmann et al. (2012).

A number of cultures aim to prevent female infidelity by subjecting women who have engaged in extra-pair copulations to harsh punishment. Historical records report practices of severe penalty for "adulterous" women: men from Inca societies were permitted to starve their wives to death for committing adultery whilst men from Aztec cultures had the right to stone or strangle their wife to death if she engaged in extra-pair copulations (Gardner 1986). A number of contemporary societies still have partial or complete legislation allowing for the death penalty for women and girls accused of committing infidelities, and whilst
these 'honour killings' have been outlawed in many other societies, they continue to be implemented (Patel & Gadit 2008). Men who have committed adultery are often afforded milder punishments and women are often punished regardless of whether their infidelities are consensual or not (Patel & Gadit 2008). The threat of honour killings may discourage women from engaging in infidelities whilst the killing or punishment of women who have committed them means that their husbands are able to avoid raising an unrelated child whilst regaining honour and status within the community (Buss 2005).

Over the past few decades there has been extensive research examining the use of behavioural tactics — more commonly referred to as ‘mate retention behaviours’ (Buss 1988b) — in humans as a means of preventing female infidelity and thus reducing or eliminating sperm competition risk. Buss (1988b) identified 19 different behavioural tactics designed to prevent sperm competition, including men being vigilant to their partner’s whereabouts, threatening or attacking rival men, and guarding their mate from rivals. Cuckoldry is only a risk when one’s partner is of reproductive age. Accordingly, the performance of mate retention behaviours are positively correlated with female reproductive value as indicated by youth and attractiveness (Buss & Shackelford 1997). Although human females have ‘concealed’ ovulation — their fertile state is not displayed with, for example, the sexual swellings found in a number of other primate species — research suggests that men are nonetheless able to detect when their partner is ovulating and increase their mate retention behaviours during this fertile period (Haselton & Gildersleeve 2011). Such data provide strong evidence that mate retention behaviours are a finely honed defensive sperm competition tactic in humans.

Much of the research on mate retention behaviours has taken place on American populations (Buss 1988b; Buss & Shackelford 1997; Gangestad et al. 2002; Havlicek et al. 2005), but research by psychologists and anthropologists show that a number of these behaviours are observable across cultures including Europe (Spain, Croatia and Slovakia respectively, de Miguel & Buss 2011; Husarova 2005; Kardun et al. 2006), the Caribbean (Trinidad, Flinn 1988) and Asian and African communities (Buunk & Solona 2012). Murdock’s (1967) *Ethnographic Atlas* — which contains detailed notes on hundreds of human societies from across the world — notes that in only four of 849 societies did men not show any behaviour related to mate guarding. One cultural factor that appears
to affect the inclination to perform mate retention behaviours is whether a man is allowed to freely choose his partner, or whether his union is arranged by his kin. Previous reports suggest that men from Islamic cultures (where marriage is often arranged) perform more guarding behaviours, than men from cultures where they have freedom to choose their partner (Dickemann 1997). In a cross-cultural study conducted by Buunk and Solona (2012), men from cultures in which arranged marriages are common reported higher levels of possessive jealousy, possibly due to the fact that the spouse did not enter the marriage out of love and might therefore become sexually involved with, or defect from the relationship for, a rival man. However, the actual performance of mate retention behaviours induced by this jealousy, including both the frequency and types of behaviours performed, were not recorded. Investigating mate retention behaviours using a standardized metric, such as the Mate Retention Inventory (Buss 1988b; Buss et al. 2008) will allow for more accurate and revealing research on mate retention behaviours across cultures. It is also important to note that many studies reporting mate retention behaviours are observational (e.g. Murdock, 1967) with experimental evidence only collected where natural experiments have occurred, such as in the case of Strassmann et al. (2012) who were able to take advantage of the natural religious transition of the Dogon people. Nevertheless, the observational data collected from Western populations by psychologists and anthropologists suggest that mate retention behaviours are not simply the product of culture or social learning but are an evolved, behavioural response to sperm competition risk.

1.4.2. Offensive sperm competition strategies in humans

**In-pair copulations**

Socially monogamous birds have been shown to increase in-pair copulation frequency as the risk of females engaging in extra-pair copulations increases, such as after the intrusion of a rival male (Mougeot et al. 2001) or after female absence (Barash 1977). A similar strategy has been suggested to occur humans, whereby men who spend a greater proportion of their time away from their partners since the couple's last copulation report greater sexual interest in their partner, greater distress in response to their partner's sexual rejection, and a greater sexual
persistence in response to their partner’s sexual rejection (Shackelford et al. 2007).

Forced in-pair copulations have also been reported in humans, whereby men force their partner to copulate when they perceive an elevated risk of extra-pair paternity (Wilson & Daly 1992). Although it can be difficult to interpret behaviours as forced or resistant in non-human animals, we are able to do so with human behaviours as women often self-report forced interactions. Approximately 10-14% of married women will experience forced copulation from their husbands (Finkelhor & Yllo 1985; Russell 1990) and most forced in-pair copulations in humans follow accusations of female infidelity (Finkelhor & Yllo 1985; Russell 1990). Furthermore, men who are partnered to women who have been known to be unfaithful in the past, tend to employ forced copulations as well as less aggressive forms of sexual coercion (withholding benefits or threatening to defect from the relationship unless granted sexual benefits) more than men whose partners have not been unfaithful (Goetz & Shackelford 2006).

**Copulatory behaviour and genital morphology**

Men are reported to adjust copulatory behaviours at times of high levels of sperm competition, for example after a perceived female infidelity or period of female absence, by thrusting deeper, more quickly, and more vigorously (Gallup et al. 2003). However, these authors rightly pointed out that periods of separation might be confounded with time since last ejaculation, and thus sexual motivation. Others have suggested that copulatory behaviour may be involved in sperm displacement.

Like many non-human primates, humans have a piston-shaped penis with the coronal glans diameter greater than the shaft diameter. This configuration has been argued to be optimal for producing the suction forces required to promote semen displacement, and that the human penis may therefore have evolved in response to sperm competition (Simmons & Jones, 2007). Gallup et al. (2003) tested the semen-displacement hypothesis by simulating intromission with artificial penes and vaginae, and recording the proportion of simulated semen displaced. Gallup et al. (2003) reported that artificial penes with a coronal glans were able to remove up to 90% of the simulated semen occupying an artificial vagina compared to penes lacking a coronal glans, which displaced only 35.3%.
However, there are many caveats to the biological interpretation of these observations. For example, it is estimated that approximately 35% of semen is ejected from the female reproductive tract within the first 30 minutes after intercourse (Baker & Bellis 1993). The fact that in humans, females eject semen from their reproductive tract after copulation, a well-characterized mechanism of cryptic female choice in non-human animals (Eberhard 1996; Pizzari & Birkhead 2000), questions whether selection for sperm displacement mechanisms is likely. More importantly, in the highly promiscuous bonobo, *Pan paniscus*, in which sperm competition is intense, the penis lacks a coronal glans, and a coronal glans is common amongst old world primates independent of their mating system (Dixson 2012). These macroevolutionary patterns suggest that the coronal glans is unrelated to sperm competition in humans or primates more generally.

Humans lack many of the penile complexities found in primate species that experience high levels of sperm competition, although genomic research indicates that the genes coding for these traits are present in the human genome. Recent research comparing the genomes of chimpanzees, *Pan troglodytes*, and humans has identified the presence of genes coding for penile spines in humans, but the regulatory DNA that ‘switches on’ these genes and result in the expression of penile spines has been lost (McLean et al. 2011). The presence of genes that encode penile spines suggest that these traits were important in species ancestral to humans. The reason for the loss of expression in humans remains unknown, although the authors suggest that it may be due to the origin of a monogamous mating system and subsequent relaxation of selection from sperm competition (McLean et al. 2011). Indeed, the evolution of defensive sperm competition tactics within a socially monogamous mating system may have reduced selection on offensive sperm competition strategies more generally.

*Testes size and ejaculate production*

Human testis size varies widely, both within and among populations (Diamond 1986). Based on a sample of just 14 men, Baker and Bellis (1995) argued that variation in human testis size reflected variation in male mating tactics, whereby men who routinely engaged in extra-pair copulations had larger testes and produced ejaculates with more sperm than men who adopted monogamous mating tactics. Simmons et al. (2004) examined patterns of testis
size, sperm production and rates of extra-pair copulations in a population of 222 Australian men. Of these, 116 men provided measures of testes size, and 50 provided semen samples. As would be expected, men with larger testes did indeed produce ejaculates containing greater numbers of sperm. However men who reported engaging in extra-pair copulations did not have larger testes than monogamous men (Figure 1.2).

Human testes are intermediate relative to body size, lying closer to the monogamous gorilla, *Gorilla gorilla*, than the polygamous chimpanzee (Harcourt et al. 1995). This suggests that humans, like gorilla, may not have been subject to selection from sperm competition for high levels of ejaculate production (Simmons et al. 2004). However, molecular evidence for the strength of selection acting on the human ejaculate is mixed. Wyckoff et al. (2000) examined the rates of nucleotide substitutions in protamine genes (genes involved in the production of functional spermatozoa), finding that the ratio of non-synonymous (substitutions that change the protein product of the gene) to synonymous (substitutions that do not change the protein product) changes was high among humans and chimpanzee, but low in gorilla. High rates of non-synonymous substitutions are characteristic of selection, and indeed, the rates of non-synonymous substitutions in protamine genes have since been found to be associated with the strength of selection from sperm competition among rodents (Martin-Coello et al. 2009). The data might thus suggest that humans have been subject to levels of sperm competition closer to polygamous chimpanzees than monogamous gorilla.

Contrasting evidence comes from studies of genes that encode human seminal fluid proteins. Clark and Swanson (2005) found at least 7 seminal fluid protein genes that exhibited significant selection among humans and chimpanzee, suggesting that they may be subject to selection via sperm competition. Indeed, the rate of evolution of one of these genes, semenogelin II (*SEMG2*), is positively correlated with the levels of sperm competition among primates generally, with humans showing only moderate rates of *SEMG2* evolution (Dorus et al. 2004). Semenogelin is involved in the formation of the semen coagulum within the female reproductive tract shortly after ejaculation. The coagulum gradually liquefies via the action of a prostate-derived seminal fluid protein, kallikrein 3, and sperm are released. The semen coagulum (also referred to as a mating plug) is thought to play a role in the successful transport of sperm through the female reproductive
tract, including the prevention of sperm transport from rival males who may mate subsequently (Dorus et al. 2004). That SEMG2 shows rates of evolution in humans closer to gorilla than chimpanzee are more consistent with data on testes size, which suggest humans have relatively weak selection on the ejaculate from sperm competition. Alongside these contradictory patterns of evolutionary change in protamine and seminal fluid genes, a recent analysis based on sequence data from 285 genes suggests that in general, the rates of evolution of genes involved in spermatogenesis and seminal fluid production may be unrelated to the strength of selection from sperm competition imposed by different primate mating systems (Good et al. 2013). Clearly more work is needed in this area before firm conclusions can be drawn concerning the relative strengths of selection from sperm competition acting on ejaculate features of human and non-human primates.

**Figure 1.2.** Testes size and the number of sperm ejaculated in relation to men’s self-reported engagement in extra-pair copulations (EPCs). Among 116 men, combined testis volume did not differ between men who reported to engage in extra-pair copulations relative to those who did not. Fifty of these men provided semen samples. The number of sperm ejaculated increased with testis volume but did not differ between men who engaged in extra-pair copulations (closed symbols) and men who did not (open symbols). Data from Simmons et al., (2004).
**Sperm morphology**

Human sperm morphology is similar to that of other mammals, consisting of a head, mid-piece and flagellum. As discussed previously, comparative research on mammals has suggested that mid-piece volume has evolved under selection from sperm competition, with larger volumes indicating increased investment in mitochondrial loading and high levels of sperm competition (Anderson et al. 2007b; Anderson & Dixon 2002; Anderson et al. 2005). Compared to other primates, humans have a relatively small mid-piece volume (Anderson et al. 2005) and human sperm show significantly lower mitochondrial membrane potential than the sperm of the polygamous chimpanzee (Anderson et al. 2007b), perhaps suggesting that the human mid-piece volume has not been subject to intense selection from offensive sperm competition. However, it seems unlikely that mitochondria are solely responsible for providing the energy needed for human sperm to be motile, as glycolysis has also been implicated to play an important role in energy production by mammalian sperm (Storey 2008). Despite many years of research, the relative importance of each of these components in the production of energy by human sperm is still subject to debate (Piomboni et al. 2012). Nevertheless, the ability to produce competitively motile sperm may not be determined by mitochondria numbers alone as seminal fluid components also have a significant impact on sperm motility (Simmons & Fitzpatrick 2012). Thus, although the human mid-piece volume is small, this fact alone is perhaps insufficient to conclude that men have not been under strong selective pressure to produce competitive sperm.

Humans show a high percentage of morphologically abnormal sperm, especially when compared to other primate species that are known to experience high levels of sperm competition (Bedford 1974; Seuanez et al. 1977). Baker and Bellis (1988) argued that these abnormal sperm are morphs that have resulted from the selective pressure to produce non-fertilizing sperm that function in offensive sperm competition. They argued that these abnormal sperm include ‘kamikaze’ sperm, designed to ‘block’ parts of the female reproductive tract so as to reduce the chances of rival sperm accessing the female’s eggs, and ‘killer’ sperm, designed to attack and kill rival male sperm that may be present in the female’s reproductive tract, thus giving the fertilizing sperm a greater chance of fertilization success. Despite achieving much public attention, there has been little scientific
support for specialized sperm morphs in the human ejaculate. Indeed, experimental studies that have focused on identifying kamikaze and killer sperm have failed to find any evidence of their existence (Moore et al. 1999). Furthermore, if abnormal sperm were, in fact, specialized sperm morphs designed to assist in sperm competition, then we would expect to find a greater, not lesser, proportion of these sperm in highly polygamous species that regularly experience a high level of sperm competition (Harcourt 1991). It is more likely then, that the high numbers of abnormal sperm represent relatively relaxed selection on the human ejaculate, rather than intense sperm competition.

**Strategic ejaculation in response to sperm competition cues**

Humans have been reported to exhibit phenotypic plasticity in sperm allocation depending on variation in sociosexual situations. There is evidence of ejaculate adjustment in response to erotic stimuli in fertility studies; men responding to sexually explicit material ejaculate a greater number of sperm and a greater percentage of motile sperm compared to men producing a semen sample without stimuli (Yamamoto et al. 2000). Surveys of preferences for erotic literature have shown that men prefer images that depict a woman with multiple men compared to a man with multiple women (McKibbin et al. 2013; Pound 2002). These researchers suggest that the appeal of such images lies in their depiction of sperm competition, which, like many non-human animals, may result in an increased sexual arousal due to man’s evolutionary instinct to compete for paternity. This hypothesis was tested experimentally by Kilgallon and Simmons (2005) who asked participants to obtain a semen sample while viewing one of two sexually explicit image sets: one depicted rival males (two males, one female) whilst the other did not (three females). As predicted, men responding to the images depicting rival males produced a higher percentage of motile sperm in their ejaculate. This result suggests that men might be capable of adjusting their short-term investment in the ejaculate based on their perceptions of sperm competition (Figure 1.3). A stronger effect in the data however, was whether participants were currently in a sexual relationship; men in a sexual relationship ejaculated sperm of greater motility than did single men, even though the experimental protocol controlled for time since last ejaculation (Figure 1.3). Of course there may be many
Figure 1.3. Some partial effect sizes and their 95% confidence intervals from Kilgallon and Simmons (2005) study on how men's perception of sperm-competition scenarios influence the motility of sperm in semen samples collected via masturbation. Men viewing images containing men and women produced ejaculates with faster swimming sperm, and men in stable sexual relationships produced ejaculates with faster swimming sperm than single men. The figure shows that phenotypic variables such as testes size and age can also be associated with semen quality. Procedural variables such as the time taken to collect the semen sample and to deliver it to the laboratory, and the extent to which the sample liquefies in vivo can have stronger effects on the outcome variable than the treatment itself. Likewise, lifestyle variables, such as stress or the use of cigarettes and alcohol which all decreased sperm motility, can have larger effects than the variables of interest. Given how sensitive semen quality can be to intrinsic and extrinsic factors, studies that aim to examine men's response to sperm-competition cues must take such factors into account.

Potential explanations for this effect, including men increasing their semen quality when in a sexual relationship as a defence against potential sperm competitors. Although this data should be viewed as preliminary, it should encourage further research examining strategic adjustments in human ejaculate quality.

Previous research investigating strategic ejaculation in humans has suggested that men may be sensitive to the proportion of time they spend with their partner since their last copulation, adjusting sperm numbers in accordance with sperm competition theory (Parker & Pizzari 2010). Baker and Bellis (1989)
thus reported a negative relationship between proportion of time spent together since last copulation and sperm numbers inseminated during the next copulation. Their study had many limitations, including a sample size of just 10 couples, and no controlled period of abstinence prior to the experimental ejaculation. Moreover, it did not account for important lifestyle factors that can influence men’s semen quality (see below) and that may covary with the time men spend with their partners. Furthermore, it is worth noting that Baker and Bellis (1989) use time spent together since last copulation as a measure for the risk of sperm competition, based on the assumption that if men have less time to physically guard their partner, then their partner will have more opportunities to engage in extra-pair copulations with rival males. There is no evidence that time spent together since last copulation is a reliable measure of sperm competition risk however. Indeed, in their study of the Dogan, Strassmann et al. (2012) found that the time pairs spent apart had no impact on non-paternity. Unfortunately a number of other studies investigating psychological and behavioural sperm competition mechanisms in men have since used time spent apart/together since last copulation as a proxy for sperm competition risk without any justification for doing so (McKibbin et al. 2010; McKibbin et al. 2011; Starratt et al. 2013).

As discussed previously, in non-human animals, males are regularly found to increase sperm numbers or quality as female attractiveness increases, because males choose to invest maximally in females of high reproductive value and/or because attractive females may represent an increased likelihood of encountering rival sperm (Kelly & Jennions 2011; Wedell et al. 2002). In a number of non-human animals, size is an indicator of female attractiveness and males will invest greater sperm numbers or better quality sperm when mating with large females (e.g. Gage & Barnard 1996; Rubolini et al. 2006). Baker and Bellis (1993) hypothesized that men would increase sperm expenditure on larger women citing a positive association between fertility and fecundity with large body size, including decreased rates of miscarriage, faster fetus growth and heavier birth weight. Data collected from 35 couples found a positive correlation between female body size and numbers of sperm ejaculated, but again methodological limitations, including variations in sample collection methods and an absence of control for lifestyle factors, mean that the results must be viewed with caution. Moreover, these results are at odds with other research that has found that body
size negatively affects female attractiveness. Cross-cultural research has shown that men tend to rate women with a high body mass index (BMI) as less attractive (Richmond et al. 2012) and obese women actually show a decrease in their ability to become pregnant (Luke 2009), and children born to obese mothers tend to show low birth weight and increased chances of cognitive deficits (Helderman et al. 2012). Ratings of female attractiveness in humans are more accurately predicted by variations in secondary sexual traits, including breast size and waist-to-hip ratio (Dixson et al. 2011; Singh et al. 2010) as well as attractive facial features including sexual dimorphism, symmetry and averageness (Baudouin & Tiberghien 2004; Rhodes 2006). Women possessing these attractive traits are preferred as both long and short-term sexual partners (Regan 2000) and, if men do possess the ability to adjust sperm allocation in response to female attractiveness, it is more likely that men should allocate a greater number of, or better quality sperm to, women who display these attractive features. Research examining the influence of female attractiveness (as determined by secondary sexual traits) on sperm allocation has never been conducted.

The importance of lifestyle factors in studies of semen quality

It is important to note that humans show considerable variation in both sperm concentration and ejaculate volume and that these parameters can be strongly affected by environmental factors such as diet (Vujkovic et al. 2009), exposure to chemicals (Mathur & D'Cruz 2011), medications (Tanrikut & Schlegel 2007) and stress (Clarke et al. 1999) (Figure 1.3). Many studies have failed to account for lifestyle factors (e.g. Baker & Bellis 1989, 1993), and the results of these studies could be explained by lifestyle factors that covary with men’s behaviour. For example, in their study of the relationship between ejaculated sperm numbers and time a couple spent together, Baker and Bellis (1989) did not control for period of abstinence between ejaculations which can significantly affect sperm numbers (De Jonge et al. 2004).

Variability in sperm parameters may also be affected by methodological factors, including the methods used to obtain the sample, and the location where experimental samples are collected. Semen collection methods differ between, and sometimes within, studies, imposing limitations on how the research findings can be compared and generalised. Collection methods are an important consideration.
The best method for collecting semen is through complete coitus using semen collection devices (Zavos et al. 1994), but this is rarely practical. Some studies have suggested that ejaculates collected via masturbation are of low quality compared to ejaculates collection via coitus (Sofikitis & Miyagawa 1993). Nonetheless, samples collected by masturbation can be of a quality more typical of those collected in coitus when men are provided with erotic material, thereby placing ejaculation within an appropriate context (Wylie & Pacey 2011). The use of masturbation makes obtaining a sample easier and more practical in an experimental setting, although the location of collection is an important consideration. Stress can reduce semen quality, and there is evidence suggesting that better quality samples are produced when a man is in a familiar setting, such as his home, compared to samples collected at a clinic (Elzanaty & Malm 2008).

Future research into strategic ejaculation needs to use standardized methods, both in terms of the collection procedure and location of collection, and ensure that other significant environmental factors related to ejaculate quality are accounted for, for example through the routine use of lifestyle questionnaires (Kilgallon and Simmons 2005).

1.4.3. Cryptic female choice in humans

Although mechanisms of cryptic female choice are less well documented in mammals, there has been some evidence that non-human primates may have evolved behavioural, physiological and morphological mechanisms to bias paternity toward preferred males (Reeder 2003). Within human research, the function of the female orgasm has received considerable attention as a possible mechanism for cryptic female choice, with one of the most discussed hypotheses suggesting that it may have evolved to produce an ‘up suck’ effect, drawing semen up through the cervix and into the uterus (Baker & Bellis 1993). Previously, there was only limited evidence that the uterine contractions experienced during female orgasm result in the movement of semen into the uterus (see Lloyd 2005). However, more recent evidence using hysterosalpingoscintigraphy (HSS) has suggested that when these contractions are experienced during the fertile phase of the ovulatory cycle, and without sexual stimulation, they assist with the movement
of sperm into the oviduct ipsilateral and to the ovaries (Zervomanolakis et al. 2007). The application of the hormone oxytocin has been shown to increase these contractions. Oxytocin is released during orgasm and so might act as the mechanism through which orgasm facilitates cryptic female choice (Zervomanolakis et al. 2007).

The upsuck hypothesis remains controversial. Some have cited evidence from the oxytocin and uterine contraction studies as evidence for the adaptive function of the female orgasm, suggesting also that the orgasm works as a cryptic female choice mechanism because women are more likely to experience orgasm when copulating with men of high mate value (e.g. Puts et al. 2012b). Nonetheless, the subject requires considerably more research. Most studies reporting the effects of oxytocin and uterine contractions have studied women who are not sexually aroused, and also tend to neglect the negative effects of increased sperm uptake, including the risk of polyspermy and sperm enzyme release which could result in decreased fertility (Levin 2011a, b). Recent research also suggests that there is no link between rates of orgasm and female fertility, which questions the functional significance of the "upsuck" effect (Zietsch & Santtila 2013).

Other hypotheses propose that the female orgasm is merely a by-product of the male orgasm, as the structure that develops into the clitoris or penis is bipotential in embryo development (Symons 1979). However, recent studies have provided evidence against this hypothesis, with self-reported data on orgasmic function from twins and full-siblings suggesting that different genetic factors underlie male and female orgasmic function (Zietsch & Santtila 2011). Wallen et al. (2012) argue that Zietsch et al.’s (2011) study had limitations, including the use of different metrics to measure orgasm function in men and women that are not correlated (time to orgasm and likelihood of orgasm for men and women respectively). A follow-up study showed that time to orgasm and likelihood of orgasm are highly correlated in women (Zietsch & Santtila 2012), but researchers must be careful in identifying analogous metrics to measure orgasm in men and women when comparing orgasmic function. Whilst one sexes’ response to a question may have great variance, the other’s response may have very little, which makes the likelihood of finding a correlation between the responses small. For example, when responding to questions on the likelihood of experiencing orgasm during sex, there is almost no variation in the response of men (Zietsch & Santtila
2012), but significant variation in the response of women (Dawood et al. 2005; Dunn et al. 2005).

Further research is required to ascertain the function—should one exist—of the female orgasm and if this relates to cryptic female choice. Non-human primates that also display female orgasm, such as the stump-tailed, *Macaca arctoides* (Goldfoot et al. 1980) and Japanese macaques, *Macaca fuscata* (Troisi & Carosi 1998) may be useful as model species for research, and provide comparative data. A complete review of the functional significance of the human female orgasm is beyond the scope of the current review. However, the interested reader is directed to a thorough review of this literature provided by Puts et al. (2012a).

### 1.5. Conclusions and directions for future research

The extent to which sperm competition has acted as a selective force during human evolution has remained controversial (Dixson 2009; Shackelford et al. 2002; Simmons et al. 2004). Comparative analysis of physiological and morphological traits associated with sperm competition can be useful in identifying the role that sperm competition has played during human evolution. These physiological and morphological traits — testes size, penile morphology, sperm morphology, sperm numbers and sperm quality — are generally associated with offensive sperm competition tactics, designed to increase sperm competitiveness when competing against rival sperm in the female’s reproductive tract (Dixson 2009; Harcourt et al. 1995; Parker et al. 1997; Stockley 2002; Tourmente et al. 2011). Comparative research indicates that, in general, these traits are relatively less well developed in humans, leading some researchers to argue that selection for offensive sperm competition has been weak or absent during human evolution (Dixson 2009). Recent genome research showing that humans possess the genes that encode penile spines, but have lost the regulatory DNA for their expression, supports this view (McLean et al. 2011).

Whilst offensive sperm competition tactics appear relatively weak in contemporary human populations, it cannot be inferred that sperm competition has not been a significant selective pressure on the evolution of the human mating
system. Human populations do show low levels of extra-pair paternity (Anderson 2006; Anderson et al. 2007a; Simmons et al. 2004), and self-reported extra-pair copulation behaviours demonstrate that women do mate with more than one partner during any one fertile window (Javanbakht et al. 2010; Johnson et al. 2001; Steffenson et al. 2011). There is considerable evidence to suggest that men have evolved mechanisms to detect and anticipate female infidelity (Andrews et al. 2008; O’Connor et al. 2011; Shackelford & Buss 1997), and apply defensive behavioural tactics designed to prevent such infidelity thereby reducing the chances of having to compete with rival sperm (Buss 1988b; Buss & Shackelford 1997; de Miguel & Buss 2011; Shackelford et al. 2002). If these defensive tactics are successful in minimizing female infidelity, then selection on offensive sperm competition mechanisms is expected to be relaxed, leading to a reduction or even loss of offensive sperm competition traits.

Although further research is clearly necessary, men do appear to show some accuracy in predicting likelihood of female infidelity in relationships (Andrews et al. 2008) and even from limited sensory information, such as the voice (O’Connor et al. 2011). Whether mate retention behaviours are effective in preventing female infidelity has rarely been studied directly, but bird species that share a broadly similar mating system to that of humans do show a positive relationship between mate guarding and female fidelity as measured through rates of extra-pair paternity (Chuang-Dobbs et al. 2001; Westneat & Webster 1994). Studies that investigate the direct relationship between the performance of mate retention behaviours and levels of female infidelity across human populations would help ascertain the effectiveness of defensive sperm competition strategies.

Defensive behaviours may be the dominant method by which human males react to female infidelity in humans. However, continuous mate guarding is not a viable strategy due to the costs associated with prolonged investment; for example a man is unable to gather resources if he invests all his time and energy in guarding his partner and, despite his best efforts when with his partner, preventative measures are not fool proof (Shackelford 2003). Given that mate guarding may not always be possible and/or effective, humans might retain some forms of offensive sperm competition tactics to counter immediate female infidelity. Whilst, offensive behavioural tactics, such as forced in-pair copulations, have received some attention in the literature (Finkelhor & Yllo 1985; Gallup et al.
studies of the use of offensive physiological tactics are scant. Some evidence that humans may adjust their ejaculate expenditure comes from the few studies that show men's ability to adjust their sperm quality dependent upon visual stimuli during ejaculation (Kilgallon & Simmons 2005; Yamamoto et al. 2000). Whether increased sperm allocation can also be affected by female attractiveness — another sperm competition cue in non-human animals — is yet to be properly investigated. Increases in the performance of defensive behaviours can be attributed to increases in female partner attractiveness and attractive women are often considered as more likely to be unfaithful (O’Connor et al. 2011; Singh 2004), so it would be interesting to determine whether men adjust their ejaculates in response to female attractiveness.

Although the attractiveness or mate value of the female has long been considered an important factor influencing ejaculate expenditure, the value or attractiveness of the male himself can also be an important factor to consider (Cornwallis & Birkhead 2007a; Mautz et al. 2013; Tazzyman et al. 2009). In humans, a man’s value as a mate is strongly determined by his status/prestige (Kruger & Fitzgerald 2011) and his ability to acquire resources (Buss 1989; Li et al. 2002), although other traits including dominance (Kruger & Fitzgerald 2011) and attractiveness (Li & Kenrick 2006; Regan 2000) have also been shown to contribute. Men who possess desired traits are preferred as sexual partners (Regan 2000), and men with high status and/or wealth have a greater number of sexual partners (Perusse 1994) and a greater number of surviving offspring (Hopcroft 2006) than men who lack in these traits. As discussed above, sperm is a limited resource. In humans, men suffer a post-ejaculatory refractory period in which they cannot remate (see Levin 2009), and without a period of ‘sexual rest’, a man’s semen quality is reduced (De Jonge et al. 2004). Due to these physiological constraints, high quality men who have sexual access to many women via female mate choice may strategically adjust their ejaculate investment into each mating opportunity dependent upon the mate value of their current partner. Men who lack these desirable traits may experience more difficulty in attracting and retaining sexual partners and thus invest fully in each mating opportunity, regardless of female attractiveness. Male mate value has been shown to influence the performance of defensive behavioural tactics in humans with high value males performing more ‘benefit-provisioning’ and fewer ‘cost-inflicting’ mate retention
behaviours (Miner et al. 2009), but whether male mate value can affect men’s allocation to the ejaculation has yet to be explored.

Finally, an equally important selection pressure arising from multiple mating by females is cryptic female choice. An increasing number of studies of non-human animals are uncovering mechanisms of cryptic female choice that bias paternity toward some males and away from others. Cryptic female choice has rarely been studied in humans. Some researchers have argued that the female orgasm functions as a mechanism of cryptic female choice (Puts et al. 2012a; Puts et al. 2012b; Zervomanolakis et al. 2007) but this work is by no means conclusive. Research on the mechanisms for cryptic female choice in women will be necessary for a complete understanding of the role of sperm competition in human evolution.
CHAPTER TWO

Men's sexual faithfulness judgements show a kernel of truth
2.1. Abstract

Mechanisms enabling men to identify women likely to engage in extra-pair copulations would be advantageous in avoiding cuckoldry. Men’s judgements of female sexual faithfulness often show high consensus, but the accuracy of these judgements appears poor. I examined whether accuracy of judgements made to images of women could be improved through i) employing a forced choice task, in which men were asked to select the more faithful of two women, ii) providing men with full person images from which to make judgements and iii) priming men to a mating environment depicting male sexual competition. In Experiment 1, men rated 34 women, for whom I had self-reported extra-pair copulation behaviour, for faithfulness, trustworthiness or attractiveness from either face or full person photographs. This was followed by a forced choice task in which men were asked to select the more faithful woman from 17 pairs of images, one of a woman who had reported no extra-pair copulations and the other of a woman who had reported two or more extra-pair copulations. Men were unable to judge faithfulness of individual women with any accuracy, replicating previous findings. However, when asked to choose the more faithful of two women, they performed significantly above chance. Although there was no significant difference in accuracy for face and full person image pairs, only judgements from faces were significantly above chance. In Experiment 2, men completed the faces forced choice task before and after exposure to images depicting alternative mating environments (sexual competition, no sexual competition, control). Again, men chose the more faithful model significantly above chance level. However, exposure to images depicting sexual competition did not improve their accuracy. In both experiments, accuracy was related to the perceived difference in trustworthiness of the two models. These results show that men’s judgements of faithfulness made from faces of unfamiliar women can contain a kernel of truth.
2.2. Introduction

Across species, males and females show preferences for particular traits in potential partners that are believed to advertise mate quality (Andersson, 1994). In humans, women value traits such as dominance and the ability to accrue resources, whereas men predominantly value youth and attractiveness (Buss, 1989; Geary et al., 2004; Regan, 2000). However, one trait that both sexes value in a potential mate is faithfulness (i.e. being sexual exclusive to one’s partner, Buston & Emlen, 2003). In socially monogamous species—such as humans—where both the male and female invest resources in offspring for an extended period of time, pairing with a mate that engages in extra-pair copulations may result in fitness costs for either sex. However, males are likely to suffer the greater evolutionary cost as they risk raising genetically unrelated offspring (cuckoldry).

Due to the significant fitness cost associated with cuckoldry, it would be adaptive for men to have evolved the ability to predict or detect unfaithfulness in a potential partner. There is some evidence that men can accurately judge female faithfulness (Anderson, 2006; Andrews et al., 2008), based on the behaviours of, and interactions with, their partners. However, people can make many trait judgements from only limited sensory information—such as images— and some of these judgements show real life accuracy (Mueller & Mazur, 1997; Wilson & Eckel, 2006). Faithfulness can also be judged from limited sensory information (O’Connor et al., 2011; Rhodes et al., 2013; Singh, 2004). However, although men often show high consensus on these judgements, little is known about whether these first impressions of faithfulness are accurate.

Accuracy of faithfulness judgements

Judgements of faithfulness can only be adaptive if they are accurate and thus prevent cuckoldry, but the accuracy of faithfulness judgements is relatively unknown. One study that directly compared perceived and actual faithfulness found that men’s ratings of faithfulness made from women’s faces did not correlate with the self-reported extra-pair copulation behaviour of those women (Rhodes et al., 2013). It is possible, however, that if men are able to directly compare women, they may be able to perceive subtle visual cues that lead to accurate judgements of faithfulness that would otherwise be overlooked in rating tasks. A forced choice
task in which men are required to choose the more faithful of two women may be a more sensitive test of men’s accuracy in faithfulness judgements as it forces the participant to discriminate. Indeed, forced choice tasks are widely used in perception research to test for discrimination ability. Here I test whether men show accuracy in their judgements of faithfulness when asked to choose the more faithful of two women who differ in self-reported extra-pair copulation behaviour.

I also asked whether accuracy could be improved by showing full person images of the women. We often use information from the body as well as the face when making judgements of people. For example, the face and body make independent contributions to judgements of attractiveness (Dixson et al., 2011; Peters et al., 2007). Here I asked whether men can assess faithfulness more accurately from full person than from face only images.

I also asked whether men may be able to show accuracy in their judgements of faithfulness if they have been primed to an appropriate mate choice environment. Individuals show preferences for many traits in potential mates, but preferences for these traits can vary across individuals. One explanation for variation in trait preference is the environment in which an individual makes their mate choice. For example, women from nations with poorer health show a stronger preference for masculinity than women from healthier nations (DeBruine et al., 2010; Penton-Voak et al., 2004) and, in an experimental context, women’s preferences for masculinity can be manipulated by exposing them to images depicting direct male competition (Little et al., 2013). Here I asked whether priming men to a mating environment depicting sexual competition and thus highlighting the potential for female unfaithfulness can increase the accuracy of their judgements of faithfulness. I hypothesized that priming men to such a context might focus men’s attention on cues to potential infidelity and thus increase the accuracy of their faithfulness judgements.

**Visual cues and traits influencing faithfulness judgements**

Little is known about the visual cues that men may use to judge faithfulness. One cue that men appear to use is female attractiveness, with more attractive women often rated as less likely to be faithful (O’Connor et al., 2011; Rhodes et al., 2013; Singh, 2004). Judging attractive women as less faithful might result in accuracy because attractive women are preferred as sexual partners and thus may
have more opportunity to engage in extra-pair copulations. Indeed, attractive women report having men attempt to poach them from relationships more often than less attractive women (Regan, 2000; Schmitt & Buss, 2001). However, data are mixed as to whether attractive individuals actually are less faithful (Rhodes et al., 2013; Hughes et al., 2004; Shackelford & Buss, 1997).

Judgements of other traits might also influence judgements of faithfulness. For example, men could potentially use perceived trustworthiness to make judgements of faithfulness. Trustworthiness has received considerable attention in trait-judgement research (Efferson & Vogt, 2013; Rule et al., 2013; Todorov, 2008; Zaidel et al., 2003). Trustworthiness is a trait with many dimensions. For example, faithfulness could be considered an aspect of 'sexual' trustworthiness and, if an individual is considered generally trustworthy, they may in turn be considered to be more faithful. However, Rhodes et al. (2013) found that women’s judgements of male trustworthiness were independent of their ratings of male faithfulness. As women showed accuracy in their judgements of faithfulness in this study, these findings suggest that trustworthiness judgements do not aid in making accurate judgements of faithfulness. As men showed no accuracy in their ratings of faithfulness in Rhodes et al. (2013), the extent to which perceived trustworthiness might be related to men’s accurate judgements of faithfulness is unknown.

The extent to which men may use judgements of attractiveness and trustworthiness to make accurate judgements of faithfulness requires further research, and is examined in this study.

The current study

I investigated whether men are able to make accurate judgements of faithfulness from images of women and examined what cues and traits they use to make these judgements. In Experiment 1, I asked whether use of a forced choice task, which allows for direct comparison between pairs of women, increases accuracy above the chance levels found when rating individual face images in Rhodes et al. (2013). I included full person images as well as face images, to see whether accuracy would improve when the body as well as the face was shown. I also examined how judgements of attractiveness and trustworthiness relate to the accuracy of faithfulness judgements. In Experiment 2, I investigated whether
priming men to an environment depicting sexual competition can improve the accuracy of their judgements of faithfulness.

2.3. Experiment 1

Participants were asked to complete two tasks: a ratings task where they rated individual women for faithfulness, and a forced choice task, in which they chose the more faithful of two women who differed in their number of self-reported extra-pair copulations. I included the ratings task to allow direct comparison with the findings of Rhodes et al. (2013). Following Rhodes et al. (2013), I did not expect to find any accuracy in this task. I included the forced choice task to determine whether men can judge faithfulness with any accuracy when they have the opportunity to directly compare women. I had self-reported extra-pair copulation behaviour for each of the models judged which allowed me to examine the accuracy of these judgements in both tasks (Rhodes et al., 2005). Participants completed these two tasks using either face images or full person images to determine whether the use of full person images (face and body) can improve accuracy of faithfulness judgements. Other male participants rated the female models for attractiveness and perceived trustworthiness, to determine whether these relate to accurate judgements of faithfulness.

2.3.1. Methods

Participants

Eighty-seven self-reported Caucasian, heterosexual, male participants aged between 18 and 35 years of age were recruited from the University of Western Australia community and were awarded either psychology course credits or were remunerated with AU$5 for their participation. Ethics approval for this research was granted by the University of Western Australia Human Ethics Research Committee (project number RA/4/1/4681). Participants read an information sheet detailing their role in the study and provided written consent prior to commencing the study.
**Ratings task**

I obtained coloured, front-view face and full person (face and body) digital photographs of 34 heterosexual, Caucasian women aged between 20 and 42 years from the database described in Rhodes et al. (2005) and also used by Rhodes et al. (2013). For each of these women, I had self-reported extra-pair copulation behaviour. In order to maximize honest reporting, they were informed that all responses were confidential and would be stored in a locked box. They also completed the questionnaire in isolation and could only be identified via a self-selected PIN (Rhodes et al., 2005). Photographs of each woman were taken from a fixed distance under symmetrical lighting conditions and models stood with their arms relaxed by their side and with a neutral expression. In order to standardize images, Adobe® Photoshop CS3® was used to colour clothing black, remove jewellery, and block out background features. Face images were scaled to a height of 420 pixels and width of 320 pixels and were surrounded by a black oval mask that covered most of the hair. Face images were viewed at an approximate distance of 50cm, at a vertical visual angle of approximately 8.3 degrees and a horizontal visual angle of approximately 6.3 degrees. Full person images were scaled to a height of 768 pixels and width of 512 pixels, and were viewed at an approximate distance of 50cm at a vertical visual angle of approximately 17.0 degrees and a horizontal visual angle of approximately 5.0 degrees. Photographs were rotated so that both pupil centres were located on the same y-axis and were presented at a resolution of 72 pixels/inch.

From these images, I obtained ratings of faithfulness, attractiveness and perceived trustworthiness from full person or face images. Attractiveness ratings of the face images were available from Rhodes et al. (2005) so were not collected again. Participants were assigned to one of the other five tasks. The ratings task began with three practice trials using three alternative randomly selected models from the database (Rhodes et al., 2005). A full person or face image of each model was then presented for 2 s followed by a response screen asking participants to make a rating of how faithful or trustworthy or attractive (full person only) they perceived the model to be on a Likert scale from 1 (‘Not at all’) to 7 (‘Extremely’), which was made by pressing the corresponding key on the keyboard. After making their rating, they were instructed to press the space bar to start the next trial.
Participants completed this process for all 34 models and the presentation order of the models was randomized for each participant.

**Faithfulness forced choice task**

For the forced choice task, the 34 models were matched into 17 pairs. The women in each pair were of similar age (±2 years) with one woman reporting engaging in two or more extra-pair copulations (hereafter ‘unfaithful model’) and the other reporting having never engaged in an extra-pair copulation (hereafter ‘faithful model’). The pair was displayed with one image presented on the left of the screen and the other on the right. Participants made their judgements from either face or full person images (same image type as the ratings task). Face images were presented approximately 1 - 1.5 inches apart and full person images approximately $2^{3/4} - 3$ inches apart.

The forced choice task began with three trials using six alternative randomly selected models from the database (Rhodes et al., 2005). Each trial started with a fixation cross in the middle of the display screen for 500ms followed by a pair of full person or face images. The images were presented for 4 s with the unfaithful model appearing on the left of the screen for nine trials and on the right for the other eight trials. After each pair, a response screen appeared asking the participant to choose which woman was the more faithful. Participants chose the individual on the left of the screen (by pressing ‘Z’ on the keyboard, labelled as ‘Left’) or the right (by pressing ‘M’ on the keyboard, labelled as ‘Right’) and then initiated the next trial by pressing the space bar. Participants completed the trials in a random order.

**General procedure**

All testing took place on a MacBook Pro, 15 inch, 1440 x 900 pixel resolution screen. All experimental tasks were programmed and performed using SuperLab 4.

Participants first completed the ratings task, in which they were assigned to one of five alternative judgements: faithfulness from full person images ($N=22$), faithfulness from face images ($N=21$), trustworthiness from full person images ($N=14$), trustworthiness from face images ($N=15$) or attractiveness from full person
images \((N=15)\). Once the ratings task was complete, participants rating faithfulness had a one minute break before moving onto the forced choice task.

The participants who rated faithfulness then completed the forced choice task in which they were presented with 17 pairs of women and were instructed to choose the more faithful of the two either from face or full person images. Once the forced choice task was completed, participants were thanked for their time and debriefed.

### 2.3.2. Results and discussion

Where variables did not meet the assumption of normality according to a Kolmogorov Smirnov test, parametric analysis was still used because \(z\) scores calculated from skewness and kurtosis values were less than 1.96 (Field 2013). Non-parametric analyses did not alter the results and are presented in Appendix A to allow comparison.

**Accuracy of faithfulness judgements in forced choice task**

The proportion of correct choices was defined as the proportion of trials on which the participant correctly chose the faithful model. An independent samples \(t\) test showed no significant difference between the proportion of correct choices for face and full person images \((t_{41}= 0.66, p= .515, \text{effect size: } r= 0.10, 95\% \text{ CI}= -0.21\text{-}0.39)\). Overall performance was significantly above chance (0.5) (one sample \(t\) test: \(t_{42}= 3.10, p= .003, X\pm SD= 0.55\pm 0.11\) and the effect size was medium-large \((r= 0.43, 95\% \text{ CI}= 0.15\text{-}0.65)\). Although there was no significant difference in performance on faces and full person images, planned \(t\)-tests showed that performance was significantly above chance for judgements from face images (one sample \(t\) test: \(t_{20}= 2.46, p= .023, X\pm SD= 0.57\pm 0.12\), effect size: \(r= 0.48, 95\% \text{ CI}= 0.06\text{-}0.76\) but only marginally significant from full person images (one sample \(t\) test: \(t_{21}= 1.87, p= .075, X\pm SD= 0.54\pm 0.11\), effect size: \(r= 0.38, 95\% \text{ CI}= -0.05\text{-}0.70\)). Nevertheless effect sizes were moderate in both cases. These results show that men's judgements of faithfulness have a kernel of truth, at least for judgements from women's faces.
Accuracy of faithfulness judgements in ratings task

Ratings of each judgement (faithfulness, attractiveness or trustworthiness) made from each image type (face or full person) were made by between 12 and 22 participants. Consensus for all judgements was high (Cronbach’s $\alpha$: face/faith= 0.81, full/faith= 0.88, face/trust= 0.87, full/trust= 0.87, face/attract= 0.81, full/attract= 0.97) so participant ratings were averaged to produce a mean rating of faithfulness, trustworthiness and attractiveness of the face and full person images for each of the 34 models. Correlations between ratings of faithfulness, trustworthiness and attractiveness made from both face and full person images are presented in Table 2.1 and corroborate those reported in Rhodes et al. (2013).

To examine men’s accuracy in faithfulness judgements in the ratings task, I examined the correlation between men’s faithfulness judgements and the self-reported extra-pair copulation behaviour of the models. There was a significant difference between faithfulness judgements made from face and full person images ($t_{33}= 3.28 \ p= .002$, face: $X\pm SD= 4.46\pm 0.64$, full: $X\pm SD= 4.75\pm 0.46$), so I examined correlations between faithfulness ratings and the models’ extra-pair copulation behaviour separately for each image type. There were no significant correlations between men’s ratings of faithfulness and the self-reported extra-pair copulation frequency of the female models being rated, for either face images ($r_{34}= -0.08, \ p= .667$) or full person images ($r_{34}= -0.07, \ p= .707$). Thus I replicated Rhodes et al.’s (2013) finding that men cannot accurately judge quantitative variation in extra-pair copulation behaviour from face images in a new sample of participants, and found that providing full person images did not improve accuracy.

Attractiveness as an honest cue of faithfulness

There was considerable variation between the 17 pairs of women in how likely participants were to choose the most faithful model of the pair. To explore whether differences in attractiveness were related to accuracy of faithfulness judgements to face images, I calculated the difference in attractiveness (‘attractiveness difference’) between the faces for each pair and correlated this variable with the proportion of participants who correctly chose the most faithful model from that pair. I found no significant correlations between the attractiveness difference and the proportion of participants who correctly chose the most faithful model ($r_{17}=-.15, \ p= .576$). Nor were differences in rated
femininity, averageness, or symmetry of the faces (available from Rhodes et al., 2005) significantly correlated with the proportion of participants who correctly chose the faithful model (femininity: $r_{34} = -0.16$, $p = .534$, averageness: $r_{34} = 0.22$, $p = .397$, symmetry: $r_{34} = -0.02$, $p = .934$). Therefore, although ratings of perceived faithfulness correlated positively with ratings of attractiveness (Table 2.1), neither attractiveness nor its components appear seem to have been used as cues to make faithfulness judgements in the forced choice task.

Table 2.1 Correlations between ratings of faithfulness, trustworthiness and attractiveness made from face and full person images (Pearson’s $r$ are shown above the diagonal and Spearman’s $r$ show belong the diagonal for comparison).

<table>
<thead>
<tr>
<th></th>
<th>Face</th>
<th>Full person</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Faith</td>
<td>Trust</td>
</tr>
<tr>
<td>Faith</td>
<td>.487**</td>
<td>-.424*†</td>
</tr>
<tr>
<td>Trust</td>
<td>.526**</td>
<td>.433*</td>
</tr>
<tr>
<td>Attract</td>
<td>-.300</td>
<td>.443**</td>
</tr>
<tr>
<td>Faith</td>
<td>.605**</td>
<td>.167</td>
</tr>
<tr>
<td>Trust</td>
<td>.354*</td>
<td>.484**</td>
</tr>
<tr>
<td>Attract</td>
<td>-.190</td>
<td>.327</td>
</tr>
</tbody>
</table>

** $p<.01$

* $p<.05$

$^\dagger$ $p=.052$

† Once an outlier with a with a leverage value greater than twice the average leverage value was removed from analysis, this correlation became non-significant ($r = -.267$, $p = 0.134$).
Perceived trustworthiness and faithfulness

There was a strong and significant correlation between ratings of trustworthiness and ratings of faithfulness (Table 2.1). I therefore investigated whether differences in perceived trustworthiness of the models’ faces were related to the proportion of participants who were able to accurately choose the more faithful model from each pair. I calculated the difference in perceived trustworthiness (hereafter ‘trustworthiness difference’) as described above for attractiveness difference. There was a strong and significant correlation between the trustworthiness difference and the proportion of participants who correctly chose the faithful model ($r_{17} = .76$, $p < .001$). Therefore, men may have used perceived trustworthiness as a cue to faithfulness.

2.4. Experiment 2

In this experiment, I investigated whether the accuracy of men’s judgements of faithfulness from faces could be further improved by priming them to an environment depicting sexual competition. Men completed the faithfulness forced choice task from Experiment 1 both before and after exposure to one of three image conditions. These images depicted either a mating environment in which there was sexual competition between males (sexual competition condition), a mating environment in which there was no sexual competition between males (no sexual competition condition), or control images (control condition). I predicted that men’s accuracy in faithfulness judgements would increase after exposure to images depicting sexual competition. As findings from Experiment 1 suggested that perceived trustworthiness relates to ratings of faithfulness, I further examined the relationship between perceived trustworthiness and accuracy in faithfulness judgements.

Just as men show individual differences in the traits they prefer in potential partners (Lee et al., 2014), they also vary in their preference for faithfulness. Specifically, men who have a more restricted sociosexual orientation (i.e. less willingness to engage in sexual activity outside of a committed relationship) show a greater preference for faithfulness in a potential partner than men with unrestricted sociosexual orientations (Simpson & Gangestad, 1992). One might
expect those who value faithfulness to be more sensitive to any visual cues associated with faithfulness and thus to show greater accuracy in their judgements. To test this hypothesis, I had participants rate their preference for faithfulness in a potential partner and compared these ratings with the accuracy of their faithfulness judgements. I obtained these ratings before and after exposure to images, to assess their reliability.

2.4.1. Methods

Participants

Sixty self-reported heterosexual, Caucasian male participants aged between 18 and 35 years of age were recruited from the University of Western Australia community and were awarded either psychology course credits or were remunerated with AU$5 for their participation. Participants were first provided with an information sheet detailing their role in the study and signed a consent form before participating. The information sheet stated clearly that participants might be exposed to sexually explicit images and that any participant uncomfortable with viewing such images should not continue with the experiment. No participants declined to take part in the study.

General procedure

All testing took place on a MacBook Pro, 15 inch, 1440 x 900 pixel resolution screen. All experimental tasks were programmed and performed using SuperLab 4. All participants were tested in a private room with no experimenter present.

Participants began by completing a ‘Mate Preference Questionnaire’ that measured the importance of 10 mate choice related traits in a sexual partner including faithfulness (Buston & Emlen, 2003). These traits were rated on a 9-point Likert scale from 1 (‘Not at all important’) to 9 (‘Extremely important’). Once the questionnaire had been completed, participants completed the faithfulness forced choice task using faces, as described in Experiment 1. Participants were then exposed to one of three sets of images: Twenty participants were allocated to a sexual competition image condition, 20 to a no sexual competition image condition and 20 to a control image condition. Four explicit multi-male with female
images (two men, one woman) were used for the sexual competition condition and four female only explicit images (three women) used for the no sexual competition condition. These images have been used successfully in past research to prime men to either a sexual competition or no sexual competition environment (Kilgallon & Simmons, 2005). Participants assigned to the control condition viewed four pictures of pedigree dogs found on the Internet as this provided a visual focus for the participant but was unrelated to a mating environment. Prior to the images appearing on the screen, an information screen instructed participants to look carefully at the following images. Participants initiated a slideshow of their assigned images by pressing the space bar. Following the protocol of Little et al. (2013), each of the assigned four images was shown for 3 s and was repeated two times (for a total of eight images and an total exposure time of 24 s). Once all images had been viewed, participants then repeated the faithfulness forced choice task. Finally, they completed another ‘Mate Preference Questionnaire’ to check for reliability in self-reported preference for faithfulness. This questionnaire was identical to the one completed at the start of the study except for the order in which the questions were presented.

2.4.2. Results and discussion

Where variables did not meet the assumption of normality according to a Kolmogorov Smirnov test, parametric analysis was still used because z scores calculated from skewness and kurtosis values were less than 1.96 (Field 2013) and/or non-standardized residuals after parametric analysis were normally distributed. Non-parametric analyses did not alter the results and are presented in Appendix B to allow comparison.

Accuracy of faithfulness judgements

I used a two-way repeated measures ANOVA, with test time (pre and post-exposure to images) as a within participants variable, image condition (sexual competition, no sexual competition and control) as a between participants variable, and faithfulness accuracy (proportion of trials in which the more faithful model was chosen) as the dependent variable. There was no significant main effect
of test time ($F_{1,57} = 0.07, p = .792$, pre: $X\pm SD = 0.59\pm 0.11$, post: $X\pm SD = 0.60\pm 0.12$) and no main effect of image condition ($F_{2,57} = 2.13, p = .128$, sexual competition: $X\pm SD = 0.57\pm 0.10$, no sexual competition: $X\pm SD = 0.62\pm 0.07$, control: $X\pm SD = 0.60\pm 0.10$). Nor was there any significant interaction between test time and image condition ($F_{2,57} = 0.93, p = .402$) (Fig. 2.1). These results provide no evidence that accuracy of faithfulness judgements increases when men are primed to consider sexual competition. Overall, accuracy was significantly above chance level ($t_{59} = 8.33, p < .001$, $X\pm SD = 0.60\pm 0.09$). The effect size was large ($r = 0.74$, 95% CI = 0.59-0.83). These results replicate the accuracy demonstrated in Experiment 1 with a new sample of participants.

Participant’s self-reported preference for faithfulness showed good test-retest reliability ($r_{60} = .76, p < .001$). However, this preference was unrelated to accuracy of faithfulness judgements ($r_{60} = .05, p = .708$). Accuracy was also unrelated to preference for the other nine traits measured in the Mate Preference Questionnaire, all $r s < .11, ps > .40$.

**Perceived trustworthiness and faithfulness**

Using the trustworthiness difference scores from Experiment 1, I investigated whether the difference in perceived trustworthiness was related to the proportion of participants who accurately chose the more faithful model from each pair. As there was no significant difference in the proportion of times that participants chose the faithful model between the pre and post exposure tasks (see ANOVA above), I calculated the overall mean for the proportion of times that participants correctly chose the faithful model and correlated this variable with trustworthiness difference. The correlation was large and significant ($r_{17} = 0.73, p = .001$), again replicating the results of Experiment 1 with a new sample of participants.
Figure 2.1. Faithfulness accuracy (proportion of trials in which the faithful model was correctly chosen in a forced choice task) before and after exposure to one of three image conditions. S.E bars are shown. There was no difference in the proportion of accurate choice between the pre and post exposure tasks with men choosing the most faithful model significantly above chance (0.5, represented by the x axis). There was no effect of image condition on the proportion of accurate choices.
2.5. General discussion

People show high consensus on many trait judgements, often from limited visual information, and these initial impressions can sometimes contain a kernel of truth (Mueller & Mazur, 1997; Wilson & Eckel, 2006; Todorov et al., 2011). Previous research suggests that men’s judgements of female faithfulness made from images of women show high consensus (O’Connor et al., 2011; Rhodes et al., 2013; Singh, 2004) but no accuracy (Rhodes et al., 2013). Our results provide the first evidence that such judgements can contain a kernel of truth. When asked to choose the more faithful women from pairs of images, men chose the woman who had not reported any extra-pair copulations significantly above chance level. Accuracy of judgements from faces had a moderate-large effect size and was replicated in two experiments using different samples of men. Accuracy of judgements from full person images also had a moderate effect size, but was not significant with our relatively small sample of pairs.

Although men’s judgements contained a kernel of truth when they selected the more faithful of two women in a forced choice task, they showed no accuracy in rating individual women. Their judgements of faithfulness did not correlate with the self-reported extra-pair copulation behaviour of the models. This result replicates Rhodes et al.’s (2013), using (a subset of) the faces from that study but different participants.

I examined three main ways in which men’s accuracy in faithfulness judgements might be improved: through the use of a forced choice task, by using full person images and by priming men to a mating environment depicting sexual competition. In Experiment 1, I found that men show some accuracy in their judgements of faithfulness when completing a forced choice task. I found no evidence that accuracy was better for full person than face images. If anything, the evidence for accuracy was clearer for faces, because accuracy was significant for faces, but only approached significance for full person images. This result seems somewhat paradoxical given that the full person images contained faces. However, the faces in these images were considerably smaller than in the face images, potentially making it more difficult to use any honest facial cues to faithfulness. The visual complexity of full person images would also have reduced the time available to process information from the faces.
In Experiment 2, I found no evidence that accuracy for face images was improved after being primed to a mating environment that depicted sexual competition. However, replicating the findings of Experiment 1, men's accuracy was significantly above chance level suggesting that their accuracy in faithfulness judgements when completing a forced choice task is robust. Faithfulness may be such an important trait in a potential partner (Buston & Emlen, 2003) that explicit priming to an environment depicting sexual competition is not needed to see some accuracy in faithfulness judgements (although this was not the case for ratings). Nevertheless, it cannot be ruled out that our priming manipulation was simply unsuccessful. The priming images used in this study have been used successfully in past research (Kilgallon & Simmons, 2005) and I followed the priming protocol described in Little et al. (2013), but I presented fewer images, resulting in a shorter overall priming time. It remains possible that priming men to a sexual competition context with a larger selection of images or for a longer period of time could enhance the accuracy of their faithfulness judgements.

Previous research has indicated that attractiveness can act as an honest cue to women's faithfulness (O'Connor et al., 2011; Singh, 2004). However, I found no relationship between the model's rated attractiveness and men's accuracy in their judgements of faithfulness. Nor did participants use individual components of attractiveness to make their judgements of faithfulness. Whereas Rhodes et al. (2013) found that women's accurate judgements of male faithfulness were cued by a specific component of attractiveness—sexual dimorphism (i.e. masculinity), I found no link between differences in ratings of femininity of the models and accuracy of faithfulness judgements. Nor did differences between models in other components of attractiveness (i.e. symmetry and averageness) correlate with accuracy. These results suggest that men do not use attractiveness as an accurate cue to female faithfulness.

Another trait that might relate to judgements of faithfulness is perceived trustworthiness. I found that the perceived trustworthiness of the models was related to men's accurate judgements of faithfulness: If the faithful model was perceived as more trustworthy than the unfaithful model, participants were more likely to correctly choose her as the faithful model. This finding is not in line with evidence from Rhodes et al. (2013) that indicated that women’s accurate judgements of male faithfulness were independent from their judgements of
trustworthiness. One explanation for these results is that, when asked to make trustworthiness judgements of women, men may automatically make judgements of faithfulness so that ratings of trustworthiness and faithfulness are actually capturing the same trait judgement. Why men’s perceptions of trustworthiness are related to their faithfulness judgements and women’s are not is unknown. In future research, one might provide a specific ‘trust scenario’ unrelated to mate choice to see if trustworthiness judgements still relate to faithfulness judgements. An alternative explanation for our finding is that judgements of faithfulness may be made using visual cues that are also used to make judgements of trustworthiness. For example, emotion expression has been found to influence a number of trait judgements including perceived trustworthiness (Oosterhof & Todorov, 2009; Said et al., 2009). Whether emotion expression might influence faithfulness judgements has not been explored. Although the models in this study posed with neutral facial expressions, neutral expressions can naturally resemble emotion expressions, which may in turn influence trait judgements (emotion overgeneralization, Said et al., 2009; Caulfield et al., 2014; Oosterhof & Todorov, 2008; Zebrowitz, 1996; Zebrowitz, 1997). More research is needed to further examine the visual cues that men use to make their judgements of faithfulness, including the use of emotion expression cues.

I have suggested that accuracy in faithfulness judgements could aid in assessing potential long-term partners to avoid cuckoldry. However, it could also play a role in assessing women’s willingness to engage in extra-pair copulations outside of their relationship. Mate poaching (whereby an individual attempts to engage another individual, already in a committed relationship, into a relationship or brief sexual encounter) is a prevalent mating tactic. Indeed, 60% of men admit to attempting to poach woman for a brief sexual encounter whilst 31% of women admit to being successfully poached from their committed relationship for a brief sexual encounter (Schmitt & Buss, 2001).

In summary, I show for the first time that men’s judgements of faithfulness from images of women can contain a kernel of truth when they are able to directly compare images in a forced choice task. Previously, accuracy in faithfulness judgements has only been found for women judging men’s faces (Rhodes et al., 2013). It is striking that men were able to show any accuracy from images alone after only a brief presentation, considering that accuracy in faithfulness
judgements made from behavioural information is relatively poor (Andrews et al., 2008; Rhodes et al., 2013).
CHAPTER THREE

Context dependent relationship between a composite measure of men’s mate value and ejaculate quality
3.1. Abstract

Secondary sexual traits in males are recognised as having arisen in order to gain access to reproductive opportunities, through their effects on the outcome of male-male competition and female choice. The phenotype-linked fertility hypothesis proposes that ejaculate quality is honestly advertised via secondary sexual traits. Alternatively, if males have limited resources to allocate to both pre and post-copulatory traits, males possessing attractive phenotypic or behavioural traits may produce poorer quality ejaculates. Sperm competition theory also predicts that the female phenotype will influence ejaculate quality, with males increasing investment as female attractiveness increases. However, the extent to which the male and female phenotypes interact in affecting ejaculate quality has not been widely studied. Here I examine how male and female phenotypes influence ejaculate quality in humans. Eighty-one men, for whom I had a composite measure of overall male mate value, produced a semen sample in response to images of either highly attractive or less attractive women. I found a significant relationship between male mate value and ejaculate quality that was context dependent. Sperm motility and concentration increased with male mate value but only when men viewed images of highly attractive women. Context dependence may contribute, in part, to the often conflicting patterns of variation found in studies that test the phenotype linked fertility hypothesis.
3.2. Introduction

Females typically have the greater investment in reproduction making them a limited resource over which males compete (Clutton-Brock & Parker 1992; Trivers 1972). Males gain access to reproductive opportunities through successfully competing in male-male competition and/or through female mate choice, so that males often evolve secondary sexual traits that contribute to success in defeating rival males and/or attracting females (Andersson 1994; Darwin 1871). Because females typically mate with more than one male, a male's reproductive success also depends on his ability to fertilise a female's ova, so that sexual selection continues after mating in the form of sperm competition and cryptic female choice (Eberhard 1996; Parker 1970). Recent research has begun to consider whether traits that influence a male's mating success are indicative of his post-copulatory fertilisation success (Kvarnemo & Simmons 2013).

The phenotype-linked fertility hypothesis proposes that male fertility is honestly advertised via secondary sexual traits (Sheldon 1994). A number of empirical studies have reported positive associations between male fertility parameters and the possession of attractive traits in a variety of taxa (Navara et al. 2012; Rasotto et al. 2010; Rogers et al. 2008). Although a recent meta-analysis of 21 species found a significant positive association between attractive male phenotypic traits and sperm viability, there was no evidence for a general significant relationship between attractive traits and sperm numbers, sperm size or sperm swimming speed (Mautz et al. 2013).

An alternative theory proposes that males who invest more in obtaining a mate (their pre-copulatory success) may have fewer resources available to invest in fertilisations (their post-copulatory success) (Parker et al. 2013). Life history theory posits that organisms generally have limited resources and must trade the allocation of those resources between different life history traits to maximize lifetime fitness (Roff et al. 2002). As a result, males may face a trade off between the allocation of limited resources to secondary sexual traits designed to increase their success at attracting or gaining access to mates, against post-copulatory traits that increase their chances of paternity success once a mating occurs (Parker et al. 2013). There is some empirical support for this hypothesis, with negative associations between male fertility and attractive male traits being reported from
a variety of taxa (Galeotti et al. 2012; Pitcher et al. 2009; Rowe et al. 2010), including humans (Simmons et al. 2011). Clearly the patterns of covariation between male phenotype and ejaculate quality vary greatly, and more studies are required to explore the factors responsible for this variation.

Sperm competition theory also predicts that the female phenotype will play an important role in ejaculate expenditure during a mating (Galvani & Johnstone 1998). Males make judgements of sperm competition risk using two main cues — the presence of rival males in the environment and the female’s expression of attractive phenotypic traits. There is consistent evidence that males invest more in their ejaculate when mating with attractive females (delBarco-Trillo 2011; Kelly & Jennions 2011). Increased investment may be beneficial for males if female attractiveness honestly indicates female reproductive value (Cornwallis & Birkhead 2007b; Lefranc & Bundgaard 2000; Pincheira-Donoso & Tregenza 2011), and/or if attractive females are more likely to be approached for copulations by rival males so that they impose a greater risk of sperm competition (Wedell et al. 2002).

Despite evidence that both the male and female phenotype influence ejaculate quality, only one study has examined the extent to which the two interact during a given mating event. Using chickens, Gallus gallus, Cornwallis and Birkhead (2007a) demonstrated that a male’s investment in his ejaculate was dependent upon both his value as a mate and the attractiveness of his partner. Amongst chickens, male mate value is most strongly determined by social hierarchy, with dominant males having greater access to females and controlling the mating opportunities of subordinate males (Pizzari & Birkhead 2000; Wilson et al. 2009). Female attractiveness is determined by the size of the head comb, with males preferring females possessing large head combs (Cornwallis & Birkhead 2007b). Whilst both subordinate and dominant males consistently prefer to mate with females possessing large head combs, only dominant males increase the quality of their ejaculate when mating with attractive females. Subordinate males invested equally in attractive and unattractive females. Clearly both the male and female phenotype should be considered when investigating phenotypic plasticity in ejaculate quality, and the degree to which male and female phenotypes interact requires further research.
The aim of this study was to examine if female attractiveness and men’s own phenotypic traits interact to influence ejaculate quality in humans. Sperm competition in humans is a hotly debated topic (Dixson 2009; Shackelford & Goetz 2007; Simmons et al. 2004). Patterns of variation in testes size and ejaculate quality among primates suggest that humans have not been subject to strong selection for offensive sperm competition traits (Leivers & Simmons 2014). Conversely, there is considerable evidence suggesting that men have evolved behavioural and psychological strategies designed to avoid sperm competition (Buss 1988b; Shackelford et al. 2002; Shackelford et al. 2005b). However, there has been very little research investigating phenotypic plasticity in ejaculate quality (Kilgallon & Simmons 2005; Leivers & Simmons 2014).

In humans, both morphological traits and behavioural traits are important determinants of male mate quality. Women rate symmetrical, masculine men with low-pitched voices as more attractive (Rhodes 2006; Simmons et al. 2011) and they value the ability of men to accrue resources, as well as traits such as dominance (Buss 1989; Geary et al. 2004; Waynforth 2001). Evidence that men advertise their fertility through attractive phenotypic traits remains mixed. A study conducted on 66 Spanish men found that men rated as attractive had a higher number of morphologically normal sperm and a higher proportion of motile sperm (Soler et al. 2003), although a similar study using 118 Australian men failed to replicate these findings (Peters et al. 2008). In a study investigating the relationship between attractiveness, voice pitch and ejaculate quality, Simmons et al. (2011) found that men with low-pitched voices were rated as more attractive but had lower sperm concentrations, suggesting a trade off between pre- and post-copulatory traits. However, there has been no research investigating whether behavioural traits influence ejaculate quality in humans. Dominance has been noted as a preferred trait in men and research on non-human species has indicated that dominance can influence ejaculate quality (Froman et al. 2002; Montrose et al. 2008; Pitcher et al. 2009; Thomas & Simmons 2009). Further research investigating the relationship between male quality — determined by the possession of preferred morphological and behavioural traits — and ejaculate quality in humans is warranted.

Female quality is also strongly determined by physical attractiveness as expressed through phenotypic traits such as symmetry, voice pitch and waist-to-
hip ratio (Feinberg et al. 2008; Geary et al. 2004; Rhodes 2006; Singh et al. 2010). Like many non-human species, there is evidence that women honestly indicate their reproductive value via phenotypic signals (Jasienska et al. 2004; Singh 2004). Although evidence from non-human animals strongly suggests that the female phenotype influences the ejaculate, there has been very limited research investigating this prediction in humans. Baker and Bellis (1993) reported a positive correlation between ejaculated sperm numbers and female body size. They argued that such a response could be adaptive, citing evidence that larger women have better fertility and fecundity. However, these findings are at odds with research showing that women with a large body mass index are viewed as less attractive (Richmond et al. 2012). As female attractiveness in humans is more accurately explained by variation in traits such as sexual dimorphism in the face and body (O’Connor et al. 2013; Singh et al. 2010), if men’s expenditure on their ejaculate is influenced by the female phenotype, it is more likely that men should respond to variation in female sexual dimorphism than to variation in body mass index.

Here I ask if female attractiveness and men’s own mate quality interact to influence ejaculate quality in humans. Men were asked to produce a semen sample in response to one of two sets of images of women that had been rated previously as highly attractive or of low attractiveness. I collected data on three measures of participants’ putative quality — attractiveness and dominance as rated by women from participant images, and the participants’ self perceived mate value — which were combined to provide a composite measure of male mate value.

3.3. Methods

Participants

Eighty-one male participants were recruited from the University of Western Australia community and other universities in the Perth metropolitan area. All participants were heterosexual, Caucasian and aged between 18 and 35 years of age ($X±SE=22.23±0.5$). Participants were randomly assigned to one of two groups: One group provided a semen sample when viewing images of women rated as highly attractive, the other group provided a semen sample whilst viewing images
of women rated as less attractive. Ethics approval for this research was granted by 
the University of Western Australia Human Ethics Research Committee (project 
number RA/4/1/5012).

Visual stimuli

Equal numbers of participants were assigned at random to one of two 
stimuli sets: high attractive stimuli or low attractive stimuli. The stimuli were 
comprised of front-view unclothed images of 93 women, taken with approval from 
a previous study (Thornhill & Grammer 1999). Full details on how the images 
were collected are provided in Thornhill and Grammer (1999).

Images for the high and low female attractiveness stimuli were chosen 
based on the combined ratings of attractiveness for the face and body made by 
participants in Thornhill and Grammer's (1999) study. The 15 most and least 
attractive models from that study were chosen for the high attractive (HA, $X\pm SE= 
4.93\pm0.08$) and low attractive (LA, $X\pm SE= 3.00\pm0.08$) stimuli respectively. This 
difference in mean attractiveness was significant, $t_{28}= 17.35$, $p< .001$. In order to 
confirm the difference in attractiveness between high and low attractive women in 
this study, I had participants rate their assigned images for overall attractiveness 
during the experimental procedure. Only images of Caucasian women were used 
and images were excluded if any features of the face or body were obscured.

Male mate value

Three separate measures of male quality — self perceived mate value, 
attractiveness and dominance— were used to construct a composite measure of 
male mate value

Self perceived mate value was assessed by having participants complete the 
Components of Self-Perceived Mate Value questionnaire (CSMV). The CSMV 
combines and evaluates a number of measures of self-perceived male mate value 
and outlines 7 distinct factors that account for 71% of the variance in self-
perceived male mate value (Fisher et al. 2008). These factors are sociality, looks, 
wealth, views of the opposite sex, parenting, relationship history and fear of 
failure.

Attractiveness and dominance scores were collected by having 
photographs of each male participant rated for attractiveness or dominance by 30
heterosexual, Caucasian women (15 rated attractiveness, 15 rated dominance). These ratings were made on a scale of 1 ("Not at all attractive/dominant") to 7 ("Very attractive/dominant"). Participants were instructed to wear shorts and a t-shirt and to relax their arms at their sides whilst looking straight ahead with a neutral expression. All photographs were scaled to a portrait orientation of 1232 x 816 pixels shown at a resolution of 1608 x 1050 pixels on a 20” screen iMac. Images were viewed at an approximate distance of 60cm, at a vertical visual angle of approximately 16.4 degrees and a horizontal visual angle of approximately 4.8 degrees. Photoshop was used to remove jewellery and tattoos, to colour all clothing black and to colour the background white. Images were presented for 2 seconds followed by a response screen asking raters to make their rating on the keypad. Participants were provided with no details about the men they rated but were asked if they recognised any of the men. If a rater did recognize a male participant, their rating for that participant was removed from the data set to avoid potential effects of familiarity on trait judgements (Zajonc 1968).

Procedure

i) Laboratory visit

Participants were met in the laboratory and were asked to read an information sheet and sign a consent form. To allow the cross-referencing of data and ensure anonymity (and thus encourage honest self-reported data), participants nominated a unique 4-digit participant code to be written on all materials.

Due to the significant influence of a number of lifestyle factors on semen quality (Mathur & D'Cruz 2011; Tanrikut & Schlegel 2007; Vukovic et al. 2009), participants were asked to complete a Lifestyle Survey (detailed information is available from Kilgallon and Simmons, 2005). They then completed the mate value questionnaire before having their photograph taken, which was independently rated for attractiveness and dominance at a later date.

Participants were given an envelope containing images from their assigned stimulus condition (HA or LA) and all materials needed to collect a semen sample at home. At this time they were also given verbal instructions outlining the collection process and had the opportunity to ask any questions.
ii) *Semen collection*

Participants collected their semen sample in their own home via masturbation whilst viewing the images they had been assigned. Masturbation is a commonly used collection method for experimental research of this kind (Elzanaty & Malm 2008; Kilgallon & Simmons 2005; Yamamoto et al. 2000). There is also evidence that samples collected via masturbation whilst viewing explicit images are of comparable quality to samples collected via coitus (Wylie & Pacey 2011). Subjects were instructed to abstain from all sexual activity for at least 48 hours, but no longer than six days before collection. Participants opened their envelope directly prior to collecting the sample and were asked to first complete an Attractiveness Ratings Task which was comprised of a small questionnaire asking the participant to rate each of their five assigned images for attractiveness on a scale of 1 (‘Not at all attractive’) to 7 (‘Very attractive’). This was included both to ensure that participants attended to the images prior to collecting the sample, and also to confirm post hoc that participants found the HA stimuli to be more attractive than the LA stimuli.

Participants collected their semen sample after 07:00 in a 70ml container, which was then wrapped in aluminium foil and stored in a warm place. Participants then completed the Ejaculate Information Sheet, which was included to ascertain whether the protocol had been followed and to collect information on the time the sample was collected, the time taken to collect the sample, whether any portion of the sample was not collected in the container and the period of time between sample collection and the participant’s last ejaculation. Participants were asked to return the sample to the laboratory with all other materials within 60 minutes of collection and by no later than 09:30. Participants were met in the laboratory where they received a debrief information sheet and remuneration of $10AUD.
3.4. Semen analysis

Semen quality was assessed using the Hamilton Thorne Computer Assisted Semen Analysis (CASA) system, immediately upon delivery. A note was made of any samples that were not fully liquefied.

Aliquots of 2 microliters of the semen sample were pipetted into each of the chambers of a pre-warmed Leja Standard Count 4 chamber slide which was then placed onto a pre-warmed Hamilton Thorne HTM MiniTherm® stage warmer set at 37 Celsius. Data were collected on sperm concentration, percentage of motile sperm, average path velocity (VAP), straight line velocity (VSL), velocity along the sperm cells point-to-point track (VCL), the lateral amplitude of sperm head movement (ALH), the frequency with which the sperm head crosses the average sperm path (BCF), the straightness of the sperm's path (STR), and the linearity of the sperm's path (LIN). One scan was taken from each of the four chambers followed by a further two scans from two chambers chosen at random. These six scans were then averaged to produce mean values for the sperm parameters.

If the CASA was unable to analyse a sample due to a very high sperm concentration, a proportion of the semen sample was centrifuged for six minutes at 13000RPM in an Eppendorf Centrifuge 5804 to separate the sperm and seminal plasma. The seminal plasma was then used to dilute a portion of the original sample. A normal analysis was then carried out and the correct sperm concentration was calculated.

3.5. Results

Semen quality

Four participants were excluded from analyses because they had sperm concentrations of less than 15 million sperm per ml, which is the lower reference limit for what is considered normal by the World Health Organisation (2010). Concentration values were log transformed to achieve normality. As is typically the case, semen parameters were highly correlated (Appendix C). I therefore followed the protocol recommended by Agarwal et al. (2003) whereby sperm
parameters were entered into a principal components analysis to reduce the data set and provide principle axes (PCs) of semen quality variation for analyses. Three principal components with eigenvalues greater than 1 were extracted and were found to account for 83.8% of the variance in semen quality (Table 3.1).

Sperm PC1 described variation in the concentration of sperm, the percent of sperm that were motile and the swimming speed of motile sperm, with VAP, VCL, ALH and the percent of motile sperm in the ejaculate contributing most strongly to this axis of variation. These semen parameters have been linked to fertilisation success in IVF treatments (Donnelly et al. 1998; Hirono et al. 2001). Sperm PC2 was loaded most strongly by factors related to the straightness and linearity of the sperm swimming path, whilst sperm PC3 was loaded most heavily by low concentration.

All three sperm quality variables were run independently in a stepwise GLM with all lifestyle and collection variables from the Lifestyle Survey and Ejaculate Questionnaire included. No lifestyle or collection variables were found to influence sperm PC1. Sperm PC2 was influenced by the average number of hours seated during the day, \( F_{4,64} = 3.11, p = .021 \), the amount of sexual activity undertaken during an average week, \( F_{3,64} = 2.84, p = .045 \), whether the participant regularly consumed Vitamin C rich foods or supplements, \( F_{1,64} = 6.79, p = .011 \), and the participant’s weight, \( F_{1,64} = 9.38, p = .003 \). Sperm PC3 was influenced by whether or not the participant had ever suffered testicular trauma, \( F_{1,70} = 11.00, p = .001 \), whether they had recently been ill, \( F_{1,70} = 12.20, p = .001 \), or had recently been taking medication, \( F_{1,70} = 8.10, p = .006 \), and the average amount of sexual activity undertaken during a week, \( F_{3,70} = 3.27, p = .026 \). All contributing variables were included as covariates in subsequent analyses.

**Mate value**

The participants’ dominance scores were normally distributed whilst attractiveness scores were not. However, because residuals from all analyses using male attractiveness were normally distributed, male attractiveness scores were not transformed. Female raters showed good consensus on their ratings of attractiveness and dominance (Attractiveness: Cronbach’s \( \alpha = .98 \), Dominance: Cronbach’s \( \alpha = .93 \)).
<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
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<tbody>
<tr>
<td>VAP</td>
<td>.777</td>
<td>.582</td>
<td>.117</td>
</tr>
<tr>
<td>VSL</td>
<td>.534</td>
<td>.796</td>
<td>.140</td>
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<tr>
<td>VCL</td>
<td>.941</td>
<td>.054</td>
<td>.277</td>
</tr>
<tr>
<td>ALH</td>
<td>.784</td>
<td>-.406</td>
<td>.372</td>
</tr>
<tr>
<td>BCF</td>
<td>-.055</td>
<td>.394</td>
<td>.520</td>
</tr>
<tr>
<td>STR</td>
<td>-.638</td>
<td>.625</td>
<td>.135</td>
</tr>
<tr>
<td>LIN</td>
<td>-.521</td>
<td>.817</td>
<td>-.094</td>
</tr>
<tr>
<td>% motile</td>
<td>.683</td>
<td>.242</td>
<td>-.496</td>
</tr>
<tr>
<td>concentration</td>
<td>.402</td>
<td>.175</td>
<td>-.779</td>
</tr>
<tr>
<td>% variance in sperm quality explained</td>
<td>41.1%</td>
<td>27.1%</td>
<td>15.6%</td>
</tr>
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</table>

**Table 3.1.** Principal components analysis on all sperm quality parameters to produce principal components that account for sperm quality. VAP = average path velocity, VSL = straight line velocity, VCL = velocity along the sperm cells point-to-point track, ALH = lateral amplitude of sperm head movement, BCF = frequency with which the sperm head crosses the average sperm path, STR = straightness of the sperm’s path, LIN = linearity of the sperm’s path, % motile = percentage of motile sperm in the ejaculate, concentration = concentration of sperm in the ejaculate (million sperm/ml).

Items from the CSMV questionnaire were summed to produce a ‘self perceived mate value’ score (Dunkel & Mathes 2011; Easton 2012; Fisher et al. 2008). The items “I often stay at home because I have nothing to do”, “I would like members of the opposite sex to hit on me more than they do” and “I often worry about not having a date” were reverse loaded so that high scores indicated a high self perceived mate value. Self perceived mate value was correlated with both rated attractiveness and dominance (attractiveness: $r = .42, p < .001$, dominance: $r = .23, p = .041$), and attractiveness and dominance were also positively correlated ($r = .52, p < .001$). As all three male quality measures were significantly correlated, it
was suitable to combine them into a composite factor (hereafter ‘male mate value’) using a principal components analysis. I extracted one component that accounted for 66.28% of the variance in male mate value. This component was loaded by all three male mate quality variables and was most heavily loaded by attractiveness (attractiveness, 0.86; dominance, 0.77; self perceived mate value, 0.68).

Response to visual stimuli

Using ratings from the Attractiveness Ratings Task, I found that participants assigned the HA stimuli rated their images as significantly more attractive than did participants assigned the LA stimuli, \( t_{75} = 5.17, p < .001 \), Cohen’s \( d = 1.20 \), indicating that the manipulation of men’s perceptions of stimulus attractiveness was successful (LA: \( X \pm SE = 3.26 \pm 1.00 \); HA: \( X \pm SE = 4.31 \pm 0.77 \)).

Sperm PC1 was entered as the dependent variable into a univariate GLM with stimuli attractiveness entered as a fixed factor and overall male mate value entered as a covariate. A significant main effect of stimulus attractiveness was found, \( F_{1,73} = 5.18, p = .026, \eta^2_{partial} = .066 \). However, the interaction between male mate value and stimulus attractiveness was significant, \( F_{1,73} = 4.74, p = .033, \eta^2_{partial} = .061 \) (Figure 3.1). The concentration of sperm and sperm motility increased with increasing male mate value when men viewed images of attractive women, \( \beta = .38, p = .018 \). In contrast, male mate value did not influence ejaculate quality significantly when participants viewed images of low attractive women, PC1, \( \beta = -.13, p = .447 \).

Sperm PC2 and sperm PC3 were run individually as dependent variables in the same GLM analyses described above. No significant interactions or main effects were found.
Figure 3.1. Regression model with composite male mate value entered as a predictor of semen quality (PC1). The filled circles and solid line represent participants who viewed images of highly attractive women when collecting the semen sample (N=39). The empty circles and dotted line represent those who viewed images of women of lesser attractiveness during sample collection (N=38).

3.6. Discussion

I show that variation in both the male and female phenotype interact to influence ejaculate quality in humans. I found that a composite measure of male mate value — that captures variation in attractiveness, dominance and self perceived mate value — predicted ejaculate quality but that this effect was context dependent, apparent only when men produced ejaculates in response to images of highly attractive women. Although the effect size of this interaction was small and was found to influence only the first principal component (PC1) describing ejaculate
quality, the interaction was nevertheless significant and PC1 explained considerably more variance in semen quality than both PC2 and PC3 combined.

Whilst some studies have found support for the phenotype-linked fertility hypothesis by showing positive associations between attractive phenotypic traits and ejaculate quality (Mautz et al. 2013; Navara et al. 2012; Rasotto et al. 2010; Rogers et al. 2008), others have found negative associations between these pre- and post-copulatory traits (Galeotti et al. 2012; Pitcher et al. 2009; Rowe et al. 2010) and still others have reported no relationship (for a review, see Mautz et al. 2013; Peters et al. 2008). The results of this study provide support for the phenotype-linked hypothesis with attractive men producing better quality ejaculates. However, this result was entirely dependent upon the stimuli provided. Increasingly, studies are showing that males exhibit considerable phenotypic plasticity in ejaculate quality so that tests of the phenotype-linked fertility hypothesis that fail to take into account the context within which an ejaculate is produced may be too simplistic. For example, had the study focused on the influence of the male phenotype alone on ejaculate quality, the conclusions would have differed, depending on whether the men had been provided with stimuli or not (Yamamoto et al. 2000) and, as I have shown in this study, the attractiveness of the stimuli provided. Taking into account the context in which ejaculates are assessed will undoubtedly provide new insights into factors affecting variation in ejaculate quality.

Interestingly, new research investigating the influence of female attractiveness on men’s allocation of attention has also found a significant interaction between female attractiveness and the man’s own self perceived attractiveness. Morgan and Kisley (2013) found that men showed greater attention (as measured through event-related brain potentials) when viewing images of attractive over unattractive women. However, whilst all men showed increased attention to attractive women, men who had been primed to believe that they themselves were of low attractiveness showed greater attention to images of low attractive women than men who were primed to believe themselves as being highly attractive. Thus, allocation of attention in men appears to be modulated by both the attractiveness of the female target face and their own mate value. These findings complement the results of this study by suggesting that interactions
between male and female attractiveness drive cognitive mate choice responses which then impact more cryptic, physiological responses via the ejaculate.

Evidence suggests that humans have evolved behavioural and psychological strategies in response to sperm competition risk (Buss 1988b; Shackelford et al. 2005a; Shackelford et al. 2002), but evidence for physiological adaptations is scarce (Kilgallon & Simmons 2005). Sperm competition theory predicts that males will invest more in the ejaculate when mating with attractive or otherwise preferred females, because these females will themselves have greater opportunity to mate and thereby present a greater risk of sperm competition (Galvani & Johnstone 1998; Wedell et al. 2002). The results presented here provide little evidence that female attractiveness affects men’s ejaculate quality in a manner predicted by sperm competition theory. Rather, the influence of female attractiveness on ejaculate quality was dependent upon male mate value. Qualitative examination of the data shows that men of relatively low mate value tended to produce ejaculates of lower not higher quality when viewing attractive women, while the reverse was true for men of higher mate value. Future research should consider employing a repeated measures design to further address the issue of ejaculate plasticity in men.

Our results may be in line with predictions made by assortative mating. A number of empirical studies have shown that men and women often choose to pair with an individual who shares similar genetic, phenotypic or behavioural qualities (He et al. 2013; Little et al. 2006; Taylor et al. 2011; Watson et al. 2004; Zietsch et al. 2011) and evidence from non-human animals suggests that assortative mating may in fact lead to greater reproductive success (Ariyomo & Watt 2013; Both et al. 2005; Budaev et al. 1999; Masumoto 1999). Although the participants who took part in this study rated the high attractiveness stimuli as more attractive than the low attractiveness stimuli regardless of their own mate value, the results of this study suggest that men may invest preferentially in women who are similar to their own market value. Indeed, although not statistically significant, there was a negative trend between male mate value and sperm quality in those participants who responded to the low attractiveness stimuli.

I find evidence for variation in sperm concentration and sperm motility dependent upon an interaction between male mate value and female attractiveness. Sperm concentration is currently the ejaculatory trait for
which there is the strongest evidence of socially mediated phenotypic plasticity (Kelly & Jennions 2011), although sperm motility can also be adjusted (Cornwallis & O’Connor 2009; Kilgallon & Simmons 2005). Prior to ejaculation, emission occurs whereby sperm are transported from the epididymis to the posterior urethra where they are mixed with the seminal fluid components released from the prostate, van deferens and ampulla, and seminal vesicles (Newman et al. 1982). These non-sperm components of the ejaculate include a number of proteins that influence the motility of sperm (de Lamirande 2007; Ding et al. 2007; Murdoch & Goldberg 2014). It is during emission where a mechanism is available to alter both sperm numbers and seminal fluid proteins that influence sperm motility. Indeed, studies of Drosophila have found that males do adjust the protein composition of seminal fluids in response to their perceptions of female mate value (Wigby et al. 2009). In humans, the emission phase of ejaculation is under considerable cerebral control and may be induced through genital stimulation or observing erotic stimuli (Comarr 1970; Giuliano & Clement 2005). Indeed, erotic stimuli are routinely provided to male fertility patients during ejaculate collection as it is found to improve the motility and concentration of the sperm ejaculated (Wylie & Pacey 2011; Yamamoto et al. 2000). Therefore it is possible for men to adjust their sperm concentration and motility rapidly based on their immediate sexual environment.

In conclusion, I show that both male and female phenotypes interact in their effect on ejaculate quality in humans. I show some evidence for the phenotype-linked fertility hypothesis with high value men producing better quality ejaculates. Importantly, however, this response was dependent upon the attractiveness of the female stimuli provided: High value men only produced better quality ejaculates than lower value men when responding to images of attractive women. When responding to images of women rated as being low in attractiveness, male mate value did not influence ejaculate quality. The results of this study demonstrate the importance of taking into account the context in which ejaculates are collected and assessed when investigating both sperm competition theory and the phenotype linked fertility hypothesis.
CHAPTER FOUR

Sperm competition in humans: mate guarding behaviour negatively correlates with ejaculate quality
4.1. Abstract

In species where females mate with multiple males, the sperm from these males must compete to fertilise available ova. Sexual selection from sperm competition is expected to favour opposing adaptations in males that function either in the avoidance of sperm competition (by guarding females from rival males) or in the engagement in sperm competition (by increased expenditure on the ejaculate). The extent to which males may adjust the relative use of these opposing tactics has been relatively neglected. Where males can successfully avoid sperm competition from rivals, one might expect a decrease in their expenditure on tactics for the engagement in sperm competition and vice versa. In this study, I examine the relationship between mate guarding and ejaculate quality using humans as an empirical model. I show that men who performed fewer mate guarding behaviours produced higher quality ejaculates, having a greater concentration of sperm, a higher percentage of motile sperm and sperm that swam faster and less erratically. These effects were found independent of lifestyle factors or factors related to male quality. These findings suggest that male expenditure on mate guarding and on the ejaculate may represent alternative routes to paternity assurance in humans.
4.2. Introduction

In species where females mate with multiple males, the sperm of two or more males must compete to fertilise available ova (Parker 1970). Selection from sperm competition is expected to favour opposing adaptations that function either in the avoidance of or engagement in sperm competition (Parker 1984; Simmons 2001). Adaptations for the avoidance of sperm competition can include the use of mate guarding or anti-aphrodisiac odours and copulatory plugs, while adaptations for the engagement in sperm competition include copulation frequency and duration or strategic adjustments in ejaculate quality (Dickinson & Leonard 1996; Garcia-Gonzalez & Gomendio 2004; Kelly & Jennions 2011).

Investment in behavioural mate guarding is likely to represent a significant cost for males as it reduces their ability to perform other ecologically important behaviours such as territorial patrol, foraging and pursuing additional mating partners (Alberts et al. 1996; Gangestad & Simpson 2000; Komdeur 2001; Low 2006). Therefore, males should only invest in mate guarding when the reproductive benefits of mate guarding outweigh the costs. Indeed, there is evidence to show that males will adjust their investment in mate guarding dependent on the perceived risk of sperm competition from rival males (Kureck et al. 2011; Schofl & Taborsky 2002; Simmons 2001). Likewise, physiological investments into ejaculate production are costly for males, and there is widespread evidence that males will also adjust their investment into the ejaculate dependent on their perceptions of sperm competition risk (for a review, see Kelly & Jennions 2011). However, little is known about how individual males might balance their investments into tactics for the engagement in and avoidance of sperm competition when paired with a given female. Where mate guarding is highly effective we might expect males to reduce their investment into physiologically expensive ejaculates. Conversely, were males unable to effectively guard their mates, we might expect them to increase their expenditure on the ejaculate.

Some evidence is available to suggest that male expenditure on the engagement in sperm competition may be negatively associated with their expenditure on its avoidance. For example, in a number of colonial bird species, at least one member of the breeding pair is required to protect the nest site from
intruders, resulting in periods of time in which a male is unable to guard his mate (Birkhead et al. 1987). Therefore, preventing the female from engaging in extra-pair copulations through mate guarding can be compromised, so that males may increase the use of tactics for the engagement in sperm competition. Indeed, in a comparative study of 173 bird species, Møller and Birkhead (1991) found that species in which males were limited in their use of mate guarding had an increased frequency of in-pair copulations (IPCs). As the outcome of sperm competition is often influenced by the quantity of a male's sperm in the female's reproductive tract (Birkhead & Møller 1998; Boschetto et al. 2011; Martin et al. 1974; Wedell et al. 2002), the increased use of IPCs likely functions in competing for paternity when males are unable to avoid sperm competition through mate guarding.

Further evidence can be found within species where males adopt alternative mating tactics (Simmons et al. 2007b). For example, in the Mediterranean wrasse (Alonzo & Warner 2000) there are three distinct male phenotypes that differ in their reproductive strategies for achieving paternity success. Satellite and nesting males actively guard their mates from rival males whilst sneaker males ‘sneak’ copulations and therefore gain reproductive success through sperm competition alone. Sneaker males produce ejaculates of higher quality than both satellite and nesting males, suggesting that male investment in tactics for the engagement in sperm competition and its avoidance are dependent upon the mating strategy adopted. Whether a negative association between tactics for the avoidance of and engagement in sperm competition is present within species that lack discreet alternative reproductive tactics has not been studied.

Here, I examine the association between expenditure on mate guarding and the ejaculate using humans as an empirical model. Human sperm competition is a hotly debated topic (for a review, see Leivers & Simmons 2014). Humans are generally considered socially monogamous, with limited evidence for polygyny (Dixson 2009; Gray & Garcia 2013), suggesting that humans are subject to relatively weak selection from sperm competition. Indeed, humans lack morphological indicators of sperm competition, such as large relative testes size (Harcourt et al. 1995; Simmons et al. 2004). However, female extra-pair copulations in humans are relatively common with approximately 20% of women reporting cases of sexual infidelities (Johnson et al. 2001; Simmons et al. 2004) and there is considerable evidence that men have evolved behavioural adaptations that
function in the prevention of extra-pair copulations (Buss 1988b; Buss & Shackelford 1997; Strassmann et al. 2012). For example, mate guarding has been well studied in humans and has been documented across cultures as a tactic that functions to avoid sperm competition by preventing females from engaging in copulations with rival males (Buss 1988b; Buss & Shackelford 1997; de Miguel & Buss 2011; Flinn 1988; Murdock 1967). Men may also have developed behavioural and physiological tactics for the engagement in sperm competition. Men show an increased interest in IPCs as the period of time between the couple’s last copulation increases (Shackelford et al. 2007) and there is also evidence to suggest that men increase their investment in ejaculate quality when responding to explicit images depicting sperm competition (Kilgallon & Simmons 2005).

Considering our hunter-gatherer origins, it seems likely that men would have been limited in their ability to continuously guard their mates from rival males due to ecological constraints. Anthropological data suggest that extra-pair sex was prevalent across many preindustrial societies (Broude 2003; Broude & Greene 1976) so that humans, like other animals, are expected to have evolved mechanisms for the engagement in and avoidance of sperm competition (Leivers & Simmons 2014). When the relationship between mate guarding and IPC frequency was explored in humans, it was found that those men who performed a high number of mate guarding behaviours also engaged in more frequent IPCs (Shackelford et al. 2006). These findings might suggest a positive relationship between tactics for the engagement in sperm competition in humans. However, IPC frequency may be a poor indicator of a man’s investment in tactics for the engagement in sperm competition as women can also initiate copulations (Bullivant et al. 2004). Furthermore, mate guarding and copulation are not necessarily mutually exclusive behaviours; the more time a man spends with his mate, the greater opportunity he has to pursue copulations with her. Indeed, IPC frequency could arguably be considered a form of mate guarding, potentially reducing a female’s tendency to seek extra-pair copulations, which would account for the positive relationship between mate guarding behaviour and IPC frequency. A physiological mechanism for the engagement in sperm competition that has been widely researched in non-human animals, but rarely in humans, is strategic adjustment in ejaculate quality (Kelly & Jennions 2011). Here I examined the relationship between mate guarding and ejaculate quality in humans and
hypothesize that men will show a negative correlation between their use of mate guarding behaviours and ejaculate quality because men who spend more effort guarding are expected to face a lower risk of sperm competition.

Forty-five male participants in committed heterosexual relationships were asked to provide a semen sample and information about their use of mate guarding behaviours. Research on both human and non-human animals has suggested that male quality can be associated with both ejaculate quality and mate guarding behaviour (Alonzo & Warner 2000; Graham-Kevan & Archer 2009; Kelly & Jennions 2011; Miner et al. 2009; Simmons et al. 2011; Soler et al. 2003). I therefore determined whether male mate value might account for variation in ejaculate quality and mate guarding by collecting information on three measures of male quality — self-perceived mate value, and female perceived dominance and attractiveness.

4.3. Methods

Participants

Forty-five male participants who were in committed heterosexual relationships were recruited from the University of Western Australia community and other universities in the Perth metro area. All participants were Caucasian in order to control for the possible influence of race on ejaculate parameters (Redmon et al. 2013; Swan et al. 2003). Participants were aged between 18 and 35 years ($X \pm SD = 24.20 \pm 4.72$), as sperm quality is known to decline after the age of 35 years (Neaves et al. 1984).

Ethics approval for this research was granted by the University of Western Australia Human Ethics Research Committee (project number RA/4/1/5012). Participants read an information sheet detailing their role in the study and provided written consent prior to commencing the study. Participants nominated a unique 4-digit participant code, which was written on all materials in order to allow the cross-referencing of data, and to ensure anonymity.
Procedure

i) Laboratory visit

Participants were first asked to read an information sheet and sign a consent form. Participants then completed a Lifestyle Survey in order to take into account the influence of environmental factors on sperm quality (Kilgallon & Simmons 2005). For example, participants reported their frequency of sexual activity during an average week so that this could be controlled statistically in analyses. After the Lifestyle Survey, men completed the Mate Retention Inventory-Short Form designed to measure their use of mate guarding behaviours (MRI-SF, Buss et al. 2008). The MRI-SF is a shortened form of the original Mate Retention Inventory (MRI) that assesses the frequency with which an individual performs a number of mate guarding behaviours (Buss 1988a, b). The MRI-SF assesses the performance of 38 behaviours, and responses from the MRI-SF have been shown to have good validity, strong internal consistency and a positive relationship with responses collected from the original 104-item MRI (Buss et al. 2008). MRI-SF scores (hereafter ‘mate guarding’) were calculated by summing responses so that high scores indicated high use of mate guarding behaviours.

To obtain measures of self-perceived mate value, participants completed the Components of Self-Perceived Mate Value questionnaire (CSMV). The CSMV combines and evaluates a number of pre-existing measures of self-perceived male mate value and produces distinct factors that account for variance in self-perceived male mate value (Fisher et al. 2008). Items from the CSMV questionnaire were summed to produce an overall CSMV score (hereafter 'mate value', Dunkel & Mathes 2011; Easton 2012; Fisher et al. 2008). The items “I often stay at home because I have nothing to do”, “I would like members of the opposite sex to hit on me more than they do” and “I often worry about not having a date” were reverse loaded so that high scores indicated a high self-perceived mate value.

Full-body photographs of each participant were taken and rated at a later date for attractiveness or dominance by 30 heterosexual, Caucasian women (15 rated attractiveness, 15 rated dominance) on a scale of 1 (“Not at all attractive/dominant”) to 7 (“Very attractive/dominant”).
Attractiveness is well known as a component of mate value (Barber 1995; Honekopp et al. 2007) and is associated with male mating success (Jokela 2009; Prokop & Fedor 2011). Dominance is also an important factor that contributes to male mate value (Hill et al. 2013; Kruger & Fitzgerald 2011). Rated dominance from images has been linked with real-life dominance in the workplace (Mueller & Mazur 1997) and mating success (Hill et al. 2013). Participants wore shorts and a t-shirt for the photograph and were told to assume a neutral expression. Photographs were scaled to a portrait orientation of 1232 x 816 pixels and shown at a resolution of 1608 x 1050 pixels on a 20” screen iMac. Images were viewed at an approximate distance of 60cm, at a vertical visual angle of approximately 16.4 degrees and a horizontal visual angle of approximately 4.8 degrees. Photoshop was used to remove jewellery and tattoos, colour clothing black and to colour the background white.

Participants were given an envelope containing a 70ml container for sample collection, aluminium foil and an Ejaculate Information Sheet, which was used to collect information on the time the sample was collected, the proportion of the sample collected and the time taken to collect the sample. Participants also reported how long it had been since their last ejaculate. This allowed me to take into account the participant’s most recent sexual activity and thus control statistically for the possible effects of sperm depletion in subsequent analyses. Participants were given verbal instructions outlining the collection process at this time and had the opportunity to ask any questions.

**ii) Semen collection**

Participants collected their semen sample in their own home via masturbation. Subjects were instructed not to use any erotic stimuli during collection and were asked to abstain from all sexual activity for at least 48 hours, but no longer than 6 days before collection. Samples were produced after 07:00 and deposited in the container provided. After collection, the participants were instructed to wrap the container in the provided foil and store in a warm place whilst in transit to the laboratory. Participants then completed the Ejaculate Information Sheet. The sample was returned to the
laboratory with all other materials within 60 minutes of collection and by no later than 09:30. Upon delivery, participants received a debrief information sheet and remuneration of $20AUD.

4.4. Semen analysis

Semen analysis was conducted using Hamilton Thorne Computer Assisted Semen Analysis (CASA) immediately after delivery, following the protocols outlined by the World Health Organisation (2010). CASA technology is used in both clinical and experimental settings and there is evidence that sperm quality parameters assessed via CASA predict fertilisation success in both human and in non-human species (e.g. Broekhuijse et al. 2012; Hirono et al. 2001; Larsen et al. 2000; Lavara et al. 2005). Aliquots of 2microliters of the semen sample were pipetted into each of the chambers of a pre-warmed Leja Standard Count 4 chamber slide which was placed onto a pre-warmed Hamilton Thorne HTM MiniTherm® stage warmer set to 37 Celsius. Data were collected on sperm concentration, percentage of motile sperm, average path velocity (VAP), straight line velocity (VSL), velocity along the sperm cells point-to-point track (VCL), the lateral amplitude of sperm head movement (ALH), the frequency with which the sperm head crosses the average sperm path (BCF), the straightness of the sperm's path (STR), and the linearity of the sperm's path (LIN). One scan was taken from each of the four chambers followed by a further two scans from two chambers chosen at random, which were then averaged to produce mean values for the sperm parameters.

If the CASA was unable to analyse a sample due to a very high sperm concentration ($N= 4$), a proportion of the semen sample was centrifuged for six minutes at 13000RPM in an Eppendorf Centrifuge 5804 to separate the sperm and seminal plasma. The seminal plasma was then used to dilute a known volume of the original sample. A normal analysis was then carried out and the correct sperm concentration was calculated after analysis.

After analysis, all contaminated materials were sanitized in a 1:10 mix of household bleach and water before being disposed of in a laboratory bin.
4.5. Results

Semen quality

Four subjects were excluded from analysis (leaving 41 participants) because their semen samples had concentration values of less than 15 million sperm per ml, which is below the lower reference limit for a normal sample according to the World Health Organisation (2010). Concentration values were log transformed to achieve normality. As semen parameters were highly correlated (Appendix D), I followed the protocol employed by Agarwal et al. (2003) whereby all sperm quality parameters were entered into a principal components analysis to produce principal components that accounted for variance in ejaculate quality. Three principal components with eigenvalues greater than 1 were extracted and were found to account for 88.48% of the variance in ejaculate quality (Table 4.1).

PC1 described ejaculates with high motility and high swimming speeds, being most heavily loaded by the percentage of motile sperm in the ejaculate, VAP, VSL and LIN, which have all been linked to fertilisation success in IVF treatments (Donnelly et al. 1998; Hirono et al. 2001). PC2 described the curvature of the sperm path, being positively loaded by VCL and ALH and negatively loaded by LIN. PC3 was positively loaded by BCF and negatively loaded by concentration and described samples characterized by low concentration with erratically moving sperm. PC3 was reversed scored so that high values indicated high concentration and less erratic sperm in order to allow direct comparisons with PC1 and PC2.

All three sperm quality variables were run independently in General Linear Models (GLM) with all lifestyle and collection variables from the Lifestyle Survey and Ejaculate Questionnaire included. Non-significant terms were removed from the model in a stepwise procedure (Crawley 1993). PC1 was influenced by the period of time between the semen sample’s collection and its analysis ($F_{1,29} = 10.96, p = .002$), by how much alcohol the participant consumed in an average week ($F_{2,29} = 5.63, p = .009$), and whether or not the participant consumed caffeinated beverages ($F_{1,29} = 11.78, p = .002$). PC2 was influenced by the length of time between the participant’s experimental sample and their last ejaculation ($F_{1,31} = 7.14, p = .012$) and by the participant’s frequency of sexual activity in an average week ($F_{1,31} = 20.46, p < .001$). PC3 was influenced by the length of time between the participant’s experimental sample and their last ejaculation ($F_{1,32} = $
4.75, p= .037). All contributing lifestyle and collection variables were controlled for in subsequent analyses.

**Mate guarding and mate value**

In all subsequent analysis, a subset of 34 participants were analysed as seven participants had missing or incomplete independent variables that necessitated exclusion. Female raters showed good consensus on their ratings of attractiveness (\(X \pm SD= 2.9 \pm 0.9\), Cronbach’s alpha= .97) and dominance (\(X \pm SD= 4.0 \pm 1.1\), Cronbach’s alpha= .89). Self perceived mate value did not correlate with either attractiveness (\(r_{34} = -.13, p = .468\)) or dominance scores (\(r_{34} = .03, p = .853\)).

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
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<tbody>
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<tr>
<td>LIN</td>
<td>.700</td>
<td>-.701</td>
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</tr>
<tr>
<td>concentration</td>
<td>.532</td>
<td>.078</td>
<td>-.689</td>
</tr>
</tbody>
</table>

**Table 4.1.** Principal components analysis on all sperm quality parameters to produce principal components that account for sperm quality. VAP= average path velocity, VSL= straight line velocity, VCL= velocity along the sperm cells point-to-point track, ALH= lateral amplitude of sperm head movement, BCF= frequency with which the sperm head crosses the average sperm path, STR= straightness of the sperm’s path, LIN= linearity of the sperm’s path, % motile= percentage of motile sperm in the ejaculate, concentration= concentration of sperm in the ejaculate (million sperm/ml).
but attractiveness and dominance were positively correlated ($r_{34} = .45, p < .001$). There was no evidence of a relationship between mate guarding and male quality, with mate guarding showing no significant correlations with self-perceived mate value ($r_{34} = .13, p = .481$), attractiveness ($r_{34} = -.16, p = .376$) or dominance ($r_{34} = -.27, p = .119$).

**Relationship between mate guarding and ejaculate expenditure**

PC1 was entered as the dependent variable into GLMs with all three male mate value variables (attractiveness, dominance, self-perceived mate value) and mate guarding entered as predictor variables. A significant main effect of mate guarding was found ($F_{1,28} = 4.51, p = .043$), with a negative relationship between the performance of mate guarding behaviours and PC1 (effect size: $\beta = -.03$, 95% CI [-.06, -.01], $R^2$ change = .072, Figure 4.1), indicating that participants who invested less in mate guarding behaviours produced ejaculates within which the motility of sperm was greater. None of the male mate value variables accounted for any variance in PC1 and were dropped from the final model.

The same GLM was run for both ejaculate quality PC2 and PC3. There were no significant main effects of variables of interest on PC2, but PC3 showed a significant main effect of mate guarding ($F_{1,31} = 4.89, p = .035$) with a negative relationship between the performance of mate guarding behaviours and PC3 (effect size: $\beta = -.04$, 95% CI [-.07, -.01], $R^2$ change = .12, Figure 4.2). This indicated that participants who invested less in mate guarding behaviours had higher numbers of sperm in their ejaculate and sperm that moved less erratically. Again, male mate value variables were not significant and were dropped from the final model.

According to guidelines from Field (2013), PC1 and PC2 were acceptable for analysis as both PCs had high factor loadings with at least four loadings of 0.6 or greater. However, PC3 had only two factor loadings greater than 0.6: concentration and BCF. For this reason, to confirm the significance of the observed patterns of variation, I also analysed concentration independently. Concentration is the strongest predictor of male fertility in men (Larsen et al. 2000) and is the most widely used indicator of ejaculate quality in sperm competition research (Kelly & Jennions 2011). Concentration was not influenced by any lifestyle variables and showed a significant main effect of mate guarding ($F_{1,32} = 5.09, p=$
.031, effect size: \( \beta = -.01, \) 95% CI \([-0.03, -0.01]\), \( R^2 = .14 \), indicating that participants who invested more in mate guarding behaviours had lower numbers of sperm in their ejaculate. This analysis corroborates the analyses based on principal components.

**Figure 4.1.** Relationship between mate guarding frequency and PC1 (after accounting for the influence of lifestyle and collection variables), which describes ejaculates with a high percentage of motile sperm and high swimming speed.
Figure 4.2. Relationship between mate guarding frequency and the unstandardized residuals of PC3 (after accounting for the influence of lifestyle and collection variables), which describes ejaculates with a high concentration of sperm and sperm that do not move erratically.

4.6. Discussion

Our study tested the general hypothesis that among males there would be a negative relationship between the use of tactics for the engagement in and avoidance of sperm competition, by examining the relationship between mate guarding and ejaculate quality in humans. The results of this study provide support for this hypothesis. Men who performed more mate guarding behaviours produced lower quality ejaculates, having a lower concentration of sperm, a lower percentage of motile sperm and sperm that swam slowly and erratically. These effects were independent of lifestyle or collection variables, and were not
predicted by men’s self-perceived mate value, attractiveness or dominance. Given
the personal nature of the task required, recruitment of subjects for studies such
as these is difficult, and this study was limited in its sample size so that the 95% CIs
on the observed effect sizes were broad. Nonetheless, the relationship was
confirmed using two independent sperm quality indices, which together
accounted for 59.1% of the variance in ejaculate quality. Previous research has
found evidence for a negative relationship between male expenditure on tactics
for the engagement in and avoidance of sperm competition, both across species
(Møller & Birkhead 1991), and within species with discrete alternative mating
strategies (Alonzo & Warner 2000). The results of this study provide evidence for
a continuous negative relationship between these opposing sperm competition
tactics in a species without discrete alternative tactics (Labuda et al. 2010;
Simmons et al. 2004).

Shackelford et al. (2006) found a positive relationship between the use of
mate guarding and IPCs in humans. However, their use of IPC frequency as a
measure of male engagement in sperm competition assumes that men control the
rate of IPCs, which is not necessarily the case. Females will play a significant role
in sperm competition and its avoidance (Eberhard 1996), and women will initiate
IPCs, particularly when at the most fertile point of their cycle (Bullivant et al.
2004). The fact that women can initiate IPCs makes IPC frequency a relatively poor
measure of male expenditure on sperm competition compared with ejaculate
quality. Indeed, women may be selected to initiate more IPCs with males who
show high use of mate guarding behaviours in order to ensure fertility, precisely
because such males invest less in their ejaculate. For example, work on fishes has
shown that male expenditure on mate guarding comes at a cost of reduced
expenditure on the ejaculate with the consequence that female fertility is reduced
(Warner 1997).

Unlike IPC frequency, ejaculate quality is unlikely to be directly influenced
by the female and certainly not in the context of the experimental design of this
study. For example, one possible reason for the negative relationship between
mate guarding behaviour and ejaculate quality could be sperm depletion. If
frequent IPC is a behaviour used by males as part of their mate guarding, or if
females initiate more IPCs with mate guarding males, then those males who guard
more strongly would be expected to have lower semen quality because of their
greater mating frequency. However, I controlled statistically for variation in ejaculate quality that was due to the total amount of sexual activity men reported per week, and importantly the time since their last ejaculation. Therefore, the pattern of correlation observed is independent of any influence of IPC frequency or sperm depletion.

The negative relationship between mate guarding and sperm quality obtained here could potentially be explained by their mutual covariation with male mate value. High quality men (with better quality ejaculates) may invest less in mate guarding because their partners are less likely to seek extra-pair copulations. Conversely, men of low mate value (with poorer quality ejaculates) may invest more in mate guarding because they are at a greater risk of having their mate defect from the relationship. The mate value parameters measured in this study included independently female assessed measures of mate quality (attractiveness and dominance) as well as a measure of men's self-perceived mate value. These measures are likely to capture much of the variance in male mate value, yet none of them were associated with ejaculate quality or mate guarding behaviour. The negative association between ejaculate quality and mate guarding behaviour presented in this study is thus unlikely to be mediated by their mutual covariation with mate value.

The correlation between mate guarding and ejaculate quality shown in this study could arise because of fixed genetic differences among men in their expenditure on these traits and/or through socially cued phenotypic plasticity. Cross cultural studies have shown how both men and women's sociosexuality — their tendency to engage in behaviours that generate sperm competition — are linked to personality types (Schmitt & Shackelford 2008) that exhibit some degree of underlying genetic variation (de Moor et al. 2012) and twin studies have found significant additive genetic variation for sociosexuality itself (Bailey et al. 2000; Cherkas et al. 2004; Lyons et al. 2004). Likewise, ejaculate quality has been shown to exhibit significant additive genetic variance (Storgaard et al. 2006) Thus, on the one hand it is possible that men may have fixed, genetically determined expenditures on mate guarding and ejaculate quality, and future work should establish the extent to which mate guarding exhibits genetic versus environmental variation and the extent to which mate guarding and ejaculate quality are genetically correlated. On the other hand, men can also show phenotypic plasticity
in ejaculate quality. There is considerable research to show that ejaculate quality can be context dependent (Leivers et al. 2014; Wylie & Pacey 2011). For example, Kilgallon and Simmons (2005) found that both among and within subjects, when men viewed images depicting sperm competition scenarios they produced ejaculates containing sperm of greater motility than when they viewed images of women alone. Thus, environmental constraints on a male’s ability to mate guard might generate plasticity in ejaculate quality. For example, males might respond to direct feedback from their mate; if a man’s partner were to actively avoid being mate guarded, he may invest more in his ejaculate. Further research examining socially cued plasticity in both mate guarding and ejaculate quality is warranted.

In conclusion, the findings of this study suggest that male expenditure on mate guarding and on the ejaculate can represent alternative means by which males respond to sperm competition. Men who performed fewer mate guarding behaviours to avoid sperm competition had higher quality ejaculates for the engagement in sperm competition. This relationship between mate guarding and ejaculate quality was independent of male quality. Future research is needed, to replicate these findings, to determine the extent to which this correlated expenditure occurs across other taxa, and to identify the genetic, and environmental and ecological factors that influence the relationship between the use of tactics for the engagement in and avoidance of sperm competition.
Epilogue

In this thesis, I investigated the potential role of sperm competition in human evolution. Each chapter in this thesis provides us with new insights into human sperm competition but also raises many questions, some of which I shall address in this epilogue.

Human sperm competition research is highly contentious and there have been many criticisms levelled at past human sperm competition literature. Taking evidence from across the psychology, biology and anthropology literature, Chapter 1 argues that men have evolved strategies that function to avoid and prevent sperm competition, which may have relaxed selection on adaptations for the engagement in sperm competition. However, I also discuss the gaps in our knowledge, including men’s use of physiological adaptations to sperm competition.

My review of the literature revealed considerable evidence from the evolutionary psychology literature that men have evolved psychological adaptations that function to anticipate and avoid sperm competition, and my first experimental chapter, Chapter 2, aimed at extending our understanding of the cues used by men in assessing sperm competition risk. For example, men show some accuracy in their judgements of their female partner’s faithfulness through interactions with their partner (Anderson 2006; Andrews et al. 2008). However, men can also make judgements of faithfulness of unfamiliar women from limited sensory information and these judgements often show high consensus among men although evidence for accuracy of judgements remains mixed (O’Connor et al. 2011; Rhodes et al. 2013; Singh 2004). The results in Chapter 2 provided novel evidence that men are able to show accuracy in their judgements of faithfulness from images of unfamiliar women. However, this accuracy was only apparent when men were given the opportunity to directly compare women in a forced choice task. Furthermore, I showed that men’s accuracy was related to the perceived trustworthiness of the models being judged but was not related to the attractiveness of the models. This result is not in line with previous research that reported that women’s accurate judgements of men’s faithfulness were not related to the perceived trustworthiness of the model (Rhodes et al. 2013). One explanation for the correlation between trustworthiness and faithfulness is that, when asked to make trustworthiness judgements of women, men may automatically make judgements of faithfulness, and vice versa. Certainly in this
instance, participants were aware that the experiments were related to person perception and human mate choice (due to the information that I was required to provide participants prior to testing), which may have encouraged participants to think about trustworthiness in a mating context (i.e. sexual trustworthiness). In future research, one might provide a specific trustworthiness scenario unrelated to mate choice (e.g. “Would you trust this person with a secret?”) to see if trustworthiness judgements still relate to faithfulness judgements. An alternative explanation for the relationship between faithfulness and trustworthiness is that faithfulness judgements may be made using some of the same cues used to make trustworthiness judgements. For example, emotion expression is closely linked with perceived trustworthiness, with neutral faces that look slightly happy being judged as more trustworthy than those that look slightly angry (Oosterhof & Todorov 2009; Said et al. 2009). Perhaps men may view an individual with an angry or unhappy countenance as less likely to be faithful as these expressions convey unhappiness, while a happy expression may portray contentment. Future research should explore the facial cues that affect accuracy in the judgements of unfaithful behaviour in women.

In Chapters 3 and 4, I changed my focus to men’s use of physiological sperm competition tactics, specifically their investment in ejaculate quality. In non-human animals, female attractiveness is often used as a cue to sperm competition risk and males will generally increase their investment in physiological adaptations (such as their expenditure on the ejaculate) when mating with attractive, or otherwise preferred, females (Kelly & Jennions 2011). However, more recently researchers have noted the possible influence of intrinsic factors (such as male quality) on the ejaculate (Kvarnemo & Simmons 2013; Parker et al. 2013; Sheldon 1994). Unfortunately, most researchers tend to overlook the possible interaction between male and female quality and how this might influence ejaculate quality. Research investigating the influence of sperm competition cues on the ejaculate of humans has been scarce and is often undermined by methodological limitations (see Chapter 1). Similarly, research investigating the relationship between male quality and ejaculate quality in humans remains inconclusive (Peters et al. 2008; Simmons et al. 2011; Soler et al. 2003). In Chapter 3, I show an interaction between female attractiveness and male quality that predicts ejaculate quality in men: higher quality men produced better quality
ejaculates, but only when responding to images of attractive women. This result provides little evidence that female attractiveness affects men’s ejaculate quality in a manner predicted by sperm competition theory. Rather, the influence of female attractiveness on ejaculate quality was dependent on male mate value, suggesting that this effect may be more suitably explained by assortative mating (whereby organisms preferentially mate with an individual that shares similar phenotypic traits).

An important question raised by the results of Chapter 3 is whether men show plasticity in their ejaculate quality. In humans, emission occurs prior to ejaculation, during which sperm are transferred from the epididymis to the posterior urethra where they are mixed with the seminal fluid components that are released from the prostate, van deferens and ampulla, and seminal vesicles (Newman et al. 1982). These seminal fluid components include proteins that influence the motility of sperm (de Lamirande 2007; Ding et al. 2007; Murdoch & Goldberg 2014). It is during emission that a mechanism is available to alter both sperm concentration and seminal fluid proteins that influence sperm motility. This suggests that it is possible for men to adjust their sperm concentration and motility rapidly based on their immediate sexual environment. Sperm concentration is currently the ejaculatory trait for which there is the strongest evidence of phenotypic plasticity across taxa (Kelly & Jennions 2011), although sperm motility can also be adjusted (Cornwallis & O’Connor 2009; Kilgallon & Simmons 2005). In Chapter 3, I had initially hoped to employ a within subjects design with men producing semen samples to both high attractive and low attractive women. Unfortunately, a within subjects design was not feasible as a large number of participants were unwilling to return a second sample for analysis. A few participants did produce samples to both high and low attractive images, but this sample size was too small for analysis. Furthermore—in those few participants who did return two semen samples for this study—it was not possible to control the period of time between the two samples being produced and changes in lifestyle factors that could potentially impact ejaculate quality. Due to these limitations, I used a between subjects design with participants producing samples in response to either high attractive or low attractive women. Future research would do well to employ a repeated measures design to investigate the issue of ejaculate plasticity in men, although this design would require a more...
rigorous protocol (e.g. controlling lifestyle and environmental factors between samples) which could reduce participant interest in a research area that already suffers difficulties recruiting volunteers.

In Chapter 4 I explored the association between traits for the engagement in sperm competition and its avoidance. Sperm competition adaptations can be morphological, behavioural or physiological. These adaptations improve a male's chances of paternity in two ways—the avoidance or prevention of sperm competition and the engagement in sperm competition by improving sperm competitiveness. Investment in both tactic types can be costly (Kelly & Jennions 2011; Kureck et al. 2011; SchoFL & Taborsky 2002; Simmons 2001), so one might expect that males will balance their investment in each tactic dependent upon the successful use of the other. I found an association between investment in mate guarding behaviour and ejaculate quality in men, with those who perform more mate guarding behaviours producing ejaculates of poorer quality. These results might suggest that men balance their investment in tactics for the avoidance of sperm competition and tactics for the engagement in sperm competition, and provide a novel insight into the possible influence of sperm competition on variation in ejaculate quality in humans. However, the mechanism by which this negative correlation between mate guarding and ejaculate quality is generated remains unknown. One option is that both mate guarding and ejaculate quality are stable traits, determined by genetic variation in which males invest a fixed amount in each trait. In species with alternative mating phenotypes, this may well be the case, with males investing in ejaculate quality or mate guarding behaviours dependent upon the mating strategy adopted (Alonzo & Warner 2000). In humans, ejaculate quality has been shown to exhibit significant additive genetic variance (Storgaard et al. 2006) suggesting that investment in the ejaculate may be genetically determined.

An alternative explanation is that mate guarding and ejaculate quality are not fixed, but in fact show phenotypic plasticity. There is considerable research to show that ejaculate quality can be context dependent (see Chapter 3, Wylie & Pacey 2011). Indeed, previous research has suggested phenotypic plasticity in ejaculate quality in humans that can be attributed to perceptions of sperm competition (Kilgallon & Simmons 2005). Males may be constrained in their ability to mate guard by their environment, or may receive cues from their environment...
to the prevailing risk of sperm competition, which might in turn generate plasticity in ejaculate quality. For example, if one’s mate actively avoids being mate guarded, the male’s perceived risk of sperm competition may increase resulting in greater investment in the ejaculate. Experimentally investigating plasticity in the relationship between sperm competition tactics would undoubtedly provide interesting findings but, due to ethical limitations using humans, non-human animal models would need to be used.

Although Chapter 4 reports the relationship between mate guarding and ejaculate quality (controlling for male quality), the study was initially designed for couples with the hope of examining the influence of female attractiveness on mate guarding and ejaculate quality in men also. Certainly there is evidence to suggest a positive relationship between mate guarding and female attractiveness (Buss 1988b; Buss & Shackelford 1997), although the results I present in Chapter 3 suggest that the influence of female attractiveness on ejaculate quality is more complex and not necessarily fully explained by sperm competition theory (which proposes that males increase investment in the ejaculate when mating with attractive females). Once again, I suffered recruitment difficulties with many women unwilling or unable to take part in the experiment, so that I was unable to examine the influence of female attractiveness on mate guarding and ejaculate quality. Including female attractiveness as a factor in this research could provide interesting insights that might explain the correlation between mate guarding and ejaculate quality that I found. In Chapter 1, I suggested that men have principally evolved mechanisms that function to avoid sperm competition over those that function to engage in sperm competition. Therefore, when mated to a woman of high mate value, men may preferentially invest in these more finely honed tactics for the avoidance of sperm competition (such as mate guarding) over tactics for the engagement of sperm competition (such as ejaculate quality).

There are many avenues for future research in human sperm competition, one of which is investigating whether men are able to show plasticity in their ejaculate and the mechanisms by which this plasticity is achieved. In relation to this question, further research should be undertaken to investigate the role of seminal fluids in adjustments in ejaculate quality. Seminal fluid proteins can influence sperm motility in humans (de Lamirande 2007; Ding et al. 2007; Murdoch & Goldberg 2014) and researchers are now beginning to understand the
importance of seminal fluids in sperm competition research (Simmons & Fitzpatrick 2012). Another area for future research is cryptic female choice in women. If sperm competition provides the opportunity for males to influence paternity at the post-copulatory level, we might also expect females to have evolved post-copulatory adaptations to bias paternity (Eberhard, 1996). Studies examining cryptic female choice in women are scarce and understanding more about the mechanisms through which women might show cryptic female choice might shed further light on human sperm competition and human post copulatory processes more broadly.

In summary, this thesis provides novel insights into the role that sperm competition may play in human mating systems. I add to the evidence that men have evolved psychological adaptations designed to avoid and prevent sperm competition by showing that men are able to show accuracy in their judgements of faithfulness. I also provide evidence that men have evolved physiological adaptations to sperm competition by demonstrating that variation in ejaculate quality can be attributed— in part— to men’s perceptions of sperm competition risk. However, the relationship between ejaculate quality and sperm competition is likely a complex one, influenced by the man’s own mate quality, as well as investment in other sperm competition adaptations, such as mate guarding behaviours.
References


Levin, R. J. 2011a. Can the controversy about the putative role of the human female orgasm in sperm transport be settled with our current physiological


Appendices
Appendix A: Non parametric analysis of Experiment 1, Chapter 2

Accuracy of faithfulness judgements

The proportion of correct choices was defined as the proportion of times the participant correctly chose the faithful model. There was no significant difference in accuracy when judgements were made from face and full person images (Mann-Whitney U Test, \( U_{43} = -0.62, p = .536 \)). Overall, accuracy was significantly above chance (0.5) (Wilcoxon Signed Rank test: \( W_{43} = 2.75, p = .006, X_{\pm SD} = 0.55\pm0.11 \)). Although there was no significant difference in performance on faces and full person images, planned tests showed that performance was significantly above chance for judgements from face images (Wilcoxon Signed Rank test: \( W_{21} = 2.18, p = .030, X_{\pm SD} = 0.57\pm0.12 \)) but only marginally significant from full person images (Wilcoxon Signed Rank test: \( W_{22} = 1.71, p = .087, X_{\pm SD} = 0.54\pm0.11 \)). These results show that men’s judgements of faithfulness have a kernel of truth, at least for judgements from women’s faces.

To examine men’s accuracy in faithfulness judgements in the ratings task, I examined the correlation between men’s faithfulness judgements and the self-reported extra-pair copulation behaviour of the models. There was a significant difference between faithfulness judgements made from face and full person images (Wilcoxon Signed Rank test: face: \( W_{34} = -3.08, p = .002, X_{\pm SD} = 4.46\pm0.64, \) full: \( X_{\pm SD} = 4.75\pm0.46 \)), so we examined the correlation between faithfulness ratings and the models’ extra-pair copulation behaviour separately for each image type. There were no significant correlations between men’s ratings of faithfulness and the self-reported extra-pair copulation frequency of the female models being rated, for either face images (Spearman’s \( r_{34} = -0.26, p = .135 \)) or full person images (Spearman’s \( r_{34} = -0.14, p = .419 \)).

Attractiveness as an honest cue of faithfulness

I investigated whether attractiveness ratings of the models were related to the proportion of participants who accurately chose the faithful model from the pair. There were no significant correlations between the attractiveness difference and accuracy (face: Spearman’s \( r_{17} = -0.16, p = .542 \), full-person: Spearman’s \( r_{17} = -0.12, p = .656 \)). Nor did differences in components of attractiveness (facial femininity/averageness/symmetry) correlate significantly with accuracy
(femininity: Spearman’s $r_{34} = -0.20, p = .453$, averageness: Spearman’s $r_{34} = 0.22, p = .387$, symmetry: Spearman’s $r_{34} = 0.04, p = .873$).

**Trustworthiness as an honest cue of faithfulness**

There were significant correlations between the trustworthiness difference of the models and the proportion of participants who accurately chose the most faithful model (face: Spearman’s $r_{17} = 0.76, p < .001$, full-person: Spearman’s $r_{17} = 0.83, p < .001$): If the faithful model looked more trustworthy than the unfaithful model, participants were more likely to correctly choose the faithful model as the more faithful of the pair.
Appendix B: Non parametric analysis of Experiment 2, Chapter 2

Accuracy of faithfulness judgements

As I could not compute a non-parametric 2-way mixed ANOVA, I calculated a ‘difference in accuracy’ score so that a positive value indicated that participants made more accurate choices in the post exposure task. There was no significant effect of image condition on difference in accuracy, (Kruskal-Wallis Test, H_{2,60}= 1.61, p = .447). Indeed, there was no significant difference between faithfulness accuracy between the pre and post exposure tasks (Wilcoxon Signed Rank Test, Z_{60}= 0.28, p= .777) so we collapsed accuracy across test time to calculate an overall mean. I found that accuracy was significantly above chance (0.5) (Wilcoxon Signed Rank Test, Z_{60}= 5.74, p< .001, X±SD= 0.60±0.09).

Participant’s self-reported preference for faithfulness was reliable across test time (Spearman’s r_{60}= .77, p< .001). Overall, participant accuracy was unrelated to their self-reported preference for faithfulness (Spearman’s r_{60}= .08, p= .523). Participant accuracy was also unrelated to preference for the other traits nine traits measured in the Mate Preference Questionnaire, all Spearman’s rs < .15, ps > .30.

Perceived trustworthiness as an honest cue of faithfulness

Using the trustworthiness difference scores from Experiment 1, I investigated whether trustworthiness ratings of the models were related to the proportion of participants who were able to accurately choose the faithful model from the pair. As there was no significant difference in the proportion of times that participants chose the faithful model between the pre and post exposure tasks (Wilcoxon Signed Rank Test, Z_{60}= 0.28, p= .777, pre: X±SD= 0.59±0.19, post: X±SD= 0.60±0.16) I calculated the overall mean for the proportion of times that participants correctly chose the faithful model and correlated this variable with trustworthiness difference. The correlation was large and significant (Spearman’s r_{17}= 0.64, p=.006).
### Appendix C: Correlation matrix between all sperm parameters for Chapter 3 (Pearson's correlations are shown above the diagonal and Spearman's correlations are included below the diagonal for comparison).

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<thead>
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<th>VAP</th>
<th>VSL</th>
<th>VCL</th>
<th>ALH</th>
<th>BCF</th>
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<td>.190</td>
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<td>.943**</td>
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<td>.807**</td>
<td>.642**</td>
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<td>.067</td>
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<td>-.492**</td>
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<td>.777*</td>
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N=77
** p< .01
*p< .05

VAP= average path velocity, VSL= straight line velocity, VCL= velocity along the sperm cells point-to-point track, ALH= lateral amplitude of sperm head movement, BCF= frequency with which the sperm head crosses the average sperm path, STR= straightness of the sperm's path, LIN= linearity of the sperm's path, % motile= percentage of motile sperm in the ejaculate, concentration= concentration of sperm in the ejaculate (million sperm/ml).
**Appendix D:** Correlation matrix between all sperm parameters (Pearson’s correlations are shown above the diagonal and Spearman’s correlations are included below the diagonal for comparison).

<table>
<thead>
<tr>
<th></th>
<th>Concentration</th>
<th>% motile</th>
<th>VAP</th>
<th>VSL</th>
<th>VCL</th>
<th>ALH</th>
<th>BCF</th>
<th>STR</th>
<th>LIN</th>
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<td>.578**</td>
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<td>.354*</td>
<td>.538**</td>
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<td>-.682**</td>
<td>-.157</td>
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</table>

N=41
** p< .01
*p< .05

VAP= average path velocity, VSL= straight line velocity, VCL= velocity along the sperm cells point-to-point track, ALH= lateral amplitude of sperm head movement, BCF= frequency with which the sperm head crosses the average sperm path, STR= straightness of the sperm's path, LIN= linearity of the sperm's path, % motile= percentage of motile sperm in the ejaculate, concentration= concentration of sperm in the ejaculate (million sperm/ml).