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**PHYSIOLOGICAL, PSYCHOLOGICAL AND BEHAVIOURAL RESPONSES
OF MALES TO CUES OF SPERM COMPETITION**

By

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A Thesis

Submitted to the School of Graduate Studies

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MALE RESPONSES TO CUES OF SPERM COMPETITION

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ABSTRACT

Sperm competition theory predicts that males should adjust the number of sperm they inseminate according to the risk of sperm competition. There is experimental evidence that adaptive sperm allocation occurs in many species. However, little attention has been paid to the physiological, psychological and behavioural mechanisms that may allow males to regulate the number of sperm they deliver from one copulation to the next in response to cues of sperm competition risk. The focus of the research reported in this thesis was the elucidation of such mechanisms. A comparative electrophysiological study is reported that demonstrates that the reproductive systems of two related rodent species differ in a way that can be interpreted as a reflection of differential exposure to sperm competition as a selective pressure during their evolutionary histories. Based on this finding it is argued that endogenous opioid systems may be involved in adaptive sperm allocation. In addition, data are presented that indicate that human males are sexually aroused by visual stimuli that would have been reliable cues of increased sperm competition risk in ancestral environments along with an experimental demonstration that human semen parameters can be affected by the nature of the visual stimulation present during specimen production, a finding that may have important clinical implications. Finally, it is shown that there is a relationship between the duration of pre-ejaculatory arousal and the number of sperm in a human male's ejaculate. Consequently, behavioural

changes that affect the duration of pre-ejaculatory sexual arousal could potentially be involved in the adaptive regulation of semen parameters in response to changes in the risk of sperm competition.

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CHAPTER 1

INTRODUCTION

Sexual selection favours those males who are successful in competing with same-sex conspecifics for mating opportunities (Darwin, 1871). However, in many species it is difficult for males to ensure exclusive paternity of a female's offspring since under certain circumstances, it may be advantageous for her to mate with multiple males. The potential direct and indirect benefits that a female may derive from facultative polyandry were first outlined by Smith (1984). Multiple mates may provide a female with direct benefits in the form of enhanced social status, additional material resources, and protection from intra-specific aggression and predation. Potential indirect benefits include genetic diversity for offspring as an "evolutionary hedge" against unpredictable environments or genetic material that is somehow superior to that available from a primary mate. Finally, a female may mate with multiple males to provide "fertility backup" as insurance against a primary mate's possible sterility, reduced fertility, or gametic incompatibility.

Given that females may benefit from facultative polyandry, in a species with internal fertilisation and paternal investment in young, males are at risk of cuckoldry, i.e., being deceived into helping rear offspring sired by other males.

Consequently, sexual selection will favour those males who engage in behaviours that tend to reduce the risk of cuckoldry. For example, in the case of the barn swallow (*Hirundo rustica*), these include aggressive behaviour directed towards rival males, defence of breeding territories from intrusions, and guarding of fertile females to prevent extra-pair copulations (Møller, 1984).

Evolutionary psychologists have argued that female facultative polyandry has also been an important selective pressure during human evolution, and that consequently psychological mechanisms have evolved in men to motivate behaviours that reduce the risk of cuckoldry (e.g. Daly *et al.*, 1982; Wilson & Daly, 1992; Buss *et al.*, 1992). Like males of many other species, men may use aggression directed towards rivals, mate guarding, and coercive restraint of fertile females as anti-cuckoldry tactics. Each of these may be effective at reducing the risk that a female will copulate with other males. However, if she does mate polyandrously, these tactics may fail to prevent her from conceiving a child sired by another male. So in the event that a female does mate with multiple males, further competition between them may take place within her reproduction tract, as sperm competition.

Sperm competition is the competition between the sperm of different males to fertilise a single female's gamete(s) (Parker, 1970). In species with internal fertilisation, sperm competition may occur whenever a female engages in "double-mating", i.e. copulates with multiple males such that live sperm from two

(or more) are present within her reproductive tract. Sperm competition can thus be viewed as nothing but sexual selection within the reproductive tract of females (Møller, 1994). Indeed, it is difficult to explain why the female reproductive tract is such a hostile environment for sperm without recourse to sexual selection theory (Birkhead *et al.*, 1993).

Mating order effects notwithstanding, success in sperm competition depends on a “raffle principle”; i.e. a given male can increase the probability of siring a female's offspring by inseminating more sperm (Parker, 1970, 1990a). However, since the costs of ejaculate production are non-trivial (Dewsbury, 1982) these must be traded-off against the risk of sperm competition. Following from this, an early prediction of sperm competition theory was that males should inseminate more sperm when the risk of “double-mating”, and hence of sperm competition, is high (Parker, 1982; 1990a,b; Baker & Bellis, 1995).

Two more specific predictions that can be derived from sperm competition theory are that, a) investment in sperm production should be greater in species with high levels of sperm competition, and b) within species, males exposed to chronically high levels of sperm competition should exhibit increased investment in sperm production. Experimental evidence supporting both these predictions is briefly reviewed in Chapter 3. However, the primary focus of the original research reported in this thesis is the elucidation of the physiological, psychological and behavioural mechanisms by which human and non-human

males may achieve adaptive regulation of the number of sperm inseminated from one copulation to the next in response to changes in the risk of sperm competition. Some of the cues that males may use to assess the risk of sperm competition have been examined, along with some of the proximal mechanisms that may be involved in adaptive regulation of the number of sperm inseminated.

CUES OF SPERM COMPETITION RISK

A reliable cue of sperm competition risk is one that provides information about the likelihood that a female's reproductive tract contains, or will soon contain, live sperm from another male. Direct inspection for visual, tactile or olfactory cues may be important in some species. For example, in some rodent species, males typically complete a series of intromissions before ejaculating and these are often separated by bouts of genital grooming during which males may pick up important olfactory information about the contents of the female reproductive tract. However, there is experimental evidence that in some species, males use less direct sources of information such as the mere presence of male rivals, the operational sex ratio, and/or whether or not the male has spent time guarding a particular female prior to copulation.

In Chapter 3, I review some of the published studies that have demonstrated that males can adjust the number of sperm they deliver in response to indirect cues of sperm competition risk. Moreover, experimental data are presented that indicate that human males are sexually aroused by visual stimuli

that would have been reliable cues of increased sperm competition risk in ancestral environments. It is argued that sexual arousal in response to visual cues of sperm competition may have been an adaptive response for ancestral human males and that this may account for the prevalence of certain types of sexual activity within contemporary pornography.

In Chapter 4, I also report the first published experimental demonstration that human semen parameters can be affected by the nature of the visual stimulation present during specimen production, a finding that may have important clinical implications. The men who volunteered to participate in this study ejaculated more sperm when viewing sexual contact between a male and a female than they did when viewing sexual contact between two females and it is argued that this can be interpreted as evidence that human males can adjust their ejaculate composition in response to visual cues of sperm competition.

The argument presented in Chapter 4 is that for ancestral human males, the visual experience of witnessing sexual contact between a female and rival males might have been an important source of information about the contents of her reproductive tract. However, for a male rodent defending a territory in the wild, merely encountering, attacking, and defeating a male intruder might be predictive of sperm competition risk since he might have already copulated with a resident female. Consequently, it may be in the interests of the resident male to increase the number of sperm he inseminates after agonistic encounters with other

males. A mechanism by which such an adaptive response might be achieved is outlined in Chapter 2 where I demonstrate experimentally that the reproductive systems of two related rodent species differ in a way that can be interpreted as a reflection of differential exposure to sperm competition as a selective pressure during their evolutionary histories.

MECHANISMS INVOLVED IN THE ADAPTIVE REGULATION OF THE NUMBER OF SPERM INSEMINATED

Facultative responses of the vas deferens

Mammalian sperm must travel through a complex system of ducts and accessory glands on their journey from the testes to the potentially hostile environment of the female reproductive tract. Spermatogenesis begins in the testes and the sperm continue to mature as they migrate along the epididymis and into the vas deferens. Since maturation takes several weeks it is the structures involved in the latter stages of this journey, such as the vas deferens, that are most likely to be involved in the short-term regulation of ejaculate composition.

The vas deferens extends from the epididymis to the urethra, which in turn empties to the outside world via the penis. In the adult human male it is approximately 25 cm long (Setchell & Brooks, 1988), possesses a thick muscular wall and narrow lumen. The smooth musculature is important for ejaculation since contractions of the distal portion of the vas deferens are critical for sperm

delivery (Batra, 1974; Guha *et al.*, 1975; Hib *et al.*, 1982). Normally, hundreds of millions of mature sperm are stored in the terminal portion of the epididymis and the vas deferens. Just prior to ejaculation, peristaltic contractions of the vas deposit some of these stored sperm into the posterior urethra. Here the sperm are mixed with fluids secreted by the prostate gland and seminal vesicles. This phase of the ejaculatory sequence is widely known as “emission”, but Baker & Bellis (1995) term the process “loading”. Subsequently, during orgasm, contractions of the bulbocavernosus and ischiocavernosus muscles force the mixture of sperm and seminal fluid down the urethra and out into the potentially competitive environment of the female reproductive tract.

Baker & Bellis (1995) have suggested two possible mechanisms by which adaptive modulation of ejaculate composition might be achieved; either by adjusting the number of sperm deposited in the urethra during loading, or adjusting the proportion of loaded sperm that are ejaculated. However, the latter mechanism would seem to be rather wasteful since any sperm retained in the urethra would be voided at the next urination. Loading fewer sperm in the first place would be a more efficient mechanism for reducing the sperm content of an ejaculate.

If alterations in the number of sperm deposited in the urethra during loading do occur as facultative responses to variations in the risk of sperm competition, then species differences in the anatomy and physiology of the vas

deferens should be expected. In a species where sperm competition has been a chronic selective force, the vas deferens might be expected to exhibit the ability to respond to cues that indicate that the sperm of a rival male are likely to be present within the reproductive tract of a female.

Electrophysiological evidence that there are important differences between the vasa deferentia of congeneric rodent species differing in sperm competition intensity is presented in Chapter 2. It is reported that electrically-evoked contractions of the vas deferens are inhibited by morphine in the non-monogamous deer mouse (*Peromyscus maniculatus*) but not in the monogamous California mouse (*Peromyscus californicus*). This is important since morphine mimics the effects of endogenous opioid peptides whose secretion can be affected by social interactions that may be predictive of sperm competition risk. In light of this finding, it is proposed that adaptive regulation of ejaculate composition may depend on opioid-regulated changes in the contractility of the vas deferens.

Facultative changes in male sexual behaviour

Frequent within-pair copulations may be an effective method of paternity assurance under certain circumstances, specifically, when the probability of siring a female's offspring is proportional to the relative number of sperm inseminated by each male who copulates with her, and/or, when the last male to copulate with a female before fertilisation is most likely to sire her offspring. Last male sperm precedence is common in birds (Birkhead & Møller, 1992) and for avian species

in which the risk of sperm competition high, males use frequent in-pair copulation as a method of paternity assurance (Birkhead *et al.*, 1987; Møller & Birkhead, 1991). Moreover, males of polyandrous rodent species are quicker to initiate copulation when introduced to a female than their counterparts from monogamous species (Dewsbury, 1981) and thus they probably achieve higher copulatory frequencies. It is unclear whether sperm precedence is a factor in human conception. Nevertheless, mating order effects notwithstanding, frequent in-pair copulations may keep a female "topped up" with a male's sperm and could serve to displace the sperm of rivals (Baker & Bellis, 1995). Consequently, sperm competition theory predicts that males could benefit from increases in the frequency of within-pair copulation when the risk of sperm competition is high.

The content analyses of contemporary pornography and sexual preference studies reported in Chapter 4 suggest that human males find visual cues of sperm competition to be sexually arousing, and thus, they may mediate adaptive increases in the frequency of within-pair copulation. Further evidence that human males can be sexually aroused by cues of female extra-pair copulation is presented in Chapter 5. It is argued that the results of the laboratory study reported in this chapter suggest that the sexual arousal produced in males in response to cues of sperm competition may motivate males to pursue in-pair copulations more eagerly.

Relationship between sexual arousal and semen parameters

While increases in the frequency of within-pair copulation can increase the number of sperm a male inseminates his partner with, other behavioural changes may achieve a similar result. For example, experimental data presented in Chapter 3 suggest that there is a relationship between the duration of pre-ejaculatory arousal and the number of sperm in a human male's ejaculate. Consequently, behavioural changes that affect the duration of pre-ejaculatory sexual arousal could potentially be involved in the adaptive regulation of semen parameters in response to changes in the risk of sperm competition. It is suggested that psychological responses to cues that would have been associated with increases in the risk of sperm competition in ancestral environments might trigger changes in sexual behaviour that increase the duration of pre-ejaculatory sexual arousal and consequently increase the number of sperm inseminated.

REFERENCES

- Baker, R. R., & Bellis, M. A. (1995). *Human sperm competition: Copulation, masturbation, and infidelity*. London, Chapman and Hall.
- Batra, S. K. (1974). Sperm transport through the vas deferens: Review of hypotheses and suggestions for a quantitative model. *Fertility and Sterility*, 25, 186-202.
- Birkhead, T. R., Atkin, L., & Møller, A. P. (1987). Copulation behaviour of birds. *Behaviour* 101, 101-138.
- Birkhead, T. R., & Møller, A. P. (1992). *Sperm competition in birds: Evolutionary causes and consequences*. London, Academic Press.
- Birkhead, T. R., Møller, A. P., & Sutherland, W. J. (1993). Why do females make it so difficult for males to fertilise their eggs? *Journal of Theoretical Biology*, 161, 31-60.
- Buss, D. M., Larsen, R. J., Westen, D., & Semmelroth, J. (1992). Sex differences in jealousy: Evolution, physiology and psychology. *Psychological Science*, 3, 251-255.
- Daly, M., Wilson, M., & Weghorst, S. J. (1982). Male sexual jealousy. *Ethology & Sociobiology*, 3, 11-27.
- Darwin, C. (1871). *The descent of man, and selection in relation to sex*. London, John Murray.

- Dewsbury, D. A. (1981). An exercise in the prediction of monogamy in the field from laboratory data on 42 species of muroid rodents. *Biologist*, 63, 138-162.
- Dewsbury, D. A. (1982). Ejaculate cost and male choice. *American Naturalist*, 119, 601-610.
- Guha, S. K., Kaur, H., & Ahmed, A. M. (1975). Mechanics of spermatic fluid transport in the vas deferens. *Medical & Biological Engineering*, 13, 518-522.
- Hib, J. Ponzio, R., & Vilar, O. (1982). Contractility of the rat cauda epididymis and vas deferens during seminal emission. *Journal of Reproduction and Fertility*, 66, 47-50.
- Møller, A. P. (1994). *Sexual selection and the barn swallow*. Oxford, Oxford University Press.
- Møller, A. P., & Birkhead, T. R. (1991). Frequent copulations and mate guarding as alternative paternity guards in birds: a comparative study. *Behaviour*, 118, 170-186.
- Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biological Reviews*, 45, 525-567.
- Parker, G. A. (1982). Why are there so many tiny sperm? Sperm competition and the maintenance of two sexes. *Journal of Theoretical Biology*, 96, 281-294.
- Parker, G. A. (1990a). Sperm competition games: raffles and roles. *Proceedings of the Royal Society: Biological Sciences*, 242, 120-126.

- Parker, G. A. (1990b). Sperm competition games: sneaks and extra-pair copulations. *Proceedings of the Royal Society: Biological Sciences*, 246, 107-115.
- Setchell, B. P., & Brooks, D. E. (1988). Anatomy, vasculature, innervation, and fluids of the male reproductive tract. In E. Knobil & J. Neil *et al.* (Eds). *The Physiology of Reproduction*. New York, Raven Press. pp 753-836.
- Smith, R. L. (1984). Human sperm competition. In R. L. Smith (Ed) *Sperm competition and the evolution of animal mating systems*. Academic Press: London. pp 601-660.
- Wilson, M., & Daly, M. (1992). The man who mistook his wife for a chattel. In J. Barkow, L. Cosmides, & J. Tooby (Eds). *The Adapted Mind*. Oxford, Oxford University Press. pp 289-322.

Running Head: *Peromyscus vas deferens*

CHAPTER 2

**EFFECTS OF MORPHINE ON ELECTRICALLY EVOKED
CONTRACTIONS OF THE VAS DEFERENS IN TWO CONGENERIC
RODENT SPECIES DIFFERING IN SPERM COMPETITION
INTENSITY.**

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SUMMARY

An early prediction of sperm competition theory was that males should adjust the number of sperm they deliver according to the risk of double mating and this has received empirical support in recent years. It has been suggested that adaptive regulation of sperm delivery in mammals may depend on changes in vas deferens contractility. In laboratory mice, the vas deferens is sensitive to opioid agonists and the secretion of endogenous opioid peptides can be affected by social interactions that may be predictive of sperm competition risk. The present experiment was conducted to determine whether morphine, an opioid agonist (at the μ -receptor), has different effects on electrically evoked contractions of the isolated vas deferens in two congeneric rodent species differing in sperm competition intensity. Morphine inhibited contractions of vas deferens in the non-monogamous deer mouse (*Peromyscus maniculatus*) but not the monogamous California mouse (*Peromyscus californicus*). This implies that the vas deferens of *P. maniculatus* possesses functional μ -receptors and, thus, should be able to respond to changes in the circulating levels of endogenous agonists whose secretion can be affected by social interactions predictive of sperm competition risk.

Keywords: morphine; sperm competition; vas deferens; *Peromyscus*; opioids; electrical stimulation

1. INTRODUCTION

Sperm competition is the competition between the sperm of different males to fertilize a single female's gamete(s) (Parker, 1970). In a species with internal fertilization, sperm competition may occur whenever a female engages in 'double-mating' such that live sperm from two (or more) males are present within her reproductive tract. Under these circumstances, notwithstanding mating order effects, a 'raffle principle' applies, i.e. a given male can increase the probability of siring her offspring by inseminating more sperm (Parker, 1970, 1990a). However, for males there is a trade-off between the non-trivial cost of ejaculate production (Dewsbury, 1982) and the risk of sperm competition. Following from this, an early prediction of sperm competition theory was that males should inseminate more sperm when the risk of double mating and, hence, of sperm competition, is high (Parker, 1982, 1990a,b; Baker & Bellis, 1995). This prediction has since been confirmed for a number of insect and mammalian species (for a review see Parker *et al.*, 1997). For example, it has been reported that male laboratory rats (*Rattus norvegicus*) ejaculate more sperm when mating with a female that they have not previously guarded (Bellis *et al.*, 1990).

It has been suggested that adaptive regulation of ejaculate composition might depend on changes in the contractility of the vas deferens (Baker & Bellis, 1995). Contractions of the distal portion of this duct are critical for sperm delivery (Batra, 1974; Guha *et al.*, 1975; Hib *et al.*, 1982). Therefore, the number

of sperm ejaculated might depend on the proportion of the sperm stored in the vas deferens that are loaded into the urethra during emission just before ejaculation. If this is the case, species differences in the ability of the vas deferens to respond to changes in the social environment should be expected. In species in which sperm competition has been a chronic selective force, the contractility of the vas deferens should be systematically related to the risk of sperm competition as indicated by changes in the social environment.

While species differences in vas deferens physiology have not been widely studied, there is evidence of genotype-dependent responses to opioid agonists in the vas deferens of inbred strains of laboratory mice (*Mus musculus*). Morphine, a μ -receptor agonist, inhibits contractions of the isolated mouse vas deferens induced by electrical stimulation of the intramural nerves (Henderson *et al.*, 1972). However, its effects are more potent in the DBA/2 strain than in the C57BL/6J strain (Berti *et al.* 1978). Such differences are difficult to explain in evolutionary terms since they are primarily the result of artificial selection within laboratory breeding programmes. Nevertheless, genotype-dependent responses to opioid agonists are particularly interesting since endogenous opioid peptides (EOPs) are involved in the regulation of male reproductive function at multiple sites within the hypothalamic-pituitary-testicular (HPT) axis (Fabbri *et al.*, 1989). Furthermore, since EOP secretion can be modulated by social stressors, these peptides may be involved in the adaptive modulation of various aspects of male

reproductive physiology in response to changes in the social environment (Knol, 1991).

In laboratory mice, social conflict within resident-intruder dyads produces potent opioid-dependent analgesia in subordinates (Rodgers & Hendrie, 1983), which is naloxone reversible and cross-tolerant with morphine (Rodgers & Randall, 1985). Moreover, dominants exhibit opioid-dependent reversible hyperalgesia (Rodgers & Hendrie, 1983), a finding that has been replicated in laboratory rats (Raab *et al.*, 1986). Pituitary secretion of EOPs into the peripheral circulation has been implicated in the antinociceptive responses to social conflict seen in defeated rodents. In particular, fighting (Huhman *et al.*, 1990) and submission (Huhman *et al.*, 1991) elevate plasma levels of the μ -receptor agonist β -endorphin in male golden hamsters (*Mesocricetus auratus*).

Social conflict within a resident-intruder paradigm incorporates cues that would be predictive of sperm competition in the wild. For a rodent defending a territory in the wild, encountering, attacking and defeating a male intruder might be predictive of sperm competition risk since the intruder could have already copulated with a resident female. Hence, such experiences should trigger adaptive changes in ejaculate composition, possibly mediated by a reduction in the level of EOP secretion and a consequent increase in vas deferens contractility.

To test the hypothesis that species differences in the sensitivity of the vas deferens to opioid agonists are related to the extent to which sperm competition

has been a selective pressure in each, two species from the *Peromyscus* genus were compared. *Peromyscus maniculatus* is probably the most polygynous species within the genus (Dewsbury, 1981a). However, it is also known that, given the opportunity, *P. maniculatus* females will copulate with more than one male during a single oestrus cycle. Consequently, they often conceive litters of multiple paternity in the wild (Birdsall & Nash, 1973) and in the laboratory (Dewsbury, 1981b). Furthermore, the males that copulate most frequently with a polyandrous female are most likely to sire her offspring (Dewsbury, 1985a). Therefore, although the mating system of *P. maniculatus* is effectively polygynous, female polyandry has been an important selective pressure for males of this species. In contrast, *Peromyscus californicus* pairs are highly, perhaps even exclusively, monogamous. There is no DNA evidence of extra-pair paternity in the wild (Ribble, 1991) and both sexes avoid extra-pair copulation (Gubernick & Nordby, 1993).

Antinociceptive responses to environmental stress (Kavaliers & Innes, 1987; Kavaliers & Galea, 1995; Kavaliers *et al.*, 1998) and novelty (Kavaliers & Innes, 1988) have been observed in *P. maniculatus*. However, the existence of social-conflict-induced, opioid-dependent analgesia has not yet been established in this species. Nevertheless, *P. maniculatus* males do form dominance relationships based on priority of residence (Dewsbury, 1985b), relationships which are associated with opioid-dependent responses in laboratory mice and rats.

Since EOP secretion depends on social experiences that are predictive of sperm competition risk, and vas deferens contractility is affected by opioid agonists in many species, it is hypothesized that EOPs are involved in the adaptive regulation of ejaculate composition. Consequently, the vas deferens should be more sensitive to opioid agonists such as morphine in species with sperm competition, such as *P. maniculatus*, than in those without, such as *P. californicus*.

2. METHODS

Sexually mature (2-12 months of age) male *Peromyscus californicus* *insignis* (44-52g) and *Peromyscus maniculatus bairdii* (20-30g) were used in the experiment (Peromyscus Genetic Stock Centre, University of South Carolina). Six animals from each species were sacrificed by cervical dislocation, and the vasa deferentia, with the prostatic end sectioned as near as possible to the seminal vesicle, were dissected from fat and connective tissue. Each was gently pressed to expel the seminal contents before being mounted vertically in a 10ml organ bath between two platinum ring electrodes (1cm apart). The prostatic end of each vas was tied with silk thread and connected to a Grass force displacement transducer model FT 03 (Grass Instrument Co., Quincey, MA, USA).

Tissues were maintained at 37°C in a modified (Mg^{2+} free) Krebs's solution (118 mmol NaCl, 4.75 mmol KCl, 2.54 mmol $CaCl_2$, 1.03 mmol KH_2PO_4 , 23 mmol $NaHCO_3$, 11 mmol glucose) which was continuously bubbled

with a mixture of 95% O₂ and 5% CO₂. A resting tension of *ca.* 200mg was applied to each vas and the tissues were allowed to equilibrate for 45 minutes before longitudinal contractions were recorded isometrically using a Grass model 7 polygraph.

To excite the intramural nerves, the electrical field stimulation parameters established by Henderson *et al.* (1972) were used (0.1 Hz, 1 ms, supramaximal voltage). Baseline twitch heights were established for each vas deferens. Then concentration-effect curves were generated cumulatively by adding morphine sulphate (Sabex) in 10 - 100 μ l volumes from 0.5 mg ml⁻¹, 5 mg ml⁻¹ and 50 mg ml⁻¹ stock solutions. The pre-incubation time at each concentration was 20 minutes. Maximum twitch height was recorded once the tissues had equilibrated at each concentration and the responses of vasa deferentia from the same animal were averaged.

3. RESULTS

The dose-response curves for *P. californicus* and *P. maniculatus* are shown in figure 1. The maximum twitch height for electrically evoked contractions of the *P. californicus* vas deferens was not inhibited by morphine at any dose. However, increasing doses of morphine progressively inhibited contractions of the *P. maniculatus* vas deferens.

Figure 1 about here

4. DISCUSSION

The vas deferens of the laboratory mouse possesses μ -receptors (Hutchinson *et al.*, 1975) and, consequently, electrically evoked contractions are inhibited by both morphine (Hughes *et al.*, 1975) and β -endorphin (Sanchez-Blazquez *et al.*, 1983). In the present experiment, the observed sensitivity of the isolated *P. maniculatus* vas deferens to the inhibitory effects of morphine *in vitro* indicates the presence of μ -receptors in this tissue. Consequently, in the intact animal the vas deferens should be able to respond to changes in the level of circulating endogenous μ -receptor agonists such as β -endorphin. Conversely, in the present experiment the isolated vas deferens of *P. californicus* was insensitive to morphine across the dose range tested, implying an absence of μ -receptors in this tissue. Lacking functional μ -receptors, the *P. californicus* vas deferens should be unable to respond to endogenous opioids that are agonists at this receptor subtype.

Previous research has shown that competitive interactions between males can affect the secretion of endogenous μ -receptor agonists such as β -endorphin (e.g. Rodgers & Hendrie, 1983). Consequently, their levels in the peripheral circulation may provide an endocrine index of sperm competition risk that can

directly affect the contractility of the vas deferens and, thus, facilitate the adaptive regulation of ejaculate volume and/or sperm concentration. Stimuli that tend to produce increases in EOP secretion will reduce the contractility of the vas deferens and inhibit sperm delivery. Conversely, stimuli that tend to produce decreases in EOP secretion will increase vas deferens contractility and stimulate sperm delivery.

Genotype-dependent responses of the vas deferens to an opioid agonist have been reported previously (Berti *et al.*, 1978). However, in the present study the observed difference was predicted *a priori* based on evolutionary theory and findings from behavioural ecology. The reproductive success of *P. maniculatus* males depends on their ability to sire offspring in an environment in which females engage in polyandrous mating. Consequently, males must balance the need to inseminate more sperm when the risk of sperm competition is high against the non-trivial costs of ejaculate production. A potential mechanism by which this might be achieved involves the regulation of vas deferens contractility and, thus, sperm delivery by EOPs such as β -endorphin. For β -endorphin to regulate sperm delivery the vas deferens must contain functional μ -receptors and the present experiment indicates that this is indeed the case for a species in which males face the selective pressures of sperm competition. In contrast, the experiment indicates that the vas deferens lacks functional μ -receptors in a species without sperm competition, *P. californicus*, in which the ability to regulate sperm delivery in response to changes in the social environment confers

no selective advantage. In light of these findings, the hypothesis that adaptive regulation of ejaculate composition depends on EOP-regulated changes in the contractility of the vas deferens warrants further investigation.

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REFERENCES

- Baker, R. R., & Bellis, M. A. (1995). *Human sperm competition: Copulation, masturbation, and infidelity*. Chapman and Hall, London.
- Batra, S. K. (1974). Sperm transport through the vas deferens: Review of hypotheses and suggestions for a quantitative model. *Fertil. Steril.* **25**, 186-202.
- Bellis, M. A., Baker, R. R., & Gage, M. J. G. (1990). Variation in rat ejaculates consistent with kamikaze-sperm hypothesis. *J. Mamm.* **71**, 479-480.
- Berti, F., Bruno, F., Omini, C., & Racagni, G. (1978). Genotype dependent responses of morphine and methionine-enkephalin on the electrically induced contractions of the mouse vas deferens. *Naunyn Schmiedebergs Arch. Pharmacol.* **305**, 5-8.
- Birdsall, D. A., & Nash, D. (1973). Occurrence of successful multiple insemination of females in natural populations of deer mice (*Peromyscus maniculatus*). *Evolution* **27**, 106-110.
- Dewsbury, D. A. (1981a). An exercise in the prediction of monogamy in the field from laboratory data on 42 species of muroid rodents. *The Biologist* **63**, 138-162.

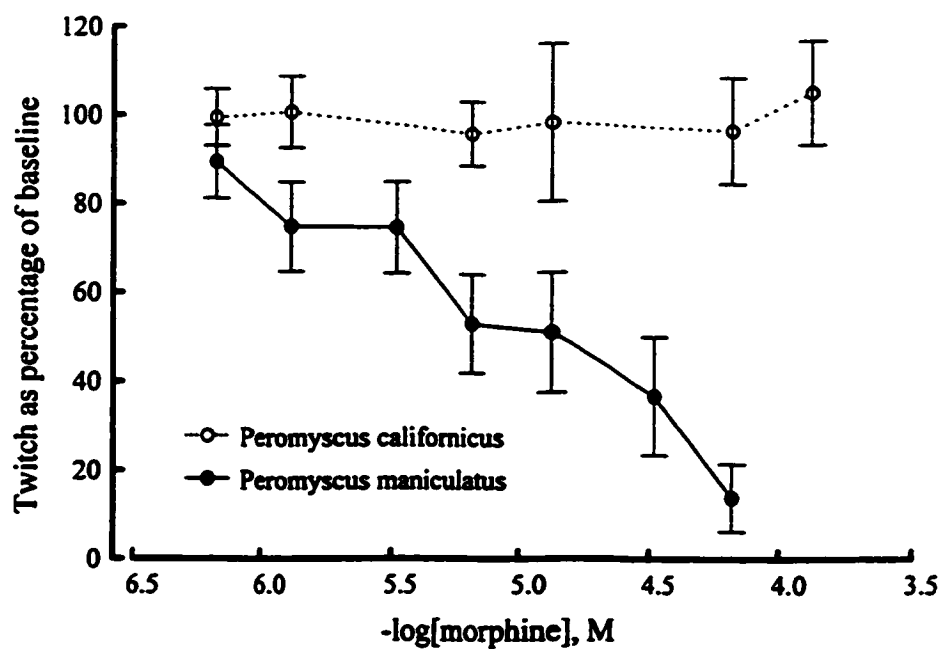
- Dewsbury, D. A. (1981b). Social dominance, copulatory behavior, and differential reproduction in deer mice (*Peromyscus maniculatus*). *J. Comp. Physiol. Psychol.* **95**, 880-895.
- Dewsbury, D. A. (1982). Ejaculate cost and male choice. *Am. Nat.* **119**, 601-610.
- Dewsbury, D. A. (1985a). Interactions between males and their sperm during multi-male copulatory episodes of deer mice (*Peromyscus maniculatus*). *Anim. Behav.* **33**, 1266-1274.
- Dewsbury, D. A. (1985b). Aggression, copulation, and differential reproduction of deer mice (*Peromyscus maniculatus*) in a semi-natural enclosure. *Behaviour* **91**, 1-23.
- Fabrizi, A., Jannini, E. A., Gnassi, L., Ulisse, S., Moretti, C., & Isidori, A. (1989). Neuroendocrine control of male reproductive function. The opioid system as a model of control at multiple sites. *J. Steroid. Biochem.* **32**, 145-150.
- Gubernick, D. J., & Nordby, J. C. (1993). Mechanisms of sexual fidelity in the monogamous California mouse, *Peromyscus californicus*. *Behav. Ecol. Sociobiol.* **32**, 211-219.
- Guha, S. K., Kaur, H., & Ahmed, A. M. (1975). Mechanics of spermatice fluid transport in the vas deferens. *Med. Biol. Eng.* **13**, 518-522.
- Henderson, G., Hughes, J., & Kosterlitz, H. W. (1972). A new example of a morphine-sensitive neuro-effector junction: Adrenergic transmission in the mouse vas deferens. *Br. J. Pharmacol.* **46**, 764-766.

- Hib, J. Ponzio, R., & Vilar, O. (1982). Contractility of the rat cauda epididymis and vas deferens during seminal emission. *Reprod. Fertil.* **66**, 47-50.
- Hughes, J., Kosterlitz, H. W., & Leslie, F. M. (1975). Effect of morphine on adrenergic transmission in the mouse vas deferens. Assessment of agonist and antagonist potencies of narcotic analgesics. *Br. J. Pharmacol.* **53**, 371-381.
- Huhman, K. L., Bunnell, B. N., Mougey, E. H., & Meyerhoff, J. L. (1990) Effects of social conflict on POMC-derived peptides and glucocorticoids in male golden hamsters. *Physiol. Behav.* **47**, 949-956.
- Huhman, K. L., Moore, T. O., Ferris, C. F., Mougey, E. H., & Meyerhoff, J. L. (1991). Acute and repeated exposure to social conflict in male golden hamsters: increases in plasma POMC-peptides and cortisol and decreases in plasma testosterone. *Horm. Behav.* **25**, 206-216.
- Hutchinson, M., Kosterlitz, H. W., Leslie, F. M., Waterfield, A. A., & Terenius, L. (1975). Assessment in the guinea-pig ileum and mouse vas deferens of benzomorphans which have strong antinociceptive activity but do not substitute for morphine in the dependent monkey. *Br. J. Pharmacol.* **55**, 541-546.
- Kavaliers, M., & Galea, L. A. (1995). Sex differences in the expression and antagonism of swim stress-induced analgesia in deer mice vary with the breeding season. *Pain* **63**, 327-334.

- Kavaliers, M., & Innes, D. G. L. (1987). Stress-induced opioid analgesia and activity in deer mice: sex and population differences. *Brain. Res.* **425**, 49-56.
- Kavaliers, M., & Innes, D. G. L. (1988). Novelty-induced analgesia in deer mice (*Peromyscus maniculatus*): sex and population differences. *Behav. Neural Biol.* **49**, 54-60.
- Kavaliers, M., Colwell, D. D., & Choleris, E. (1998). Sex differences in opioid and N-methyl-D-aspartate mediated non-opioid biting fly exposure induced analgesia in deer mice. *Pain* **77**, 163-171.
- Knol, B. W. (1991). Stress and the endocrine hypothalamus-pituitary-testis system: a review. *Vet. Q.* **13**, 104-14.
- Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* **45**, 525-67.
- Parker, G. A. (1982). Why are there so many tiny sperm? Sperm competition and the maintenance of two sexes. *J. Theor. Biol.* **96**, 281-294.
- Parker, G. A. (1990a). Sperm competition games: raffles and roles. *Proc. R. Soc. Lond. B* **242**, 120-126.
- Parker, G. A. (1990b). Sperm competition games: sneaks and extra-pair copulations. *Proc. R. Soc. Lond. B* **246**, 107-115.

- Parker, G. A., Ball, M. A., Stockley, P., & Gage, M. J. G. (1997). Sperm competition games: a prospective risk analysis assessment. *Proc. R. Soc. Lond. B* **264**, 1793-1802.
- Raab, A., Dantzer, R., Michaud, B., Mormede, P., Taghzouti, K., Simon, H., & Le Moal, M. (1986). Behavioural, physiological and immunological consequences of social status and aggression in chronically coexisting resident-intruder dyads of male rats. *Physiol. Behav.* **36**, 223-228.
- Ribble, D. O. (1991). The monogamous mating system of *Peromyscus californicus* as revealed by DNA fingerprinting. *Behav. Ecol. Sociobiol.* **29**, 161-166.
- Rodgers, R. J., & Hendrie, C. A. (1983). Social conflict activates status-dependent endogenous analgesic and hyperalgesic mechanisms in male mice: effects of naloxone on nociception and behaviour. *Physiol. Behav.* **30**, 775-780.
- Rodgers, R. J., & Randall, J. I. (1985). Social conflict analgesia: studies on naloxone antagonism and morphine cross-tolerance in male DBA/2 mice. *Pharmacol. Biochem. Behav.* **23**, 883-888.
- Sanchez-Blazquez, P., Garzon, J., Lee, N. M. (1983). Functional opiate receptor in mouse vas deferens: evidence for a complex interaction. *J. Pharmacol. Exp. Ther.* **226**, 706-711.

Figure 1. Effects of morphine on electrically stimulated twitch contractions of the vas deferens in *Peromyscus maniculatus* and *Peromyscus californicus*. Data are the means (\pm S.E.M) for six animals from each species.



Running Title: Duration of sexual arousal and semen quality

CHAPTER 3

**DURATION OF SEXUAL AROUSAL PREDICTS SEMEN PARAMETERS
FOR EJACULATES COLLECTED VIA MASTURBATION**

Submitted to Human Reproduction

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ABSTRACT

For a particular man, semen parameters may vary considerably from one specimen to the next, in part due to variability in the conditions under which the specimens are produced. In the present study, the relationship between the duration of pre-ejaculatory sexual arousal and the quality of semen produced by masturbation was investigated. Twenty-five semen donors provided a total of 300 semen specimens over a period of 4 months. Each specimen was produced after 3 days of ejaculatory abstinence and measures included the time taken to produce the specimen, ejaculate volume, sperm concentration, percent motility, and grade of motility. The time taken to produce a specimen was positively correlated with sperm concentration ($r = 0.19$; $p = 0.001$) and total sperm number ($r = 0.22$; $p = 0.0001$) but negatively correlated with sperm motility ($r = -0.21$; $p = 0.0004$). Nevertheless, there was a positive correlation between specimen production time and both motile sperm concentration ($r = 0.12$; $p = 0.04$) and the total number of motile sperm in the ejaculate ($r = 0.17$; $p = 0.003$). We conclude that the duration of pre-ejaculatory sexual arousal is an important predictor of ejaculate quality for specimens produced by masturbation.

Keywords: sexual arousal; masturbation; semen quality; sperm competition; sperm concentration

INTRODUCTION

Substantial within-subject variability in ejaculate composition is typical of studies in which human males provide multiple semen specimens over several days or weeks (e.g. Read & Schnieden, 1978; Schwartz *et al.*, 1979; Mallidis *et al.*, 1991;). For a particular donor, ejaculate volume and sperm concentration may vary considerably from one specimen to the next, partly because both parameters are affected by the duration of ejaculatory abstinence (e.g. Padova *et al.*, 1988; Sauer *et al.*, 1988; Blackwell & Zaneveld, 1992). However, the context in which an ejaculate is produced is also important. For example, ejaculates produced during intercourse are generally superior to those produced during masturbation (e.g. Zavos, 1985). Specifically, specimens obtained via intercourse have higher ejaculate volume, total sperm number, and grade of sperm motility than those obtained via masturbation (Zavos & Goodpasture, 1989). They also exhibit a greater percentage of motile and morphologically normal spermatozoa and consequently perform better on various sperm function tests (Sofikitis & Miyagawa, 1993).

The superior quality of ejaculates produced during intercourse may be attributable, in part, to the greater intensity and duration of sexual arousal that typically precedes copulatory ejaculation. There is some experimental evidence that the duration of pre-ejaculatory sexual arousal is an important determinant of semen quality for copulatory ejaculates. Specifically, increases in the duration of

pre-coital stimulation increase the number of motile sperm with normal morphology in copulatory ejaculates (Zavos, 1988). A similar relationship between duration of sexual arousal and semen quality is known to exist when specimens are collected from domestic animals for the purposes of artificial insemination. Under these circumstances, it is standard practice to intentionally prolong the duration of sexual stimulation beyond that needed for mounting and ejaculation in order to maximise the number of sperm ejaculated (Senger, 1997). This is generally achieved through a combination of restraint and "false mounts" during which the male is allowed to repeatedly mount a female without intromission. For example, sexual preparation of this type prior to ejaculation increases the number of sperm ejaculated by bulls (Almquist *et al.*, 1958; Almquist, 1973; Collins *et al.*, 1951; Hafs *et al.*, 1962), increases the number of sperm in the sperm-rich fraction of the ejaculate in boars (Hemsworth & Galloway, 1979) and increases the fluid content of the accessory sex glands and ductus deferens in stallions (Weber *et al.*, 1990).

The mechanisms involved in the improvements in semen quality associated with increases in the duration of pre-ejaculatory sexual arousal are unclear. However, it is known that sexual stimulation increases the rate of sperm transport in the vas deferens (Prins and Zaneveld, 1979; 1980) and thus it can be hypothesised that improvements in semen quality may depend on increases in the number of sperm that are moved into the distal portion of the vas deferens prior to emission. It is also conceivable that the improvements in ejaculate quality seen

with increases in the duration of pre-ejaculatory male sexual arousal might be secondary to increases in the duration of female sexual arousal. This might be the case if the intensity of the tactile, visual, olfactory and auditory stimulation provided by a female is dependent on the duration of her sexual arousal, and if sperm transport in the male is facilitated by the intensity of this stimulation at the moment of ejaculation. The finding that ejaculates obtained via uninterrupted coitus have higher semen volume, total sperm number, and sperm motility than those obtained via the coitus interruptus method (Zavos *et al.*, 1994) is consistent with this possibility and suggests that the nature of the tactile stimulation at the moment of ejaculation may be important.

Masturbatory ejaculates provide an opportunity to study the relationship between semen parameters and the duration of male sexual arousal in isolation from the potentially confounding effects of female sexual arousal. Furthermore, it is easier to obtain accurate and reliable measurements of the duration of pre-ejaculatory sexual arousal for specimens produced via masturbation in a laboratory setting than it is for copulatory ejaculates that would usually be produced in non-clinical settings. Consequently, the present study was conducted to determine whether the quality of semen specimens produced by masturbation is related to the duration of pre-ejaculatory sexual stimulation. Previously, it has been reported that neither changes in the subjective intensity of sexual arousal, nor changes in the time to taken to reach orgasm, are correlated with changes in semen parameters for ejaculates produced by masturbation (van Rooijen *et al.*,

1996). However, in that study each male provided semen specimens on only two occasions and these were at least one month apart.

MATERIALS AND METHODS

Twenty-five semen donors aged 22-40 years (median: 31 years) participated in the study between November 1998 and February 1999. Each was accepted into the semen donor programme at a Toronto-based sperm bank after completing the required screening as per official standards of Health Canada (1996) and the Canadian Fertility and Andrology Society (1996). The donors were instructed to abstain from ejaculation for 3 days before producing their specimens by masturbation in a private room while watching a sexually explicit video. Each specimen was evaluated 30 minutes after ejaculation according to the standard procedures recommended by the World Health Organisation (1992). Parameters measured were ejaculate volume, sperm concentration, percent motility, and grade of motility. The total number of sperm in the ejaculate was calculated as sperm concentration x specimen volume. The number of minutes the donor spent in the private room was recorded as the time taken to produce the specimen. For reasons of privacy, it was not possible to record directly the time spent masturbating. Statistical methods employed to analyse the relationships between semen parameters and the time taken to produce a specimen included linear regression and non-linear curve estimation models (SPSS 10.0; SPSS Inc.) and the calculation of Pearson's product moment correlation coefficients.

RESULTS

A total of 292 semen samples were collected with a median of 11 per donor. All donors reported that they had maintained at least 3 days of ejaculatory abstinence prior to specimen production. The average time taken to produce a specimen was 15.6 ± 8.0 minutes with a range of 3 - 55 minutes. Descriptive statistics for the semen parameters measured are shown in Table I together with the correlations between each parameter and the time taken to produce a specimen.

Semen specimens were divided into 4 groups according to production time and the mean sperm concentration, percent motility and motile sperm concentration for each group are depicted in Figure 1. The time taken to produce a specimen was positively correlated ($r = 0.19, p < 0.005$) with sperm concentration but unrelated ($r = 0.08, p = 0.2$) to ejaculate volume. However, there was nevertheless a positive correlation ($r = 0.22, p < 0.0005$) between specimen production time and the total number of sperm in the ejaculate. The time taken to produce a specimen was negatively correlated ($r = -0.21, p < 0.0005$) with sperm motility. However, despite this decline in sperm motility with increasing specimen production time there was nevertheless a positive correlation ($r = 0.12, p < 0.05$) between production time and the motile sperm concentration. Furthermore, there was a positive correlation ($r = 0.17, p < 0.005$) between specimen production time and the total number of motile sperm in the ejaculate.

Figure 1 about here

Linear regression analysis was used to characterise the relationship between specimen production time and sperm concentration more precisely. The significant linear relationship ($r = 0.19$, $df = 290$, $F = 10.7$, $p < 0.005$) between sperm concentration and time take to produce the specimen is described by the equation $CONC = 60.6 + 0.67(TIME)$ but this linear relationship could only account for 3.6% of the variance in sperm concentration. However, there was also a significant quadratic relationship ($r = 0.33$, $df = 289$, $F = 17.3$, $p < 0.001$) that could account for 10.7% of the total variance in sperm concentration. This relationship is described by the equation $CONC = 35.4 + 3.5(TIME) - 0.06(TIME^2)$ and is depicted in Figure 2.

Figure 2 about here

In principle, the observed relationship between specimen production time and semen quality could arise from a between-subject association between these two variables. If this is the case, then correlations between a donor's mean semen parameters and the average time taken by him to produce a specimen should be expected. To address this possibility, average values for each semen parameter were calculated for each donor. However, there were no significant correlations between the mean specimen production time for each donor and the donor-

specific average values for any of the measured semen parameters ($r < 0.1$; $p > 0.6$ for all bivariate correlations).

To determine whether the observed relationship might be due to within-subject improvements in semen parameters with increases in the time taken to produce a specimen, a fixed effects linear regression model was employed to control for between-subject differences in these variables. Inspection of the data presented in Figure 2, and the parameters of the best-fitting quadratic function, indicate that if there is a monotonic increasing relationship between specimen production time and sperm concentration it probably exists only up to about 30 minutes. Consequently, in order to assess the linear component of the relationship between specimen production time and sperm concentration, only the 275 specimens that were produced in less than 30 minutes were included in the regression analysis.

Twenty-three binary dummy variables were created to code for the 23 donors who produced multiple semen specimens. These were entered into a linear regression model along with time taken to produce the specimen as a continuous predictor and sperm concentration as the dependent variable and the results of the analysis are presented in Tables 2a, 2b and 2c. Controlling for the fixed-effects of donor identity on sperm concentration, time taken to produce the specimen was still a significant predictor of sperm concentration ($t = 2.00$; $p < 0.05$). This suggests that for specimens that are produced in less than 30 minutes,

there is an important within-subjects component to the relationship between these two variables depicted in Figures 1 and 2.

DISCUSSION

In the present study, ejaculate quality improved as the time taken to produce the specimen increased. Specifically, both sperm concentration and total sperm number were positively correlated with specimen production time. In contrast, sperm motility declined as the time taken to produce the specimen increased. Nevertheless, this decline was not sufficient to negate the improvements in sperm concentration and total sperm number associated with increases in specimen production time. Consequently, there was a positive correlation between time taken and both motile sperm concentration and motile sperm number.

If the time taken to produce a specimen is closely related to the time spent masturbating, then this variable is closely related to the time spent in a state of sexual arousal. Consequently in the present study, ejaculate quality would seem to be dependent, at least in part, on the duration of pre-ejaculatory sexual arousal. This finding is consistent with the results of a previous experimental study of ejaculates produced during copulation in which ejaculate quality improved as the duration of pre-coital stimulation was increased (Zavos, 1988), but it contradicts a more recent report that changes in the time to orgasm are not associated with changes in sperm concentration for ejaculates collected via masturbation (van

Roijen *et al.*, 1996). However, it should be noted that in this latter study each sperm donor provided only two semen specimens collected on different occasions at least one month apart whereas in the present study donors provided a median of 11 specimens each over a period of 4 months.

The finding that there is a correlation between semen quality and the duration of pre-ejaculatory sexual arousal in human males is consistent with what is known about the effects of sexual preparation on the quality of semen collected from domestic animals for the purposes of artificial insemination. Sexual preparation in non-human animals probably improves semen quality by facilitating sperm transport. Specifically, prolonged arousal may increase the magnitude and duration of contractions of the smooth musculature surrounding the caudal epididymis and ductus deferens (Senger, 1997), contractions that are known to be critical for sperm delivery (Batra, 1974; Guha *et al.*, 1975; Hib *et al.*, 1982). A similar mechanism may be involved in the improvements in human semen quality seen with increases in the duration of pre-ejaculatory sexual arousal.

The significant decrease in sperm motility seen with increased specimen production time in the present study is consistent with the marginally significant negative correlation ($r = -0.52$, $p = 0.07$) between motility and changes in time to orgasm for healthy sperm donors reported in a previous study (van Roijen *et al.*, 1996). If increased specimen production time is a reflection of anxiety on the part

of the semen donor then this may contribute to the observed decline in sperm motility since there is some evidence that psychological stress can impair semen quality. Specifically, Clarke *et al.* (1999) reported that the stress associated with providing a specimen for in-vitro fertilisation can impair total and motile sperm concentration. The mechanism by which psychological stress might affect semen quality is unclear but it is possible that anxiety-induced changes in semen parameters are in fact secondary to increases in ejaculatory latency.

If the mechanism by which increases in the duration of pre-ejaculatory sexual arousal improve semen quality involves the facilitation of sperm transport along the vas deferens and into the posterior urethra in preparation for ejaculation, then this might account for the observed decline in motility with increased specimen production time. Increases in the amount of time that sperm spend in the distal vas deferens and posterior might be associated with increases in sperm mortality and consequent declines in the number of motile sperm ejaculated. However, this decline is of limited clinical significance since, as previously noted, it is not sufficient to cause reductions in motile sperm concentration with increases in specimen production time given the substantial increases in sperm concentration associated with increases in the duration of pre-ejaculatory sexual arousal.

Perhaps of more clinical significance is the finding that the relationship between specimen production time and semen quality was not entirely linear and

had a significant quadratic component. The best-fitting quadratic functions indicate that both sperm concentration and total sperm number showed improvements with increased specimen production time up to about 30 minutes. However, the observed quadratic component appears to be attributable to the low quality of the relatively small number (about 5%) of ejaculates that took longer than 30 minutes to produce. In these cases, increased ejaculatory latency and reduced ejaculate quality might both be consequences of relatively short periods of sexual abstinence. Although all donors reported having maintained a minimum of 3 days of ejaculatory abstinence before providing each specimen, it is nevertheless likely that there were significant between-specimen differences in the exact duration of the abstinence period. This is important since not only is there a positive relationship between the duration of sexual abstinence and ejaculate quality (e.g. Schwartz *et al.*, 1979; Sauer *et al.*, 1988, Blackwell & Zaneveld, 1992), but there is also an inverse relationship between the duration of abstinence and ejaculatory latency (Tuthill, 1955; Spiess, *et al.*, 1984).

Obviously, further research is needed to disentangle the interactive effects of sexual abstinence and pre-ejaculatory sexual arousal on ejaculate quality. However, given the well-established effects of abstinence, the inverse relationship between the duration of abstinence and the ejaculatory latency would tend to mask any positive relationship between duration of pre-ejaculatory sexual arousal and the semen parameters. That such a relationship was observed in the present study suggests that it is fairly robust, and this finding, taken together with the

findings of Zavos (1988), suggests that ejaculate composition is indeed dependent on the duration of pre-ejaculatory arousal.

The present study provides some evidence that the duration of pre-ejaculatory sexual arousal can affect the composition of masturbatory ejaculates. However, since the study was correlational rather than experimental in its design it cannot be established whether the observed relationship reflects a casual link between arousal and ejaculate composition. Concomitant increases in ejaculatory latency and sperm concentration may be attributable to a common underlying cause. For example, it could be hypothesised that males who typically take a long time to produce a specimen also tend to produce high quality ejaculates. However, in the present study there was no relationship between the average time taken by each donor to produce a specimen and the mean values for his various ejaculate parameters and this suggests that the observed relationship cannot be attributed entirely to stable individual differences between males. Furthermore, when between-subject differences in sperm concentration were controlled for in the fixed effects linear regression model, time taken to produce the specimen was still a significant predictor of sperm concentration for those specimens produced in less than 30 minutes. Further research, in which individual males provide multiple specimens, is needed to determine the extent to which within-subject changes in the duration of pre-ejaculatory sexual arousal alone can affect semen parameters. If the within-subject effects are substantial, instructing semen donors

to prolong the duration of pre-ejaculatory sexual stimulation when they provide specimens by masturbation might result in improvements in semen quality.

Clinicians have generally treated differences in ejaculate parameters from one specimen to the next as a problem when attempting to establish a reliable semen profile for a particular man (e.g. Baker *et al.*, 1981; Poland *et al.*, 1985). However, behavioural ecologists have taken a rather different approach when studying variability in ejaculate composition in non-human species. Facultative adjustment of sperm delivery can be considered as a resource allocation problem for males of species that have faced the selective pressures associated with sperm competition during their evolutionary history. Sperm competition is the competition between the sperm of different males to fertilise a single female's gamete(s) (Parker, 1970). In species with internal fertilisation, sperm competition may occur whenever a female copulates with multiple males such that live sperm from two (or more) are present within her reproductive tract. Under these circumstances, notwithstanding mating order effects, a "raffle principle" applies; i.e. a given male can increase the probability of siring her offspring by inseminating more sperm (Parker, 1970; 1990a). However, for males there is a trade-off between the non-trivial cost of ejaculate production (Dewsbury, 1982) and the risk of sperm competition. Following from this, an early prediction of sperm competition theory was that males should inseminate more sperm when the risk of double mating, and hence of sperm competition, is high (Baker & Bellis, 1995; Parker, 1982; 1990a; 1990b). There is experimental evidence that this

occurs in various insect and mammalian species (for a review see Parker *et al.*, 1997) and there is also some evidence that human males, when copulating with an established partner, inseminate more sperm when the risk of sperm competition is high (Baker & Bellis, 1989; 1993). However, the psychological and physiological mechanisms involved in adaptive regulation of ejaculate composition are poorly understood.

The present study and the findings of Zavos (1988) suggest that increases in the duration of pre-ejaculatory sexual arousal are associated with improvements in semen quality for human males. This raises the intriguing possibility that changes in the intensity and duration of sexual arousal preceding ejaculation may be involved in the adaptive regulation of semen parameters in response to changes in the risk of sperm competition. Psychological responses to social situations and cues that would have been associated with increases in the risk of sperm competition in ancestral environments, might trigger changes in sexual behaviour that increase the duration of pre-ejaculatory sexual arousal and consequently increase the number of sperm inseminated.

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REFERENCES

- Almquist, J. O. (1973). Effects of sexual preparation on sperm output, semen characteristics and sexual activity of beef bulls with a comparison to dairy bulls. *J Anim Sci*, *36*, 331-336.
- Almquist, J. O., Hale, E. B., & Amann, R. P. (1958). Sperm production and fertility of dairy bulls at high collection frequencies with varying degrees of sexual preparation. *J Dairy Sci*, *41*, 733.
- Baker, H. W., Burger, H. G., de Kretser, D. M., Lording, D. W., McGowan, P., & Rennie, G. C. (1981). Factors affecting the variability of semen analysis results in infertile men. *Int J Androl*, *4*, 609-622.
- Baker, R. R., Bellis, M. A. (1995). *Human sperm competition: Copulation, masturbation, and infidelity*. Chapman and Hall, London.
- Baker, R. R., & Bellis, M. A. (1989). Number of sperm in human ejaculates varies in accordance with sperm competition theory. *Anim Behav*, *37*, 867-869.
- Baker, R. R., & Bellis, M. A. (1993). Human sperm competition: ejaculate manipulation by males and the function of masturbation. *Anim Behav*, *46*, 861-885.
- Batra, S. K. (1974). Sperm transport through the vas deferens: Review of hypotheses and suggestions for a quantitative model. *Fertil Steril*, *25*, 186-202.
- Blackwell, J. M., & Zaneveld, L. J. (1992) Effect of abstinence on sperm acrosin, hypoosmotic swelling, and other semen variables. *Fertil Steril*, *58*, 798-802.

- Canadian Fertility and Andrology Society (1996). *Guidelines for Therapeutic Donor Insemination*.
- Clarke, R. N., Klock, S. C., Geoghegan, A., & Travassos, D. E. (1999). Relationship between psychological stress and semen quality among in-vitro fertilization patients. *Hum Reprod*, *14*, 753-758.
- Collins, W. J., Bratton, R. W., & Henderson, C. R. (1951). The relationship of semen production to sexual excitement of dairy bulls. *J Dairy Sci*, *34*, 224-227.
- Dewsbury, D. A. (1982). Ejaculate cost and male choice. *Amer Nat*, *119*, 601-610.
- Guha, S. K., Kaur, H., & Ahmed, A. M. (1975). Mechanics of spermatic fluid transport in the vas deferens. *Med Biol Eng*, *13*, 518-22.
- Hafs, H. D., Kinsey, R. C., & Desjardins, C. (1962). Sperm output of dairy bulls with varying degrees of sexual preparation. *J Dairy Sci*, *45*, 788-793.
- Health Canada: Health Protection Branch (1996). *Food and Drug Act: Processing and Distribution of Semen for Assisted Conception Regulations*.
- Hemsworth, P. H., & Galloway, D. B. (1979). The effect of sexual stimulation on the sperm output of the domestic boar. *Anim Reprod Sci*, *2*, 387-394.
- Hib, J. Ponzio, R., & Vilar, O. (1982). Contractility of the rat cauda epididymis and vas deferens during seminal emission. *J Reprod Fertil*, *66*, 47-50.
- Mallidis, C., Howard, E. J., & Baker, H. W. (1991). Variation of semen quality in normal men. *Int J Androl*, *14*, 99-107.

- Padova, G., Tita, P., Briguglia, G., & Giuffrida, D. (1988). Influence of abstinence length on ejaculate characteristics. *Acta Eur Fertil*, 19, 29-31.
- Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biol Rev*, 45, 525-567.
- Parker, G. A. (1982). Why are there so many tiny sperm? Sperm competition and the maintenance of two sexes. *J Theor Biol*, 96, 281-294.
- Parker, G. A. (1990a). Sperm competition games: raffles and roles. *Proc R Soc Lond B Biol*, 242, 120-126.
- Parker, G. A. (1990b). Sperm competition games: sneaks and extra-pair copulations. *Proc R Soc Lond B Biol*, 246, 107-115.
- Parker, G. A., Ball, M. A., Stockley, P., & Gage, M. J. G. (1997). Sperm competition games: a prospective risk analysis assessment. *Proc R Soc Lond B Biol*, 264, 1793-1802.
- Poland, M. L., Moghissi, K. S., Giblin, P. T., Ager, J. W., & Olson, J. M. (1985). Variation of semen measures within normal men. *Fertil Steril*, 44, 396-400.
- Prins, G. S., & Zaneveld, L. J. (1979). Distribution of spermatozoa in the rabbit vas deferens. *Biol Reprod*, 21, 181-185.
- Prins, G. S., & Zaneveld, L. J. (1980). Radiographic study of fluid transport in the rabbit vas deferens during sexual rest and after sexual activity. *J Reprod Fertil*, 58, 311-319.

- Read, M. D., & Schnieden, H. (1978). Variations in sperm count in oligozoospermic or asthenozoospermic patients. *Andrologia*, *10*, 52-55.
- Sauer, M. V., Zeffer, K. B., Buster, J. E., & Sokol, R. Z. (1988). Effect of abstinence on sperm motility in normal men. *Am J Obstet Gynecol*, *15*, 604-607.
- Schwartz, D., Laplanche, A., Jouannet, P., & David, G. (1979). Within-subject variability of human semen in regard to sperm count, volume, total number of spermatozoa and length of abstinence. *J Reprod Fertil*, *57*, 391-395.
- Senger, P. L. (1997). *Pathways to pregnancy and parturition*. Current Conceptions, Pullman, WA.
- Sofikitis, N. V., & Miyagawa, I. (1993). Endocrinological, biophysical, and biochemical parameters of semen collected via masturbation versus sexual intercourse. *J Androl*, *14*, 366-373.
- Spiess, W. F., Geer, J. H., & O'Donohue, W. T. (1984). Premature ejaculation: Investigation of factors in ejaculatory latency. *J Abnorm Psychol*, *93*, 242-245.
- Tuthill, J.F. (1955). Impotence. *Lancet*, *268*, 124-128.
- van Roijen, J. H., Slob A. K., Gianotten, W. L., Dohle, G. R., van der Zon, A. T., Vreeburg, J. T., & Weber, R. F. (1996). Sexual arousal and the quality of semen produced by masturbation. *Hum Reprod*, *11*, 147-151.

- Weber, J. A., Geary, R. T., & Woods, G. L. (1990). Changes in accessory sex glands of stallions after sexual preparation and ejaculation. *J Am Vet Med Assoc*, 196, 1084-1089.
- World Health Organization (1992). *Laboratory Manual for the Examination of Human Semen and Sperm-Cervical Mucus Interaction*, 3rd edn. Cambridge University Press, Cambridge.
- Zavos, P.M. (1985). Seminal parameters of ejaculates collected from oligospermic and normospermic patients via masturbation and at intercourse with the use of a Silastic seminal fluid collection device. *Fertil Steril*, 44, 517-520.
- Zavos, P.M. (1988). Seminal parameters of ejaculates collected at intercourse with the use of a seminal collection device with different levels of precoital stimulation. (Abstr) *J Androl*, 9: P-36.
- Zavos, P. M., & Goodpasture, J. C. (1989). Clinical improvements of specific seminal deficiencies via intercourse with a seminal collection device versus masturbation. *Fertil Steril*, 51, 190-193.
- Zavos, P. M., Kofinas, G. D., Sofikitis, N. V., Zarmakoupis, P. N., & Miyagawa, I. (1994). Differences in seminal parameters in specimens collected via intercourse and incomplete intercourse (*coitus interruptus*). *Fertil Steril*, 61, 1174-1176.

Table 1. Ejaculate parameters and bivariate correlations with time taken to produce specimen. Pearson correlation coefficient (r) and significance (P).

Variable	N	Mean	SD	Min	Max	r	P
Time Taken to Produce Specimen (mins)	292	15.5	8.0	3.0	55.0	—	—
Ejaculate Volume (ml)	292	3.5	1.6	0.9	9.0	0.08	0.2
Sperm Concentration (millions per ml)	292	70.9	28.2	12.0	156.0	0.19	0.001
Sperm Motility (%)	292	62.9	8.7	31.0	81.0	0.21	0.0004
Motility Grade (1-4)	291	3.7	0.3	0.5	4.0	0.05	0.4
Total Sperm Number (millions)	292	236.8	124.1	26.4	834.4	0.22	0.0001
Motile Sperm Concentration (millions per ml)	292	44.4	18.2	5.6	110.2	0.12	0.04
Total Motile Sperm Number (millions)	292	148.8	79.5	16.7	433.9	0.17	0.003

Table 2a. Linear Regression Model Summary

Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
1	.719 ^a	.518	.475	19.8962

Table 2b. ANOVA^b

Model		Sum of Squares	Df	Mean Square	F	Sig.
1	Regression	105318.8	22	4787.218	12.093	.000 ^a
	Residual	98172.6	248	395.857		
	Total	203491.4	270			

Table 2c. Coefficients^b

	Unstandardized Coefficients		Standardized Coefficients	t	Sig.
	B	Std. Error	Beta		
(Constant)	50.296	4.785		10.511	.000
Time	0.671	0.335	.134	2.000	.047
D3032	15.609	10.652	.077	1.465	.144
D3038	-9.859	6.249	-.085	-1.578	.116
D3061	33.969	12.324	.130	2.756	.006
D3116	12.068	6.975	.091	1.730	.085
D3117	5.924	5.489	.065	1.079	.282
D3120	24.243	7.565	.167	3.205	.002
D3136	55.977	6.484	.481	8.633	.000
D3139	-6.282	6.376	-.052	-0.985	.325
D3140	25.233	6.431	.211	3.924	.000
D3141	35.017	7.193	.376	4.868	.000
D3142	-2.811	9.330	-.015	-0.301	.763
D3148	-7.630	6.483	-.071	-1.177	.240
D3150	-3.400	8.990	-.018	-0.378	.706
D3152	19.072	6.923	.143	2.755	.006
D3153	21.086	7.872	.138	2.679	.008
D3154	19.279	15.171	.060	1.271	.205
D3155	-4.281	7.811	-.028	-0.548	.584
D3156	-15.510	7.951	-.101	-1.951	.052
D3157	1.581	7.674	.010	0.206	.837
D3158	17.331	7.039	.135	2.462	.014
D3159	12.529	11.454	.055	1.094	.275

a. Predictors: (Constant), D3159, D3154, D3061, D3032, D3150, D3142, D3157, D3156, D3155, D3153, D3120, D3152, D3116, D3158, D3140, D3139, D3136, D3038, D3148, time taken to produce sample, D3117, D3141

b. Dependent Variable: sperm concentration (million per ml)

Figure 1. Relationship between time taken to produce a semen specimen and sperm concentration (\square), sperm motility (\bullet), and motile sperm concentration (\blacktriangle) for 292 specimens produced by 25 donors (median 11 per donor). Specimens have been divided into four groups according to production time. Parameter mean \pm SEM are shown for each group.

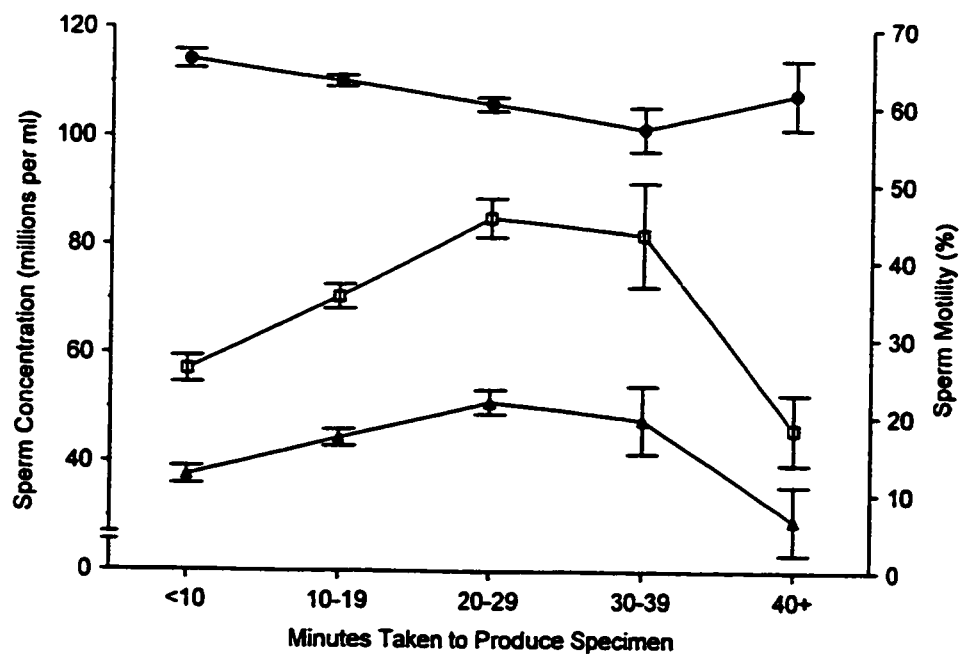
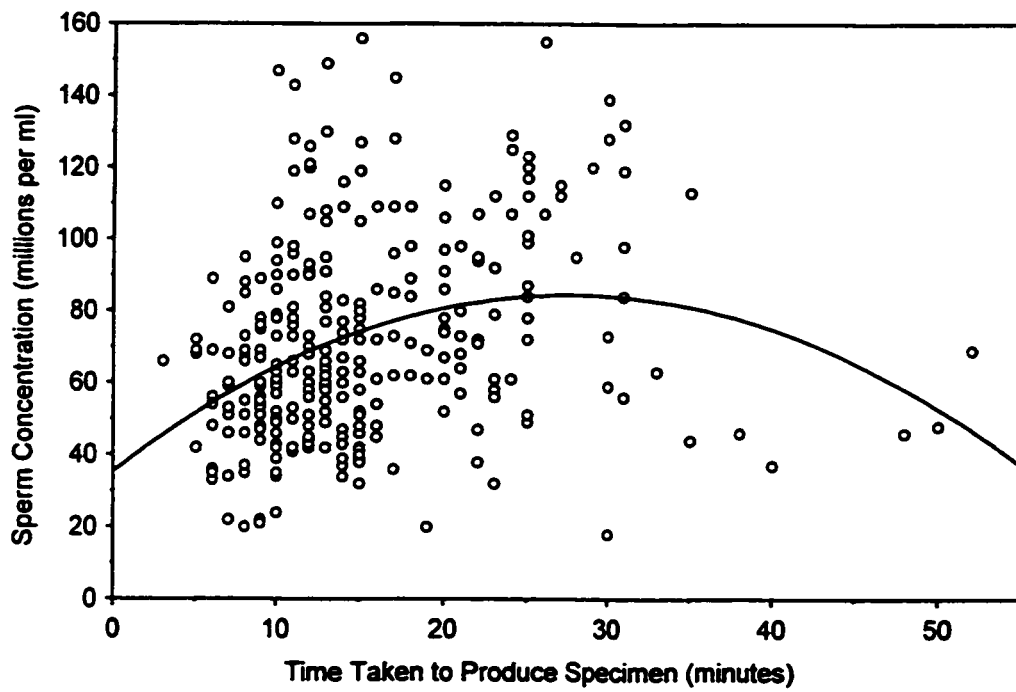


Figure 2. Scatterplot showing the relationship between sperm concentration and the time taken to produce a specimen for 292 specimens produced by 25 donors (median 11 per donor). The best-fitting quadratic regression model ($y = 35.4 + 3.5x - 0.06x^2$) is represented by the dotted line.



CHAPTER 4

**THE PREVALENCE OF POLYANDRY IN CONTEMPORARY
PORNOGRAPHY: A REFLECTION OF MALE PSYCHOLOGICAL
ADAPTATIONS TO SPERM COMPETITION?**

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ABSTRACT

Pornography is produced to sexually arouse a male audience. Hence, analysis of the types of material that are available may provide valuable insights into the nature of male sexual preferences and interests. Content analysis of pornographic images available over the Internet, sexually explicit videos and "erotic" stories revealed that depictions of polyandrous mating by females may be a significant source of sexual arousal for males. This was confirmed by a short survey of male preferences conducted using the World Wide Web. The adaptive significance of male sexual arousal in response to female polyandry will be discussed in the context of sperm competition theory.

Keywords: evolutionary psychology; men; pornography; polyandry; sperm competition.

INTRODUCTION

Men and women both show physiological signs of sexual arousal when viewing explicit depictions of sexual activity (e.g. Kelley & Byrne, 1983). However, most pornography is produced to sexually arouse men (Kinsey *et al.*, 1948) and they generally report much more exposure to, and greater interest in, sexually explicit books, photographs and films than do women (Abelson *et al.*, 1971; Nawy, 1971). It is reasonable to assume that the types of sexual activity most frequently depicted in visual pornography are those that men find most arousing to view, not least because many of the people involved in the production and distribution of the material are men themselves and therefore have first-hand knowledge of male sexual preferences and interests. Consequently, it might be expected that there would be concordance between the activities that are most frequently depicted in pornography, and those that appear most often in male sexual fantasies.

Male sexual fantasies frequently involve anonymous sex with physically attractive strangers and typically include explicit visual imagery of genitalia and sexual acts (e.g. Ellis & Symons, 1990). Furthermore, male fantasies typically involve sexual encounters with many different partners while women, in contrast, are more inclined to focus on sexual relations with a particular desirable mate (e.g. Symons, 1979). This sex difference in fantasy content is thought to reflect a real difference in the relative importance that men and women place on sexual

variety and sheer number of sexual partners. Evolutionary psychologists have argued that this difference has arisen because of the asymmetric costs associated with sexual reproduction. The nature of the menstrual cycle and the time required to carry a baby to term place important constraints on the maximum reproductive output of the human female. The male on the other hand, is essentially only limited by the number of fertile partners with whom he can mate and sire offspring. More generally, sexual access to reproductively valuable partners limits progeny more significantly for males than females in species where there are asymmetries in parental investment (Bateman, 1948; Trivers, 1972; Williams, 1975). Over successive generations, the desire to mate with multiple partners would have had significant selective consequences if males who engaged in such behaviour left more offspring than those who did not. Consequently, given the choice, human males should prefer to mate with multiple partners and in despotic societies, powerful men do just this when they monopolise the reproductive output of a harem of females (Betzig, 1986).

There is clearly concordance between pornography and male sexual fantasies in that both typically include explicit visual imagery of genitalia and sexual acts. Furthermore, given that men fantasise about sexual encounters with many different partners (Symons, 1979) pornography would also seem to cater to this aspect of evolved masculine sexual psychology simply by virtue of the sheer quantity and variety of material that is available. However, male interest in sexual variety might also be expected to manifest itself in the types of activity that

are depicted. For example, depictions of sexual activity involving a single male and several females would seem to constitute the most direct appeal to this aspect of male sexuality since all else being equal, the males of an effectively polygynous species are expected to prefer polygynous mating opportunities when given a choice. However, a cursory examination of pornographic videos and photographs reveals that they frequently depict sexual contact between one woman and several men. In its extreme form, this type of orgiastic sexual activity can involve a single female and a very large number of males. This can be thought of as somewhat surprising since such polyandrous orgiastic sexual activity might be expected to be uninteresting at the least, and possibly aversive, to human males. In the environments in which male sexual psychology evolved, such mating contexts would have been less likely to result in conception for a particular male than either monogamous or polygynous encounters. Therefore, males might be expected to prefer to mate with a single female, in isolation, or to mate with multiple females either sequentially or in an orgiastic setting. However, sperm competition theory might be able to explain why males find depictions of polyandrous orgiastic mating to be sexually arousing.

Sperm competition is the competition between the sperm of different males to fertilise a female's gamete(s) (Parker, 1970). In a species with internal fertilisation, it can occur whenever a female engages in "double-mating" such that live sperm from two (or more) males are present within her reproductive tract. Under these circumstances, notwithstanding mating order effects, a "raffle

principle” applies; that is, a particular male can increase the probability of siring a female’s offspring by inseminating more sperm (Parker, 1970, 1990a). However, for males there is a trade-off between the non-trivial cost of ejaculate production (Dewsbury, 1982) and the risk of sperm competition. Thus, an early prediction of sperm competition theory was that males will inseminate more sperm when the risk of “double-mating”, and hence sperm competition, is high (Parker, 1982, 1990a,b; Baker & Bellis, 1995).

There is abundant evidence that investment in sperm production is greater in species that experience high levels of sperm competition. For example, testis size is positively correlated with the incidence of polyandrous mating across species for primates (Short, 1979; Harcourt *et al.*, 1981; Harvey & Harcourt, 1984), birds (Møller, 1988), ungulates (Ginsberg & Rubenstein, 1990), frogs (Jennions & Passmore, 1993), and butterflies (Gage, 1994). Moreover, the fact that human testes are larger in relation to body size, than are those of monogamous primates (Short, 1981) strongly suggests that sperm competition has been an important selective pressure during human evolution (Smith, 1984).

In addition to between-species differences in investment in sperm production that are consistent with sperm competition theory, experimental evidence is accumulating that within many species, individual males are able to make adaptive, short-term adjustments in the number of sperm they produce and deliver. Specifically, from one copulation to the next, individual males can make

facultative adjustments to the number of sperm they inseminate in response to cues that provide information about the risk and/or intensity of sperm competition (for a review see Parker *et al.*, 1997). Male moths (*Plodia interpunctella*) adjust the number of eupyrene sperm they inseminate according to the number of rival sperm already present within a female's reproductive tract (Cook & Gage, 1995), perhaps making use of direct visual, tactile, or olfactory cues to determine the risk of sperm competition. However, in other species males have been shown to respond to less direct cues of sperm competition risk. Bushcrickets adjust the number of sperm they inseminate according to a female's mating status (*Kawanaphila nartee*: Simmons *et al.*, 1993) while rats are sensitive to the time they have spent guarding a particular female prior to copulation (*Rattus norvegicus*: Bellis *et al.*, 1990). Similarly, there is also some evidence that human males can regulate their ejaculate composition in an adaptive fashion. Baker and Bellis (1989, 1993) reported that men, when copulating with an established partner, inseminate more sperm when the risk of sperm competition is high. Specifically, they found a negative correlation between the number of sperm ejaculated and the proportion of time a couple has spent together since their last copulation; a parameter which is correlated with the risk that the female already contains sperm from another male (Baker & Bellis, 1995). Finally, males in some species have been shown to be sensitive to the presence of other males. For example, male beetles (*Tenebrio molitor*: Gage & Baker, 1991) and flies (*Ceratitis capitata*: Gage, 1991) inseminate more sperm in the presence of a male

rival. Moreover, male field (*Gryllodes supplicans*) and house (*Acheta domesticus*) crickets increase the number of sperm they inseminate in proportion to the number of rivals present (Gage & Barnard, 1996).

For avian species in which the risk of sperm competition high, birds use frequent in-pair copulation as a method of paternity assurance (Birkhead *et al.*, 1987; Møller & Birkhead, 1991). Similarly, in addition to adjusting ejaculate composition, human males could achieve adaptive regulation of the number of sperm inseminated by changing the frequency and timing of copulation itself (Baker & Bellis, 1995). Consequently, if prompt copulation with a female who has been inseminated by another male reduces the risk of cuckoldry then cues of sperm competition risk should produce sexual arousal and motivate behaviours likely to lead to more frequent copulation. This occurs in the walnut fly (*Rhagoletis juglandi*), a species in which males increase the amount of time spent copulating when the operational sex ratio is strongly male biased (Alonso-Pimental & Papaj, 1996). Furthermore, there is abundant evidence from the farming industry that the presence of other males can have significant stimulatory effects on sexual activity.

The sexual performance of bulls is enhanced when they mate in multiple rather than single-sire groups (Mattner *et al.*, 1974). Furthermore, when semen is collected from bulls for artificial insemination, sexual performance is improved if they are simply watched by another young "teaser" male (Foote, 1974; West,

1977). Under these circumstances, bulls are quicker to mount a female and ejaculatory latency is reduced, and their ejaculatory frequency is increased (Mader & Price, 1984). The same effect can also be used to stimulate sexual behaviour in a bull that is required to mate successively with multiple cows and might otherwise cease to show interest. As a potential rival, the teaser may stimulate the bull's evolved responses to intrasexual competition.

In light of the evidence that *Homo sapiens* have been subjected to a history of sperm competition, human males might also be expected to be aroused sexually by the presence of male rivals and other cues predictive of increased risk of sperm competition. These cues are expected to motivate more frequent in-pair copulation as insurance against the possibility that polyandrous mating has already occurred, or cannot be prevented. By keeping a female "topped up" with his sperm, a man can reduce the likelihood she will conceive a child sired by another male (Baker & Bellis, 1995). Furthermore, copulation may serve to displace rival sperm that may be present. But while the presence of male rivals may reliably predict increased risk of sperm competition, the most direct and unequivocal evidence that rival sperm are likely to be present within a female's reproductive tract may come from witnessing a sexual encounter between her and another male.

In many species, such an experience is capable of producing sexual arousal in male observers. For example, allowing them to view other males

engaged in copulatory behaviour enhances the sexual performance of domesticated farm animals. After watching another male copulate with a female, bulls ejaculate more frequently (Kerruish, 1955; Blockey, 1981) and male goats show reduced latencies to mount and ejaculate (Price *et al.*, 1984). Similar improvements in sexual performance are seen in stallions that display a lack of sexual interest (Pickett *et al.*, 1977). Crucially, the stimulatory effects associated with viewing a female copulating with another male are greater than are those of watching a restrained cow by herself (Mader & Price, 1984). Moreover, similar effects are seen in boars that have merely viewed another male mounting and ejaculating over a dummy sow. These males exhibit substantial reductions in the time taken to mount the dummy and increases in the total number of sperm ejaculated relative to controls (Hemsworth & Galloway, 1979). So it would seem that human males are not unique in their ability to become aroused simply by watching other males engaged in sexual activity (i.e. viewing pornography).

It can be argued that human males can be sexually aroused by depictions of heterosexual copulation because they contain cues that would have been predictive of increased risk of sperm competition in the ancestral environment. An alternative interpretation might be that such material sexually arouses males only because they identify with, and imagine themselves to be, the male in the depiction. However, it is difficult to extend this identification interpretation to pornography that contains representations of sexual encounters between a single female and multiple males; that is unequivocal depictions of female polyandry.

Such material provides unambiguous cues of sperm competition risk. If male sexual psychology has been shaped by an evolutionary history of sperm competition then it follows that men may find depictions of female polyandry to be a more potent source of sexual arousal than material depicting heterosexual couples alone.

To summarise, I have argued that male arousal in response to witnessing sexual encounters between females and other males may reflect an adaptation to an evolutionary history of sperm competition. Moreover, the ability of pornographic images to produce sexual arousal may depend on this aspect of male sexuality. Furthermore, if male sexual arousal is an adaptive response to female polyandry and the associated risk of sperm competition, then it might be expected that images that unequivocally depict female polyandry would be particularly potent sexual stimuli (i.e. sexual encounters between a female and multiple males). To determine whether males are interested in viewing such material, a series of content analyses were conducted. It is assumed that the relative prevalence of depictions of polyandrous sexual activity in contemporary pornography can provide an indirect index of male interest in this type of material. In addition, preference studies were conducted since these can provide direct evidence that males are interested in material containing cues of increased sperm competition risk. Finally, semen analyses were performed to determine whether the number of sperm ejaculated by human males varies according to the

presence or absence of sperm competition cues in the visual pornography they view while producing semen specimens via masturbation.

STUDY 1: CONTENT ANALYSIS OF PHOTOGRAPHS

The rapid growth of the World Wide Web (WWW) during the 1990s has created an important new route for the distribution of pornography. To the extent that prevalence reflects preferences, the relative frequency with which different types of sexually explicit material are encountered on the WWW may provide useful information about the nature of male sexual preferences. While it can be argued that Internet users are a unique subset of the male population, personal computers connected to the Internet provide access to pornography for individuals who might otherwise be reluctant to purchase such material in public. Since it is possible to download pornographic photographs and videos in relative privacy and at minimal cost, the number of males who regularly view pornographic material has likely increased substantially in recent years. Consequently, studies of pornography consumption over the Internet can be used to examine the preferences of men who might be excluded by studies that focused on more traditional media.

PROCEDURE

Many WWW sites compile and maintain lists of other sites containing pornographic photographs that are freely accessible. Once such site is known as

"Persian Kitty's Adult Links" (<http://www.persiankitty.com/>) and, according to indices such as "100hot: The Web's Popularity Guide" (<http://www.100hot.com/>) and Webcounter (<http://www.digits.com/>), it is currently one of the most popular free "adult" sites averaging over 20,000 "hits" per day. The site has an extensive alphabetical list of other sites on the WWW that offer free access to pornographic images of interest to heterosexual males. Every tenth link to a free site listed on this page was followed and the images contained within each of these sites were categorised according to the number of males and females they contained. In total, 49 sites were visited and 3188 images were categorised. The procedure was repeated for CyberPorn Sex Links (<http://www.cyberporn.inter.net/>), another popular site that averages about 30,000 hits per day. For CyberPorn, 28 sites were visited and 2286 images were categorised. The categorisation of images located using this second source of links was conducted by a research assistant who was unfamiliar with the rationale behind the study.

RESULTS

Of the 5473 images sampled, 48.5% depicted a single female while the remaining images depicted sexual activity involving two or more individuals. The results of the categorisation procedure for the 2816 images depicting sexual activity are summarised in Table 1. It is clear that the distribution of images among the categories was extremely similar for the sites located using either of the two links pages. Depictions of heterosexual couples formed the largest

category of images. However, for those images depicting three or more individuals, images in which males outnumbered females were more prevalent (61.9%) than those in which females outnumbered males (35.9%). Of those images in which there were more males than females, 86.7% depicted two males with one female, while 13.3% depicted a single female with three or more males (13 in the most extreme case). There were no images depicting more than two females with a single male.

Table 1 about here

STUDY 2: CONTENT ANALYSIS OF VIDEOS

In addition to providing rapid access to pornographic material, the Internet is also used to transmit information about pornography that is available in other, more traditional forms. In particular, a number of WWW sites and Usenet groups are dedicated to discussions about, and reviews of, pornographic videos that are available in rental stores or via mail order. These discussions and reviews can provide concise information about the content of pornographic videos and are conveniently archived by a number of websites. One of the largest archives of video reviews is CyberSpace Adult Video Reviews (<http://www.cavr.com/>). It contains several hundred reviews of pornographic videos released in the USA over the past few years and these reviews include brief descriptions of each of the different scenes in the videos.

METHOD

All the video reviews (n=169) archived between November 1996 and March 1997 were examined and the scenes that they contained were categorised according to the number of male and female participants. The vast majority of descriptions clearly identified all the scene participants and the types of activity that occurred. However, when the descriptions were ambiguous the video was not included in the analysis.

RESULTS

The average length of the videos was 86 minutes (Max. 140; Min. 25) and the median number of scenes in each was four (Max. 10; Min. 1). In total 742 scenes were categorised and the results are summarised in Table 1. Scenes involving a heterosexual couple were most common (43.4%), but males outnumbered females in the majority (62.5%) of the scenes involving three or more people. Females outnumbered males in only 29.5% of the group sex scenes.

STUDY 3: PREFERENCE QUESTIONNAIRE

Content analyses can provide information about the prevalence of certain types of sexual activity within pornography. However, inferences about male sexual preferences based on such evidence depend on the assumption that preferences are reflected in the relative prevalence of certain types of material.

Consequently, in order to assess male preferences more directly, an on-line questionnaire was set up with the co-operation of a web site that publishes pornographic stories (<http://www.xxxgroup.com/>).

METHOD

Visitors to the Free XXX Sex Stories site were invited to complete a short questionnaire. Participants were asked to indicate the types of scene they preferred when, a) reading erotic stories; b) viewing still photographs depicting sexual activity; and c) watching films or videos depicting sexual activity. For each type of pornography, respondents were able to choose from six categories that corresponded to those used in the content analyses of studies 1 and 2. These were, a) a single female, b) two or more females, c) one male and one female, d) group sex with multiple males and a single female, e) group sex with multiple females and a single male, f) group sex with equal numbers of males and females, or, g) other.

RESULTS

During a one-week period, 203 people completed the questionnaire and their responses are summarised in Table 2. For pornographic videos, photographs and stories, the most popular scenes were those involving multiple males and a single female. Notably, questionnaire respondents were approximately twice as

likely to have indicated a preference for these scenes than for depictions of multiple females and a single male.

Table 2 about here

STUDY 4: IMAGE SELECTION

The previous study involved asking participants hypothetical questions about what types of material they would view given the choice. However, expressed preferences do not necessarily perfectly reflect actual preferences since social desirability considerations may lead respondents to claim that they would choose to view a particular type of scene when they would actually choose to view something different when presented with a real choice. To address this concern, a second preference study was conducted to assess preferences more directly by asking participants what they would actually like to view at that time. This study depended on participants believing that their choice would actually determine the type of pornography they would get to view.

Previous research on sensitive issues has employed the Internet as a means of contacting potential participants. Sell (1997) conducted a survey of sexual orientation by randomly selecting participants from the pool of individuals who had posted messages to particular newsgroups. They were then contacted by email and a 56.4% response rate was achieved. The problem with this technique is that it can only identify people who have posted to newsgroups and it thus

excludes the large number of people who just read the postings without contributing themselves. Consequently, in the present study postings to relevant newsgroups were used to solicit participants.

METHOD

A web site was established in order to collect information on male preferences for certain types of visual pornography. Participants for the study were sought using a series of messages posted to newsgroups in the alt.sex.* and alt.binaries.sex.* hierarchies. These messages, like many other postings to the groups, contained information (a URL) on where to find a web site containing pornographic images. The messages indicated that the advertised site contained "100% Free Hot Sex Pictures".

Visitors to the site were warned that it contained sexually explicit material, then asked to choose what type of images they would like to view. They were offered a choice between sexually explicit images containing depictions of, a) a single female, b) two or more females, c) one male and one female, d) group sex with two males and a single female, e) group sex with two females and a single male. The alternatives were presented on the screen in this order. Once a choice was made, the visitor was informed that "the launch of the site had been postponed" and that it contained "no pictures at the current time." Only the choice made on the first visit from a particular Internet Protocol (IP) address was recorded.

RESULTS

Over a period of two weeks, 391 people responded to the postings and visited the web site. The first choices made by each visitor are summarised in Table 2. Images of two or more females were the most popular (27.5%) first choice of visitors to the web site. However, images of multiple males with a single female were the second most popular (25.2%) first choice. Images of multiple females with a single male were the fourth most popular choice.

STUDY 5: EFFECTS OF PORNOGRAPHY ON EJACULATE PARAMETERS

It has been argued that human males should respond to visual cues of sperm competition with sexual arousal and behaviours that increase the likelihood that they will deposit sperm in a female's reproductive tract. However, sperm competition theory also predicts that males should respond to cues of sperm competition with increases in the number of sperm delivered during copulation. While there is some evidence that human males are capable of adaptive modulation of ejaculate composition (Baker & Bellis, 1989, 1993) it is not known whether men can adjust their semen parameters in response to visual cues of sperm competition present during sexual arousal and ejaculation. Consequently, a study was conducted to determine whether the presence of visual cues of sperm competition in the pornographic material viewed by men during specimen production can affect their semen parameters.

METHOD

Subjects

Twenty-five regular semen donors aged 22-40 years (median: 31 years) participated in the study between November 1998 and February 1999. Each was accepted into the semen donor programme at a Toronto-based sperm bank after completing the required screening as per official standards of Health Canada and the Canadian Fertility and Andrology Society (1996). The donors were instructed to abstain from ejaculation for 3 days before producing their specimens by masturbation in a private room while watching one of four sexually explicit videos.

Procedure

Commercially available pornographic videos were edited to produce four tapes (A, B, C, D), each of which contained a compilation of scenes depicting sexual activity involving a particular number of males and females; A) 2 females, B) 1 male and 1 female, C) 1 male and 2 females; D) 2 males and 1 female. Since the scenes on each compilation were drawn from the same set of pornographic videos, the quality and style of the footage on each tape was fairly similar. Furthermore, wherever possible, each of the four tapes contained scenes involving the same females.

During the first phase of the study (November-December), donors provided semen specimens while watching either video A or B. The video provided was alternated on a weekly basis and the donors provided specimens on an irregular, self-determined, schedule. However, donors would typically visit the laboratory once a week. During the second phase of the study (January-February), donors provided semen specimens while watching either video C or D. Each specimen was evaluated 30 minutes after ejaculation according to the standard procedures recommended by the World Health Organisation (WHO, 1992). Parameters measured were ejaculate volume, sperm concentration, percent motility, and grade of motility. The total number of sperm in the ejaculate was calculated as sperm concentration x specimen volume. Logarithmic transformations were applied to sperm concentrations and total sperm numbers since both can vary across an order of magnitude. The number of minutes the donor spent in the private room was recorded as the time taken to produce the specimen. For reasons of privacy, it was not possible to record directly the time spent masturbating.

RESULTS

A total of 281 semen specimens was collected with a median of 11 per donor and median of three per donor per video. The total number of specimens provided by donors watching videos A, B, C, and D were 54, 65, 86, and 76 respectively. For each donor, the mean semen parameters for specimens

produced while watching each of the videos were calculated. During the first phase of the study, 15 donors produced specimens under both experimental conditions (A and B). Paired-samples t-tests revealed that there were no significant differences between any of the mean semen parameters for specimens produced while watching videos A and B. However, there were significant differences between the first specimens produced by each donor while watching video A and the first produced by each donor while watching video B. Table 3 contains raw and transformed values for sperm concentration and total sperm number for the first specimens produced by the each of the 15 donors under each of the experimental conditions. A within-subjects comparison of the logarithmically transformed sperm concentrations indicated that donors produced more concentrated ejaculates on their first exposure to video B than on their first exposure to video A ($t = 2.18$; $df = 14$; $p < 0.05$). Furthermore, a within-subjects comparison of the logarithmically transformed total sperm numbers indicated that donors ejaculated more sperm on their first exposure to video B ($t = 2.19$; $df = 14$; $p < 0.05$).

Table 3 about here

During the second phase of the study, 17 donors produced specimens under both experimental conditions (C and D). There were no significant differences between any of the mean semen parameters for specimens produced while watching videos C and D. Furthermore, there were no significant

differences between the specimens produced by donors on their first exposure to video C and those produced on their first exposure to video D.

DISCUSSION

The content analyses provide convergent evidence that depictions of sexual contact between a single female and multiple males are prevalent in contemporary pornography, more prevalent in fact than depictions of contact between a single male and multiple females. Therefore, if availability and prevalence can serve as indices of interest, male consumers of pornography would appear to be more interested in depictions of the former type of sexual activity. This inference is supported by the results of the two preference studies in which depictions of sexual activity involving multiple males and a single female were more popular for each category of pornographic material.

These findings are noteworthy since, as discussed previously, there are both theoretical and empirical reasons to expect that human males will have a strong aversion to "sharing" mating, and hence reproductive, opportunities with other males. Moreover, the nature of male sexual psychology is such that, given the choice males should choose to mate with, and monopolise the reproductive output of, multiple females. Consequently, it is somewhat surprising that so many males choose to use depictions of sexual contact between multiple males and one female as a source of sexual arousal, and presumably, as an adjunct or aid to masturbation. However, sperm competition theory provides a parsimonious

explanation as to why men might be sexually aroused by such material. Sexually explicit photographs, videos and stories in which a female engages in sexual activity with multiple males may provide cues that would have been reliably associated with increases in the risk of sperm competition in ancestral environments. Male sexual arousal in response to such cues would have been an adaptive response since it would have increased the probability that a particular male sired her offspring.

As Symons (1979) has noted "pornography is, in a sense, an artificial stimulus" (p172) and "a natural human habitat seldom provides pornography-like stimuli" since humans tend to prefer to copulate in private. However, it seems unlikely that ancestral humans would have been able to completely conceal their sexual activity from their peers and competitors. Moreover, in the absence of modern clothing, visual information about recent sexual arousal and copulation may have been more readily available. Consequently, visual pornography may contain some cues that are analogous to those that would have been predictive of increased risk of sperm competition in ancestral environments. For example, the relevant cues present in pornographic videos could be as simple as the mere presence of more than one male in close proximity to a female who is displaying visual and/or auditory signs of sexual arousal. In addition, the sight of another man's penis in close proximity to a female's genitalia would most likely have been a reliable cue that the risk of sperm competition is high. Finally, ancestral human males may have encountered pornography-like visual stimuli during the coercive

insemination of females by multiple males (Thornhill & Palmer, 2000), and under these circumstances paternity is likely to be determined by the outcome of the ensuing sperm competition.

It should be emphasised that sperm competition theory does not imply that males should seek out, or prefer, to mate with a female who mates with multiple males. Yet, sexual arousal may be an adaptive response when sperm competition does arise, and regular users of pornography may become aware of this aspect of their sexuality through repeated exposure to material containing cues of sperm competition risk. Following from this, it might be predicted that relatively naïve users of pornography would be less likely to express a preference for depictions of sex involving multiple males and a single female than more experienced users. The possibility that there may be a dissociation between arousal and preference in this domain deserves empirical investigation, ideally using phallometric indices of sexual arousal. Dissociations between measures of physiological arousal and affective responses have previously been identified in women. For example, when viewing male- and female-produced erotica there is discordance between the emotional responses of women and genital measures of their sexual arousal. While they claim to prefer the female-produced erotica, their genital responses to each type are indistinguishable (Laan *et al.*, 1994).

The possibility that males are sexually aroused by images of other males because their presence would have been predictive of increases in the risk of

sperm competition in the ancestral environment has some interesting implications for psychological theories of bisexuality and the psychoanalytic concept of *latent homosexuality*. Many ostensibly heterosexual males experience sexual arousal in response to, or engage in homosexual activity with, other males at some point during their lives. Kinsey, Pomeroy and Martin (1948) reported that 37% of men engage in homosexual activity to the point of orgasm at some time during their adult lives and presumably many more experience some homosexual interest that is not expressed behaviourally. However, only a small minority of these men can be described as exclusively homosexual. More recent studies indicate that 6.1% of British (Johnson *et al.*, 1992) and 4.1% of French (ACSF, 1992) men have experienced intercourse with a person of the same sex during their lifetime. Furthermore, the vast majority of men who have had at least one experience of homosexual intercourse also have experience of heterosexual intercourse (ACSF, 1992).

Psychoanalytic theories of *latent homosexuality* have generally emphasised the negative consequences of struggling to deny and repress homosexual desires (e.g. Bieber *et al.*, 1962). In fact, various attempts have been made to link *latent homosexuality* in otherwise heterosexual males with overt hostility and discrimination against homosexuals, the general theory being that the repression of homosexual urges and consequent anxiety about the possibility of being or becoming a homosexual may have a causal role in the development of homophobia (West, 1977). Such an approach has spawned studies that have

demonstrated sexual arousal in otherwise heterosexual men to erotic homosexual stimuli. For example, Adams, Wright, and Lohr (1996) showed that among exclusively heterosexual males, negative attitudes towards homosexuals and fear of homosexuality were associated with an increased erectile response to explicit depictions of homosexual activity. In demonstrating this, Adams *et al.* (1996) also showed that a significant proportion of men who claim to be exclusively heterosexual nevertheless exhibit sexual arousal in response to erotic depictions of other men. Surely, the prevalence of homosexual arousal in a substantial proportion of males who are predominantly heterosexual suggests that this may be a normal aspect of male sexuality rather than a developmental aberration and sperm competition theory can provide a parsimonious explanation for this finding. Other males, and in particular those who are sexually aroused themselves, may be a source of arousal for heterosexual males because their proximity would have been a reliable cue of increased risk of sperm competition in ancestral environments.

It could be argued that males are particularly interested in representations of sexual activity involving multiple males and a single female because such material can depict multiple types of sexual contact between males and females in a single scene. However, if this were the case then one would expect to see a greater number of scenes involving multiple males and females in roughly equal numbers. Such scenes could effectively depict multiple types of heterosexual contact while simultaneously appealing to male interests in sexual variety by

including numerous different females but despite the well-documented male interest in sexual variety, the majority of group sex scenes involved only a single female participant.

It remains to be determined exactly what cues of female polyandry and risk of sperm competition are sufficient to elicit arousal and thus form important elements of pornographic stimuli. The mere presence of other males who could be construed as potential rivals in a sexual context may be sufficient to trigger an arousal response. If this is the case then this aspect of male sexuality may form the basis for sexual arousal of heterosexual males in response to erotic depictions of other men. Psychoanalytic constructs such as *repressed* or *latent homosexuality* may be redundant if sexual arousal in response to viewing other males involved in sexual activity is simply one component of the repertoire of male responses to intra-sexual competition.

The semen analyses provide some evidence that the number of sperm ejaculated by men can be affected by the visual stimuli present during specimen production. Specifically, men ejaculated more sperm on their first exposure to a video depicting sexual contact between a man and women than they did on their first exposure to a video depicting sexual contact between two women. The fact that a significant difference was only observed for specimens produced by men on their first exposure to each video suggests that they may habituate rapidly when repeatedly exposure to the same pornographic material. However, it is an

impressive finding given that there is substantial within-subject variability in semen parameters (e.g. Read & Schnieden, 1978; Schwartz *et al.*, 1979; Mallidis *et al.*, 1991), which will tend to mask the effects of experimental manipulations. Furthermore, the simple finding that semen parameters were dependent on the type of visual stimulation present during specimen production in the present study is noteworthy since previously, it has been reported that there is no statistically significant improvement in semen quality when specimens are produced with visual erotic stimulation compared to without (van Roijen *et al.*, 1996).

The finding that there were no statistically significant differences between ejaculates produced while watching polygynous and polyandrous orgiastic sexual activity is clearly inconsistent with the prediction derived from sperm competition theory, that males should ejaculate more sperm when visual cues of sperm competition are present during specimen production. Further research is needed to establish conclusively whether visual cues of sperm competition risk can affect semen parameters. It can be argued that simply witnessing a sexual encounter between a female and a male provides direct and unequivocal evidence that rival sperm are likely to be present within that female's reproductive tract. Consequently, the finding that males ejaculate more sperm when viewing sexual contact between a male and a female than they do when viewing sexual contact between two females can be interpreted as weak support for the prediction that

human males can adjust their ejaculate composition in response to visual cues of sperm competition.

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REFERENCES

- Abelson, H., Cohen, R., Heaton, E., & Suder, C. (1971). National survey of public attitudes toward and experience with erotic materials. In *Technical Report of the Commission on Obscenity and Pornography, Vol. 4*. U.S. Government Printing Office, Washington, D.C.
- ACSF Investigators (1992). AIDS and sexual behaviour in France. *Nature* 360: 407-409.
- Adams, H. E., Wright, L. W., Lohr, B. A. (1996). Is homophobia associated with homosexual arousal. *J. Abnorm. Psych.* 105: 440-445.
- Alonso-Pimental, H., & Papaj, D. R. (1996). Operational sex ratio versus gender density as determinants of copulation duration in the walnut fly, *Rhagoletis juglandis* (Diptera: Tephritidae). *Behav. Ecol. Sociobiol.* 39: 171-180.
- Baker, R. R., & Bellis, M. A. (1989). Number of sperm in human ejaculates varies in accordance with sperm competition theory. *Anim. Behav.* 37: 867-869.
- Baker, R. R., & Bellis, M. A. (1993). Human sperm competition: ejaculate manipulation by males and the function of masturbation. *Anim. Behav.* 46: 861-885.
- Baker, R. R., & Bellis, M. A. (1995). *Human sperm competition: Copulation, masturbation, and infidelity*. Chapman and Hall, London.
- Bateman, A. J. (1948). Intra-sexual selection in *Drosophila*. *Heredity* 2: 349-368.

- Bellis, M. A., Baker, R. R., & Gage, M. J. G. (1990). Variation in rat ejaculates consistent with kamikaze-sperm hypothesis. *J. Mammal.* 71: 479-480.
- Betzig, L. L. (1986). *Despotism and Differential Reproduction: A Darwinian View of History*. Aldine, New York.
- Bieber, I., Dain, H. J., Dince P. R., Drellich, M. G., Grand, H. G., Gundlach, R. H., Kremer, M. W., Rifkin, A. H., Wilbur, C. B., & Bieber, T. B. (1962). *Homosexuality*. Basic Books, New York.
- Birkhead, T. R., Atkin, L., & Møller, A. P. (1987). Copulation behaviour of birds. *Behaviour* 101: 101-138.
- Blockey, M. A. de B. (1981). Modification of a serving capacity test for beef bulls. *Appl. Anim. Ethol.* 7: 321-336.
- Canadian Fertility and Andrology Society (1996). *Guidelines for Therapeutic Donor Insemination*. Ribosome Communications, Toronto.
- Cook, P. A., & Gage, M. J. G. (1995). Effects of risk of sperm competition on the numbers of eupyrene and apyrene sperm ejaculated in the moth *Plodia interpunctella* (Lepidoptera: Pyralidae). *Behav. Ecol. Sociobiol.* 36: 261-268.
- Cook, P. A., & Wedell, N. (1996). Ejaculate dynamics in butterflies: a strategy for maximizing fertilization success? *Proc. R. Soc. Lond. B* 263: 1047-1051.
- Dewsbury, D. A. (1982). Ejaculate cost and male choice. *Amer. Nat.* 119: 601-610.

- Ellis, B. J., & Symons, D. (1990). Sex differences in sexual fantasy: and evolutionary psychological approach. *J. Sex. Res.* 27: 527-555.
- Foote, R. H. (1974). Artificial Insemination. In E.S.E. Hafez (Ed). *Reproduction in Farm Animals*. Lea and Febiger, Philadelphia. pp 409-431.
- Gage, M. J. G. (1991). Risk of sperm competition directly affects ejaculate size in the Mediterranean fruit fly. *Anim. Behav.* 42: 1036-1037.
- Gage, M. J. G. (1994). Associations between body size, mating patterns, testis size and sperm lengths across butterflies. *Proc. R. Soc. Lond. B* 258: 247-254.
- Gage, M. J. G., & Baker, R. R. (1991). Ejaculate size varies with sociosexual situation in an insect. *Ecol. Entomol.* 16: 331-337.
- Gage, M. J. G., & Barnard, C. J. (1996). Male crickets increase sperm number in relation to competition and female size. *Behav. Ecol. Sociobiol.* 38: 349-353.
- Ginsberg, J. R., & Rubenstein, D. I. (1990). Sperm competition and variation in zebra mating behavior. *Behav. Ecol. Sociobiol.* 22: 427-434.
- Harcourt, A. H., Harvey, P. H., Larson, S. G., & Short, R. V. (1981). Testis weight, body weight, and breeding system in primates. *Nature* 293: 55-57.
- Harvey, P. H., & Harcourt, A. H. (1984). Sperm competition, testis size, and breeding systems in primates. In R. L. Smith (Ed.) *Sperm competition and the evolution of animal mating systems*. Academic Press, London. pp 589-600.

- Hemsworth, P. H., & Galloway, D. B. (1979). The effect of sexual stimulation on the sperm output of the domestic boar. *Anim. Reprod. Sci.* 2: 387-394.
- Jennions, M. D., & Passmore, N. I. (1993). Sperm competition in frogs: testis size and a 'sterile male' experiment on *Chiromantis xerampelina* (Rhacophoridae). *Biol. J. Linn. Soc.* 50: 211-220.
- Johnson, A. M., Wadsworth, J., Wellings, K., Bradshaw, S., & Field, J. (1992). Sexual lifestyles and HIV risk. *Nature* 360: 410-412.
- Kelly, K., & Byrne, D. (1983). Assessment of sexual responding: Arousal, affect, and behavior. In J. Cacioppo and R. Petty (Eds.) *Social psychophysiology*. Guilford, New York. pp 467-490.
- Kerruish, B. M. (1955). The effect of sexual stimulation prior to service on the behaviour and conception rate of bulls. *Brit. J. Anim. Behav.* 3: 125.
- Kinsey, A. C., Pomeroy, W. B., & Martin, C. E. (1948). *Sexual Behavior in the Human Male*. Saunders, Philadelphia.
- Lann, E., Everaerd, W., van Bellen, G., Hanewald, G. (1994). Women's sexual and emotional responses to male- and female-produced erotica. *Arch. Sex. Behav.* 23: 153-169.
- Mader, D. R., & Price, E. O. (1984). The effects of sexual stimulation on the sexual performance of Hereford bulls. *J. Anim. Sci.* 59: 294-300.

- Mallidis, C., Howard, E. J., & Baker, H. W. (1991). Variation of semen quality in normal men. *Int. J. Androl.* 14: 99-107.
- Mattner, P. E., George, J. M., & Braden, A. W. H. (1974). Herd mating activity in cattle. *J. Reprod. Fertil.* 36: 454-455 (abstract).
- Møller, A. P. (1988). Testis size, ejaculate quality and sperm competition in birds. *Biol. J. Linn. Soc.* 33: 273-283.
- Møller, A. P., & Birkhead, T. R. (1991). Frequent copulations and mate guarding as alternative paternity guards in birds: a comparative study. *Behaviour* 118: 170-186.
- Nawy, H. (1971). The San Francisco erotic marketplace. In *Technical Report of the Commission on Obscenity and Pornography, Vol. 4*. U.S. Government Printing Office, Washington, D.C.
- Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* 45: 525-67.
- Parker, G. A. (1982). Why are there so many tiny sperm? Sperm competition and the maintenance of two sexes. *J. Theor. Biol.* 96: 281-294.
- Parker, G. A. (1990a). Sperm competition games: raffles and roles. *Proc. R. Soc. Lond. B* 242: 120-126.
- Parker, G. A. (1990b). Sperm competition games: sneaks and extra-pair copulations. *Proc. R. Soc. Lond. B* 246: 107-115.

- Parker, G. A., Ball, M. A., Stockley, P., & Gage, M. J. G. (1997). Sperm competition games: a prospective risk analysis assessment. *Proc. R. Soc. Lond. B* 264: 1793-1802.
- Pickett, B. W., Voss, J. L., & Squires, E. L. (1977). Impotence and abnormal sexual behavior in the stallion. *Theriogenology* 8: 329-347.
- Price, E. O., Smith, V. M., Katz, L. S. (1984). Sexual stimulation of male dairy goats. *Appl. Anim. Ethol.* 13: 83-92.
- Read, M. D., & Schnieden, H. (1978). Variations in sperm count in oligozoospermic or asthenozoospermic patients. *Andrologia*, 10: 52-55.
- Schwartz, D., Laplanche, A., Jouannet, P., & David, G. (1979). Within-subject variability of human semen in regard to sperm count, volume, total number of spermatozoa and length of abstinence. *J. Reprod. Fertil.* 57: 391-395.
- Sell, R.L. (1997). Research and the Internet: Experience Conducting an E-Survey on Sexual Orientation. *Am. J. Public. Health.* 97: 297.
- Short, R. V. (1979). Sexual selection and its component parts, somatic and genital selection as illustrated by man and the great apes. *Adv. Study Behav.* 9: 131-158.
- Short, R.V. (1981). Sexual selection in man and the great apes. In C.E. Graham (Ed.) *Reproductive biology of the great apes*. Academic Press, New York. pp 319-341.

- Simmons, L. W., Craig, M., Llorens, T., Schinzig, M., & Hosken, D. (1993). Bushcricket spermatophores vary in accord with sperm competition and parental investment theory. *Proc. R. Soc. Lond. B* 251: 183-186
- Smith, R. L. (1984). Human sperm competition. In R. L. Smith (Ed.) *Sperm competition and the evolution of animal mating systems*. Academic Press, London. pp 601-660.
- Symons, D. (1979). *The evolution of human sexuality*. Oxford University Press, New York.
- Thornhill, R., & Palmer, C. T. (2000). *A Natural History of Rape: Biological Bases of Sexual Coercion*. MIT Press, Cambridge, Massachusetts.
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.) *Sexual selection and the descent of man*. Aldine, Chicago. pp 1871-1971
- van Rooijen, J. H., Slob A. K., Gianotten, W. L., Dohle, G. R., van der Zon, A. T., Vreeburg, J. T., & Weber, R. F. (1996). Sexual arousal and the quality of semen produced by masturbation. *Hum. Reprod.* 11: 147-151.
- West, D. J. (1977). *Homosexuality re-examined*. University of Minnesota Press, Minneapolis.
- Williams, G. C. (1975). *Sex and evolution*, Princeton University Press, Princeton, NJ.

World Health Organization (1992). *Laboratory Manual for the Examination of Human Semen and Sperm-Cervical Mucus Interaction*, 3rd edn. Cambridge University Press, Cambridge.

Table 1. Contents of images depicting 2 or more people engaged in sexual activity from the World Wide Web sample

Image/Scene Contents	Study 1				Study 2	
	Site A Images		Site B Images		Video Scenes	
2+ Females	463	26.7%	256	23.6%	123	18.1%
1 Female and 1 Male	877	50.7%	622	57.3%	322	47.5%
Males > Females	221	12.8%	141	13.0%	140	20.6%
Females > Males	141	8.1%	63	5.8%	66	9.7%
Males = Females	15	0.9%	4	0.3%	18	2.7%
Other/Unobtainable	13	0.8%	0	0.0%	9	1.3%
Total	1730		1086		678	

Table 2. Results of WWW preference studies

Image/Scene Contents	Study 3 (n=203) Preference Questionnaire			Study 4 (n=391) Web Choices
	Images	Videos	Stories	Images
1 Female	9.3%	4.5%	6.9%	20.8%
2+ Females	15.3%	8.9%	7.4%	27.5%
1 Female and 1 Male	11.8%	12.9%	9.9%	9.5%
Males > Females	32.0%	36.1%	35.0%	25.2%
Females > Males	16.3%	17.8%	22.2%	17.0%
Males = Females	15.3%	19.8%	18.7%	N/A

Table 3. Raw and logarithmically transformed sperm concentration and total sperm number for the first specimens produced by each of the 15 donors while watching videos A and B.

Donor	Sperm Concentration				Total Sperm Number			
	Video A		Video B		Video A		Video B	
	$\times 10^6$ per ml	log	$\times 10^6$ per ml	log	$\times 10^6$	log	$\times 10^6$	log
1	84.0	1.92	98.0	1.99	201.6	2.3	215.6	2.33
2	34.0	1.53	78.0	1.89	81.6	1.91	312.0	2.49
3	119.0	2.08	91.0	1.96	178.5	2.25	145.6	2.16
4	41.0	1.61	76.0	1.88	135.3	2.13	220.4	2.34
6	69.0	1.84	99.0	2.00	414.0	2.62	712.8	2.85
7	42.0	1.62	89.0	1.95	126.0	2.10	329.3	2.52
9	128.0	2.11	126.0	2.10	230.4	2.36	340.2	2.53
10	54.0	1.73	55.0	1.74	383.4	2.58	390.5	2.59
12	128.0	2.11	101.0	2.00	396.8	2.60	414.1	2.62
13	57.0	1.76	58.0	1.76	193.8	2.29	156.6	2.19
14	68.0	1.83	42.0	1.62	482.8	2.68	247.8	2.39
15	22.0	1.34	66.0	1.82	74.8	1.87	330.0	2.52
16	78.0	1.89	97.0	1.99	241.8	2.38	281.3	2.45
18	56.0	1.75	67.0	1.83	352.8	2.55	422.1	2.63
19	38.0	1.58	62.0	1.79	102.6	2.01	142.6	2.15

CHAPTER 5

INFIDELITY AND SEXUAL DESIRABILITY

Sperm competition theory predicts that males should adjust the number of sperm they inseminate according to the risk of sperm competition (Parker, 1982, 1990*a,b*; Baker & Bellis, 1995). This may be achieved by adaptive regulation of the number of sperm ejaculated during each copulation, but increases in the number of sperm that a male inseminates could also be produced by increases in the frequency of copulation itself. Indeed, males of avian species in which the risk of sperm competition is high use frequent in-pair copulation as a method of paternity assurance (Birkhead *et al.*, 1987; Birkhead & Møller, 1992; Møller & Birkhead, 1991). Frequent in-pair copulations may serve to displace rival sperm that may be present and keep the female “topped up” with that male's sperm, and thus reduce the likelihood she will conceive offspring sired by another.

In humans, it has been predicted that cues associated with increases in the risk of sperm competition should produce changes in male reproductive physiology and sexual behaviour that lead to more frequent in-pair copulation and thus increases in the number of sperm inseminated (Baker & Bellis, 1995). These changes may include increased male sexual interest and arousal, decreases in erectile and ejaculatory latency, and decreases in the duration of the post-

ejaculatory refractory period. Subjectively, males may report increases in their level of sexual desire for their partner and a greater willingness to copulate. They may also be more inclined to disregard female disinterest and to employ coercive tactics in order to copulate with her.

There is anecdotal evidence from men who engage in "swinging" (consensual extra-pair sexual activity) that cues indicative of sexual infidelity can stimulate sexual motivation (e.g. Gould, 1999). Specifically, when couples engage in "partner-swapping", the men apparently experience increased sexual desire for a partner when they know that she has recently had sex with someone else. This increase in desire may be particularly acute when the man actually witnesses his partner having sex with another man. Among those participating in "swinging", the sight of the partner arousing other men frequently arouses men who then may strive to "repossess" her (Talese, 1981).

The purpose of the present study was to assess experimentally whether men exhibit increased sexual desire and a greater inclination to use sexual coercion in response to cues of increases in the risk of sperm competition. Furthermore, it can be hypothesised that while cues of promiscuity should reduce a female's desirability as a long-term sexual partner, they may increase her attractiveness as a partner for a short-term sexual relationship. It appears that men who "swing" are not only acutely aware of, but actively seek, the increases in sexual arousal that they experience in response to a partner's extra-pair

copulations. However, many men, particularly those with little experience of long-term sexual relationships, may be less aware of this aspect of their sexuality. Consequently, it might be predicted that men involved in long-term sexual relationships will be more likely to report that they would experience increased sexual arousal in response to female infidelity than those men who are not.

In order to assess male responses to cues of sexual infidelity in the present study a fictive photo-story was used. A photo-story has certain advantages over narrative text. In particular, visual cues of sexual infidelity can be presented without detailed explanations that might provide normative information about typical male responses to such situations. Furthermore, photographs may be particularly effective in evoking men's emotional responses to situations involving sex, since men are more easily aroused by visual stimuli than women (Kinsey *et al.*, 1948, 1953) and male sexual fantasies typically include explicit visual imagery of genitalia and sexual acts (e.g. Ellis & Symons, 1990).

METHOD

Subjects

One hundred male students participated in the experiment in exchange for credit in an introductory undergraduate psychology course. Subjects were forewarned that participation involved answering questions about sexual relationships and were told that they could withdraw from the study at any time

without loss of credit. Subjects' ages ranged from 18 to 30 years with a mean age of 19.4. Fifty-seven subjects described themselves as "single" while the other 43 reported that they were either in a long-term sexual relationship, or cohabiting with a partner.

Procedure

In privacy in the laboratory, subjects viewed a computerised interactive photo-story that depicted events involving a heterosexual couple in a long-term committed relationship. They were instructed that they were to view a series of photos on a computer screen using mouse clicks to move from one image to the next. They were informed that they would be required to respond to a number of questions at the end of the sequence, and were assured that their responses would be treated as anonymous and confidential.

A series of 12 images with accompanying descriptive text introduced a young couple, Lucy and Steve. Several images depicted them embracing in a romantic but not sexually explicit manner while others depicted them in various situations alone together, with friends and on vacation. The text emphasised that their relationship had lasted several years and would likely lead to marriage. They were described as "loving," "very much in love," and "considering getting engaged" after "3 years together." The presentation sequence is described in Table 1.

After viewing the core images, all subjects were presented with the following text; “One evening at Lucy’s house Steve accidentally came across two photographs he hadn’t seen before”. Half the subjects then read that “Both were pictures of him with Lucy” (Fidelity Condition) while the other half read “Both were pictures of Lucy with a guy called Dave” (Infidelity Condition). The images presented subsequently were manipulated to create two alternative scenarios for a between-groups experimental design: one in which there was evidence of sexual infidelity on the part of the female, and one in which this evidence was absent.

Fidelity Condition

Subjects in the fidelity condition then viewed an image of Lucy sitting on Steve’s knee in a bar with accompanying text that read; “*The first was a photo of Lucy and Steve taken at Bar Rhumba. There was a date on the back. It had been taken only a couple of weeks earlier. Steve remembered the photograph being taken*”. They then viewed an image of Lucy, partially clothed, sitting on Steve’s knee back at her house accompanied by the following text; “*The second was a photo of Steve & Lucy at her house. It had been taken the morning after the night in Bar Rhumba*”.

Infidelity Condition

Subjects in the infidelity condition viewed a version of the image of Lucy sitting on Steve’s knee in a bar in which Steve’s face had been replaced by that of

another man. This image was accompanied with the following text; "*The first was a photo of Lucy and Dave at Bar Rhumba. There was a date on the back. It had only been taken a couple of weeks earlier. Steve hadn't been there when the photograph was taken*". They then viewed a version of the image of Lucy, partially clothed, sitting on Steve's knee in which Steve's face had also been replaced by that of the other man. The accompanying text read; "*The second was a photo of Dave & Lucy at her house. It had been taken the morning after the night in Bar Rhumba*".

Questionnaire

After viewing the photo story subjects were presented with a series of 7 questions about the female protagonist (Table 2). Responses were recorded using a 7-point Likert scale specific to each question. Additional questions gathered demographic information about the subjects, including age and marital status.

RESULTS

Fifty men viewed the photo story containing cues of infidelity. Twenty-eight of these men were "single" and 22 were either in a long-term relationship or cohabiting with a partner. Fifty men viewed the photo story in which cues of infidelity were absent. Twenty-nine of these men were "single" and 22 were either in a long-term relationship or cohabiting with a partner. Descriptive statistics for responses to the seven questions are presented in Table 3. In general,

the female protagonist in the photo story was rated as highly attractive (mean = 5.54 ; s.d. = 0.88) and sexy (mean = 5.32 ; s.d.= 1.14). Furthermore, subjects reported that they were very likely to want to have sex with her (mean = 5.29; s.d. = 1.70).

The effects of infidelity on desirability as a partner

Subjects ratings of the female protagonist's desirability as a partner were analysed using a 2 x 2 x 2 ANOVA with Relationship Type (short-term vs long term), Fidelity Condition, and Subject's Status ("single" vs not "single") as factors. There was a main-effect of Relationship Type on the female protagonist's desirability as a partner across all conditions. Specifically, whether or not there were cues of sexual infidelity, subjects reported that she was more desirable as a partner for a short-term sexual relationship than a long-term committed relationship ($F = 31.9$; $df = 1,96$; $p < 0.001$). However, subjects who were presented with images indicative of sexual infidelity on the part of the female protagonist reported that she was less desirable as a partner for a long-term committed relationship and more desirable as a partner for a short-term sexual relationship than did subjects in the fidelity condition (Figure 1). Moreover, this interaction (Relationship Type x Fidelity Condition) was highly significant ($F = 18.0$; $df = 1,96$; $p < 0.001$).

The effects of being single

The mean responses to the questionnaire items addressing the sexual desirability of the female protagonist given by men who were "single" and those who were in long-term relationships are depicted in Figure 2. Multivariate ANOVA revealed that "single" males tended to rate the female protagonist as *more sexy* ($F = 3.62$; $df = 1,96$; $p = 0.060$), to report that they would be more likely to *want to have sex with her* ($F = 2.63$; $df = 1,96$; $p = 0.11$); and to report that they would be more likely to *try to persuade her to have sex* ($F = 3.38$; $df = 1,96$; $p = 0.069$). However, these differences did not reach statistical significance.

There was a tendency for "single" males to report that they would be less likely to want to have sex with the female protagonist when cues of infidelity were present than when they were absent. In contrast, males who were involved in a relationship tended to report that they would be more likely to want to have sex with her in the infidelity condition than in the fidelity condition. However, this interaction between subject's relationship status and the fidelity of the female protagonist, depicted in Figure 3, did not reach statistical significance ($F = 2.94$; $df = 1,92$; $p = 0.090$).

DISCUSSION

Subjects who were presented with images indicative of sexual infidelity on the part of the female protagonist in a fictive photo-story found her to be less

desirable as a partner for a long-term committed relationship than those who were not. This is not surprising since sexual fidelity is a highly valued by men as a trait in a potential partner (Buss & Schmitt, 1993) and premarital sexual permissiveness is a good predictor of the risk that someone will engage in extramarital sex (Weiss & Slosnernick, 1981; Thompson, 1983). This finding is also consistent with evolutionary theories of human sexuality since men who choose to establish long-term relationships with women who are likely to engage in extra-pair copulation (EPC) are at risk of cuckoldry and desertion. Selection will have favoured those males who prefer to seek out and establish committed relationships with women who are less inclined to engage in EPC.

In general, the female protagonist was rated as more desirable as a partner for a short-term relationship than for a long-term relationship. However, subjects presented with cues of sexual infidelity rated her as more desirable as a partner for a short-term sexual relationship than did those who were not. Whereas men value sexual fidelity in a potential mate, they tend to relax their standards for a wide variety of characteristics when it comes to choosing partners for casual sex (Buss, 1999; Buss & Schmitt, 1993). Consequently, cues of a female's promiscuity are less likely to reduce her attractiveness in a short-term mating context and may even raise it.

Since cues of sexual infidelity may be predictive that a female is willing to engage in extra-pair copulation or casual sex without commitment, it might be

expected that they would stimulate sexual interest in males who are otherwise mate deprived. However, the findings of the present study are inconsistent with this view. "Single" males reported that they were less likely to want to have sex with the female protagonist when cues of infidelity were present than when they were absent, while this pattern was reversed for men who were involved in relationships (Figure 3). While this interaction only approached significance, it is consistent with the prediction that men in committed relationships should experience increased sexual arousal when there is a risk of sperm competition.

More generally, it may be the case that men think about and respond to cues of infidelity rather differently depending on their current mating status. It is possible that the "single" males in the present study just did not have sufficient experience of sexual relationships to know how they would actually respond when confronted with cues of infidelity. While men who participate in "swinging" may be acutely aware that female extra-pair copulation can lead to increased male sexual desire (Gould, 1999) this may seem fairly counter-intuitive to males who have little experience of the phenomenon themselves. Moreover, it may be only when men are involved in long-term sexual relationships that they start to exhibit adaptive responses to cues of sperm competition risk that function to keep their partners "topped up" with sperm. Thus, when males are involved in a long-term committed relationship they may be in a qualitatively different psychological and physiological state than when they are single and the finding that testosterone levels are reduced in married men, but return to pre-marriage

levels on divorce or separation (Mazur & Booth, 1998) is consistent with this view.

There were some apparent differences between the responses of "single" men and men involved in long-term relationships (Figure 2) which, although non-significant in the present study may warrant further investigation. Men who were not currently involved in a relationship tended to rate the female protagonist as being more sexy than did those who were. Furthermore, they reported that they were more likely to want to have sex with her. Taken together these data suggest that male ratings of sexual attractiveness and desirability might be context-dependent, which is interesting since most studies of human mating preferences have tended to focus on characteristics intrinsic to the individual being selected rather than the status of the selector.

According to the *mate deprivation hypothesis* of sexual coercion, the threshold for sexual coercion and rape is lowered in males who lack alternative reproductive options (Thornhill & Thornhill, 1983, 1992; Thornhill & Palmer, 2000). The tendency for "single" men in the present study to report that they would be more likely to try to persuade the female protagonist to have sex if she refused is consistent with this hypothesis. However, it is inconsistent with a report by Lalumière *et al.* (1996) that males who identify themselves as sexually coercive actually have higher self-perceived mating success, as indicated by reports of more extensive sexual histories, than those who do not. Of course, it is

not possible to determine whether the "single" males in the present study responded to the questionnaire items in the way that they did because they are single. It is equally plausible that the attitudes and behavioural inclinations that led them to respond as they did directly contributed to their "single" status. Furthermore, it must also be acknowledged that increased willingness to "try to persuade" a female to have sex may not inevitably lead to the use of physical coercion and violence. Instead, sexual coercion may be particularly common in a sub-group of men who share a constellation of developmental experiences such as rejection by potential mates and a history of non-committal heterosexual relationships (Malamuth, 1996, 1998).

To summarise: the present study provides some evidence that cues that a female has engaged in an extra-pair copulation can stimulate male sexual arousal and increase her desirability as a partner for a short-term sexual relationship while decreasing her desirability as a partner for a long-term relationship. Furthermore, it provides some weak evidence that men respond rather differently to cues of female promiscuity depending on whether they are currently involved in a long-term sexual relationship themselves.

REFERENCES

- Baker, R. R., & Bellis, M. A. (1995). *Human sperm competition: Copulation, masturbation, and infidelity*. Chapman and Hall, London.
- Birkhead, T. R., Atkin, L., & Møller, A. P. (1987). Copulation behaviour of birds. *Behaviour*, 101, 101-138.
- Birkhead, T. R., & Møller, A. P. (1992). *Sperm competition in birds: Evolutionary causes and consequences*. Academic Press, London.
- Buss, D. M. (1999). *Evolutionary psychology: The new science of the mind*. Allyn and Bacon, Boston.
- Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, 100, 204-232.
- Ellis, B. J., & Symons, D. (1990). Sex differences in sexual fantasy: and evolutionary psychological approach. *Journal of Sex Research*, 27, 527-555.
- Gould, T. (1999). *The lifestyle: A look at the erotic rites of swingers*. Random House of Canada.
- Kinsey, A. C., Pomeroy, W. B., & Martin, C. E. (1948). *Sexual Behavior in the Human Male*. Saunders, Philadelphia.
- Kinsey, A. C., Pomeroy, W. B., Martin, C. E., & Gebhard, P. H. (1953). *Sexual Behavior in the Human Female*. Saunders, Philadelphia.

- Lalumière, M. L., Chalmers, L. J., Quinsey, Vernon, L., & Seto, M. C. A. (1996). A test of the mate deprivation hypothesis of sexual coercion. *Ethology and Sociobiology*, 17, 299-318.
- Malamuth, N. (1996). Research on the confluence model of sexual aggression based on feminist and evolutionary perspectives. In D. Buss, & N. Malamuth, (Eds.). *Sex, power, conflict: Evolutionary and feminist perspectives*. Oxford University Press, New York. pp 269-295.
- Malamuth, N. (1998). An evolutionary-based model integrating research on the characteristics of sexually coercive men. In J. Adair, K. Dion, & D. Belanger, D. (Eds.) *Advances in Psychological Science (Vol. 2): Personal, Social, and Developmental Aspects*. Psychology Press, Hove. pp 151-184.
- Mazur, A., & Booth, A. (1998). Testosterone and dominance in men. *Behavioural and Brain Sciences*, 21, 353-363.
- Møller, A. P., & Birkhead, T. R. (1991). Frequent copulations and mate guarding as alternative paternity guards in birds: a comparative study. *Behaviour*, 118, 170-186.
- Parker, G. A. (1982). Why are there so many tiny sperm? Sperm competition and the maintenance of two sexes. *Journal of Theoretical Biology*, 96, 281-294.
- Parker, G. A. (1990a). Sperm competition games: raffles and roles. *Proceedings of the Royal Society: Biological Sciences*, 242, 120-126.

- Parker, G. A. (1990b). Sperm competition games: sneaks and extra-pair copulations. *Proceedings of the Royal Society: Biological Sciences*, 246, 107-115.
- Talese, G. (1981). *Thy Neighbor's Wife*. Ballantine, New York.
- Thompson, A. P. (1983). Extramarital sex: A review of the research literature. *Journal of Sex Research*, 19, 1-22.
- Thornhill, R. (1980). Rape in *Panorpa* scorpionflies and a general rape hypothesis. *Animal Behaviour*, 28, 52-59.
- Thornhill, R., & Palmer, C. T. (2000). *A Natural History of Rape: Biological Bases of Sexual Coercion*. MIT Press, Cambridge, Massachusetts
- Thornhill, R., & Thornhill, N. M. (1983). Human rape: An evolutionary analysis. *Ethology and Sociobiology*, 4, 137-173.
- Thornhill, R., & Thornhill, N. M. (1992). The evolutionary psychology of men's coercive sexuality. *Behavior and Brain Sciences*, 15, 363-421.
- Weiss, D. L., & Slosnernick, M. (1981). Attitudes toward sexual and nonsexual extramarital involvements among a sample of college students. *Journal of Marriage and the Family*, 43, 349-358.

Table 1. Image Presentation Sequence

Screen	Image(s)	Text
Title Screen		A Loving Couple
Introduction	1) Steve's face 2) Lucy's face 3) Steve & Lucy embracing	This is the story of Steve and Lucy. Please read any text that appears with the pictures. At the end you will be asked about your impressions of Steve and Lucy.
1	Together on a sunny balcony. Steve has arm around her waist.	Lucy and Steve met while studying at McMaster University.
2	Lucy sitting on a step with 3 dogs.	Lucy was in her third year studying Biology when they met.
3	Steve sitting on same step with same 3 dogs	Steve was in his fourth year studying English when they met.
4	Together dressed formally. Steve in suit, Lucy in summer dress. His arm around her waist.	After graduating Steve got a job working with a publishing company. When Lucy graduated a year later they took some time off to travel.
5	Together unwrapping presents	Christmas Day with Steve's relatives in San Francisco.
6	Together unwrapping presents	Steve liked to buy her presents.
7	Together in front of St Paul's Cathedral.	Here they are visiting Lucy's relatives in England.
8	Together on beach.	Lucy especially liked holidays on the beach.
9	Together on boat, Steve holding fishing rod and fish.	Steve welcomed the chance to try a little fishing.
10	Close embrace. Her arms around his neck. Steve in shirt and tie, Lucy in dress.	After 3 years together they were very much in love and considering getting engaged.
11	Lucy on sofa with 5 female friends.	And Lucy still liked to party with her girlfriends.
12	Steve with 3 male friends.	Although Steve spent a lot of time with Lucy he still liked to go out drinking with his old friends.

Table 2. Questionnaire Items

Questionnaire Item	Left	Right
	Anchor	Anchor
1. How attractive is Lucy?	Not at all attractive	Extremely attractive
2. How sexy is Lucy?	Not at all sexy	Extremely sexy
3. If you had just been out to dinner with Lucy and were back at her house for coffee how likely is it that you would want to have sex with her?	Not at all likely	Extremely likely
4. If Lucy did not seem interested how likely is it that you would try to persuade her to have sex with you?	Not at all likely	Extremely likely
5. How angry would you be if Lucy refused to have sex with you?	Not at all angry	Extremely angry
6. How desirable is Lucy as a partner in a long-term committed relationship?	Not at all desirable	Extremely desirable
7. How desirable is Lucy as a partner for a brief sexual relationship?	Not at all desirable	Extremely desirable

Table 3. Descriptive statistics for responses.

	Mean	S.D.	Distribution of Responses						
			← Not at all			Extremely →			
			1	2	3	4	5	6	7
1. How attractive is Lucy?	5.54	.88	1	0	0	8	33	50	8
2. How sexy is Lucy?	5.32	1.14	2	1	2	11	37	36	11
3. If you had just been out to dinner with Lucy and went back to her house for coffee how likely is it that you would want to have sex with her?	5.29	1.70	4	8	3	9	19	30	27
4. If Lucy did not seem interested how likely is it that you would try to persuade her to have sex with you?	2.33	1.57	40	28	11	9	6	4	2
5. How angry would you be if Lucy refused to have sex with you?	1.77	1.11	55	25	13	4	2	0	1
6. How desirable is Lucy as a partner in a long-term committed relationship?	4.21	1.83	11	13	8	17	22	21	8
7. How desirable is Lucy as a partner for a brief sexual relationship?	5.53	1.53	4	3	2	8	24	28	31

Figure 1. The effects of visual and narrative cues of infidelity on mean ratings of female protagonist's desirability as a partner for a short-term sexual and long-term committed relationship. Error bars indicate SE.

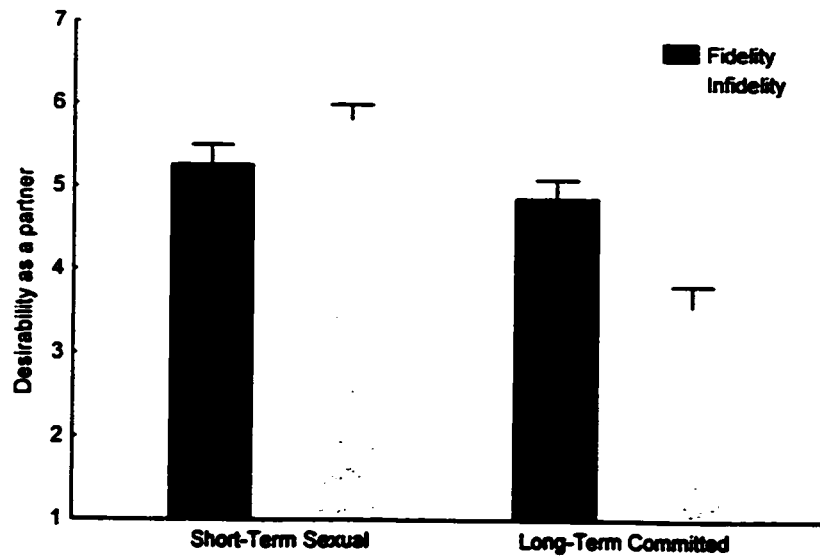
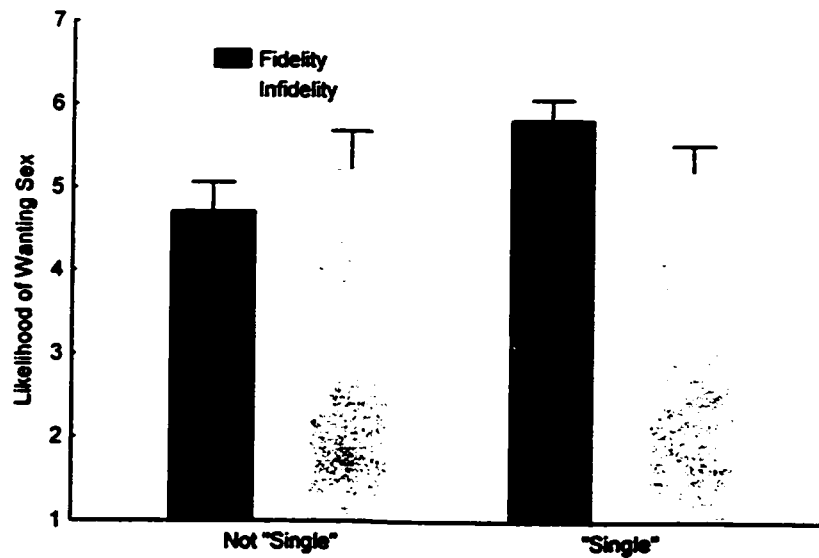


Figure 2. The effects of subject's relationship status on mean ratings of female protagonist's sexual attractiveness, desire for sex, and the likelihood that a man will try to persuade her to have sex if she was not interested. Error bars indicate SE.



Figure 3. The interactive effects of cues of infidelity and subject's relationship status on mean ratings of the likelihood of wanting sex with the female protagonist. Error bars indicate SE.



CHAPTER 6

CONCLUDING COMMENTS AND FUTURE RESEARCH DIRECTIONS

The prediction that males should inseminate more sperm when the risk of sperm competition is high has been tested extensively, at the inter-specific, intra-specific, and intra-individual levels. In particular, experimental evidence is accumulating that in species where the risk of sperm competition can vary from one copulation to the next, males are capable of adjusting the number of sperm they deliver in response to relevant cues (for a review see Parker *et al.*, 1997). However, little attention has been paid to the physiological, psychological, and behavioural mechanisms that may be involved in adaptive sperm allocation. Hence, the research reported in this thesis was conducted to identify some potential sperm allocation mechanisms in humans and other mammals.

A number of possible mediating processes have been identified at the physiological, psychological, and behavioural levels. In Chapter 4 it is reported that human males ejaculate more sperm when viewing sexual contact between a male and a female than they do when viewing sexual contact between two females. It is argued that this can be interpreted as evidence that human males can adjust their ejaculate composition in response to visual cues of sperm

competition. Alternative interpretations are possible, but this finding is nevertheless of some significance since it is the first published demonstration that the number of sperm ejaculated by men can be affected by the visual stimuli present during specimen production.

Data presented in Chapters 4 and 5 suggest that human males find visual and narrative cues of sperm competition risk to be sexually arousing and it is argued that consequently, such cues may motivate males to pursue more frequent within-pair copulations when the risk that the female partner has copulated with another male is elevated. Sexual arousal may thus be conceived of as the proximal psychological mechanism mediating the relationship between cues of sperm competition risk and the adaptive response, i.e., increases in the number of sperm inseminated. Further research is needed to isolate the specific visual cues that males rely on to assess sperm competition risk. Additionally, the possibility that males use cues in other sensory modalities needs to be examined. In a number of nonhuman primate species, females make loud vocalisations during copulation and it has been suggested that these may function to incite behavioural and sperm competition between males (Harcourt et al., 1981; O'Connell & Cowlshaw, 1994). Vocalisations made by human females during copulation may have served a similar function in ancestral environments so they may have facilitatory effects on male sexual behaviour and sperm delivery. In addition, the olfactory system may also provide human males with a rich source of information about the risk of sperm competition. When the female reproductive tract contains

sperm from one or more rival males, olfactory cues may be available that males could use to adjust their sexual behaviour and semen parameters in an adaptive fashion.

The data presented in Chapter 3 raise the intriguing possibility that behavioural changes that increase the duration of pre-ejaculatory male sexual arousal could be involved in the adaptive regulation of semen parameters in response to changes in the risk of sperm competition. However, this finding needs to be reconciled with the view that rapid and frequent copulations are the appropriate response to increases in the risk of sperm competition. It may be the case that physiological constraints in human males are such that the most efficient way to deliver a large number of sperm is in a single, prolonged copulatory episode rather than in a series of intromissions of shorter duration. Moreover, prolonged sexual intercourse may have other benefits for men such as the removal of rival sperm or the stimulation of female orgasm and consequent increases in sperm uptake (Baker & Bellis, 1995).

It is acknowledged that further work is needed to disentangle the within- and between-subjects sources of variance in ejaculatory latency and semen parameters. However, if the within-subject relationship between ejaculatory latency and semen quality ultimately turns out to be robust then this work may have important clinical implications. For example, instructing semen donors to prolong the duration of pre-ejaculatory sexual stimulation when they provide

specimens by masturbation might result in improvements in semen quality for oligospermic men.

The data reported in Chapter 3 also have some important implications for adaptationist accounts of human female sexuality. It has been suggested that the human female orgasm is an adaptation for post-copulatory female choice between rival ejaculates and hence between potential sires. Specifically, it has been argued that since the female orgasm can cause sperm to be sucked up into the uterus during copulation (Fox, 1970; Singer, 1973), females can selectively retain the sperm of particular males by adjusting the occurrence and timing of their orgasm in relation to male ejaculation (Baker & Bellis, 1989, 1993, 1995). Thus, they may be able to bias sperm competition in favour of males possessing heritable fitness indicators such as low fluctuating asymmetry (FA), and the finding that women are more likely to have an orgasm during intercourse when copulating with a male possessing low FA (Thornhill *et al.*, 1995) is consistent with this possibility.

The relationship between the duration of pre-ejaculatory male sexual arousal and ejaculate composition reported in Chapter 3 suggests an alternative explanation for evidence that has been used in support of the hypothesis that women can and do bias the outcome of sperm competition by changes in orgasmic timing (Pound & Daly, 2000). Baker & Bellis (1993) reported that when women experience an orgasm between about 1 minute before and 45

minutes after their partner ejaculates, they retain more sperm than if they have an orgasm earlier or not at all. In that study, the number of sperm retained was computed from an estimate of the number of sperm ejaculated minus the number ejected by the female from her vagina after copulation (the "flowback") and, thus, was based on the assumption that the number of sperm ejaculated is identical regardless of whether or when female orgasm occurs. However, this may not be true since the duration of pre-ejaculatory male sexual arousal is most likely confounded with female orgasm timing.

The duration of pre-ejaculatory male sexual arousal is likely to be shorter for ejaculations that occur before female orgasm than for those that occur afterwards. This is important since the data reported in Chapter 3, and the findings of Zavos (1988), indicate that the number of sperm ejaculated by human males is positively correlated with the duration of pre-ejaculatory sexual arousal. Consequently, Baker & Bellis' estimates of the number of sperm retained for copulatory episodes during which the female has an orgasm after the male are likely to be based on overestimates of the number of sperm ejaculated. It may indeed be the case that the "flowbacks" associated with female orgasms that occur after male ejaculation are smaller than those associated with orgasms that occur before. However, this difference may arise as a consequence of differences in the number of sperm inseminated rather than in the number of sperm retained. The "high sperm retention" orgasm may thus be simply an artefact of a method that fails to take into account an important determinant of ejaculate composition.

Finally, it was argued in Chapter 2 that adaptive regulation of ejaculate composition in *Peromyscus maniculatus* might depend on changes in the contractility of the vas deferens regulated by endogenous opioid peptides (EOPs) and their antagonists. Obviously, further comparative work is needed to determine whether this proposed mechanism could exist in other mammalian species. Specifically, it needs to be determined whether other monogamous and non-monogamous species differ systematically in the extent to which opioid receptors are expressed in the vas deferens.

The physiological mechanism for adaptive modulation of ejaculate composition in mammals proposed in Chapter 2 has two key elements. These are that a) social events that may be predictive of sperm competition risk can cause changes in the circulating levels of endogenous opioid peptides (EOPs) and their antagonists, and b) these substances can affect vas deferens contractility and, thus, semen parameters. However, EOPs and their antagonists may also be involved in the adaptive regulation of many other aspects of sexual behaviour and reproductive physiology in males of many species, including humans.

During the course of mammalian evolution EOPs seem to have come to assume neuromodulatory, paracrine and endocrine roles in controlling and integrating the activity of a diverse set of structures that are functionally related. They are involved in the control of many aspects of reproductive functioning, at multiple sites (for a review see Fabbri *et al.*, 1989b), including the central nervous

system, the peripheral nervous system, secretory tissues, and (as demonstrated in Chapter 2) the muscular ducts involved in sperm transport.

Opiate drugs that mimic the effects of opioid peptides by binding to the same receptors are known to be potent inhibitors of many aspects of human reproduction including sexual behaviour. Male heroin addicts often experience clinically significant sexual dysfunctions such as diminished sexual desire, increased latency to erection, increased ejaculation latency and extended post-ejaculatory refractory periods (e.g. Bolelli *et al.*, 1979; Mirin *et al.*, 1980). Furthermore, individuals tolerant to the effects of opiates often experience increased sexual motivation and responsiveness during drug withdrawal. Males may experience frequent spontaneous erections and even spontaneous ejaculations while the post-ejaculatory refractory period may also be substantially reduced.

If tolerance to opiate administration depends on chronic increases in the secretion of endogenous opioid antagonists, then exogenous opioid antagonists should be expected to stimulate male sexual behaviour and reproductive functions and there is experimental evidence that they do (e.g. Fabbri *et al.*, 1989a; Van Ahlen *et al.*, 1995). Naloxone in particular, has been used with some success as a treatment for idiopathic impotence, leading to either an increase in the frequency of spontaneous early morning erections (Brennemann, 1993) or the full return of erectile function (Goldstein, 1986). Furthermore, it can also induce spontaneous penile erection in normal adult men (Mendelson *et al.*, 1979).

Since it is known that social events and stressors can affect the activity of opioid systems (e.g. Rodgers & Hendrie, 1983; Rodgers & Randall, 1985; Raab *et al.*, 1986; Huhman *et al.*, 1990, 1991), the possibility that opioid mediated processes may be involved in the adaptive regulation of male sexual behaviour and reproductive functions needs further examination. In particular, it is important to determine whether such things as adaptive increases in copulatory frequency, and most importantly, increases in the number of sperm inseminated can be attenuated by opiate administration. The fact that opioid agonists tend to delay ejaculation is somewhat problematic for the argument that they have a general role in adaptive sperm allocation since it has been argued that prolonged pre-ejaculatory sexual arousal may be important for increases in the number of sperm delivered. However, since opioids also tend to increase erectile latency their effects on the duration of sexual arousal may be neutral. This, too, needs to be examined empirically.

Ultimately, other endocrine and neurotransmitter systems may also turn out to be involved in adaptive sperm allocation. However, the data reported in this thesis are initial steps in the formation of an integrated account of how and when males of human and non-human mammalian species adjust the number of sperm they inseminate in response to cues of changes in the risk of sperm competition.

REFERENCES

- Baker, R. R., & Bellis, M. A. (1989). Number of sperm in human ejaculates varies in accordance with sperm competition theory. *Animal Behaviour*, 37, 867-869.
- Baker, R. R., & Bellis, M. A. (1993). Human sperm competition: ejaculate manipulation by females and a function for the female orgasm. *Animal Behaviour*, 46, 887-909.
- Baker, R. R., & Bellis, M. A. (1995). *Human sperm competition: Copulation, masturbation, and infidelity*. Chapman and Hall, London.
- Bolelli, G., Lafisca, S., Flamigni, C., Lodi, S., Franceschetti, F., Filicori, M., & Mosca, R. (1979). Heroin addiction: relationship between the plasma levels of testosterone, dihydrotestosterone, androstenedione, LH, FSH, and the plasma concentration of heroin. *Toxicology*, 15, 19-29.
- Brennemann, W., Stitz, B., Van Ahlen, H., Brensing, K. A., & Klingmuller, D. (1993). Treatment of idiopathic erectile dysfunction in men with the opiate antagonist naltrexone: A double blind study. *Journal of Andrology*, 14, 407-410.
- Fabbri, A., Jannini, E. A., Gnassi, L., Moretti, C., Ulisse, S., Franzese, A., Lazzari, R., Fraioli, F., Frajese, G., & Isidori, A. (1989a). Endorphins in male impotence: evidence for naltrexone stimulation of erectile activity in patient therapy. *Psychoneuroendocrinology*, 14, 103-111.

- Fabbri, A., Jannini, E. A., Gnnessi, L., Ulisse, S., Moretti, C., & Isidori, A. (1989b). Neuroendocrine control of male reproductive function. The opioid system as a model of control at multiple sites. *Journal of Steroid Biochemistry*, 32, 145-150.
- Fox, C. A., Wolff, H. S., & Baker, J. A. (1970). Measurement of intra-vaginal and intra-uterine pressures during human coitus by radio-telemetry. *Journal of Reproduction & Fertility*, 22, 243-251.
- Goldstein, J. A. (1986). Erectile function and naltrexone. *Annals of Internal Medicine*, 105, 799.
- Harcourt, A. H., Harvey, P. H., Larson, S. G., & Short, R. V. (1981). Testis weight, body weight, and breeding system in primates. *Nature*, 293, 55-57.
- Huhman, K. L., Bunnell, B. N., Mougey, E. H., & Meyerhoff, J. L. (1990). Effects of social conflict on POMC-derived peptides and glucocorticoids in male golden hamsters. *Physiology & Behavior*, 47, 949-956.
- Huhman, K. L., Moore, T. O., Ferris, C. F., Mougey, E. H., & Meyerhoff, J. L. (1991). Acute and repeated exposure to social conflict in male golden hamsters: increases in plasma POMC-peptides and cortisol and decreases in plasma testosterone. *Hormones & Behavior*, 25, 206-216.
- Mendelson, J. H., Ellingboe, J., Kehule, J. C. & Mello, N. K. (1979). Effects of naltrexone on mood and neuroendocrine function in normal and adult males. *Psychoneuroendocrinology*, 3, 231-236.

- Mirin, S. M., Meyer, R. E., Mendelson, J. H. & Ellingboe, J. (1980). Opiate use and sexual function. *American Journal of Psychiatry*, 137, 909-915.
- O'Connell, S. M., & Cowlshaw, G. (1994). Infanticide avoidance, sperm competition and mate choice: The function of copulation calls in female baboons. *Animal Behaviour*, 48, 687-694.
- Parker, G. A., Ball, M. A., Stockley, P., & Gage, M. J. G. (1997). Sperm competition games: a prospective risk analysis assessment. *Proceedings of the Royal Society: Biological Sciences*, 264, 1793-1802.
- Pound, N., & Daly, M. (2000). Functional significance of human female orgasm still hypothetical. *Behavioral and Brain Sciences*, 23, xxx-xxx.
- Raab, A., Dantzer, R., Michaud, B., Mormede, P., Taghzouti, K., Simon, H., & Le Moal, M. (1986). Behavioural, physiological and immunological consequences of social status and aggression in chronically coexisting resident-intruder dyads of male rats. *Physiology & Behavior*, 36, 223-228.
- Rodgers, R. J., & Hendrie, C. A. (1983). Social conflict activates status-dependent endogenous analgesic and hyperalgesic mechanisms in male mice: effects of naloxone on nociception and behaviour. *Physiology & Behavior*, 30, 775-780.
- Rodgers, R. J., & Randall, J. I. (1985). Social conflict analgesia: studies on naloxone antagonism and morphine cross-tolerance in male DBA/2 mice. *Pharmacology, Biochemistry & Behavior*, 23, 883-888.

- Singer, I. (1973). Fertility and the female orgasm. In I. Singer (Ed.) *The Goals of Human Sexuality*. Wildwood House, London. pp 159-197.
- Thornhill, R., Gangestad, S. W., & Comer, R. (1995). Human female orgasm and mate fluctuating asymmetry. *Animal Behaviour*, 50, 1601-1615.
- Van Ahlen, H., Piechota, H. J., Kias, H. J., Brennemann, W., & Klingmuller, D. (1995). Opiate antagonists in erectile dysfunction: a possible new treatment option? Results of a pilot study with naltrexone. *European Urology*, 28, 246-250.
- Zavos, P.M. (1988). Seminal parameters of ejaculates collected at intercourse with the use of a seminal collection device with different levels of precoital stimulation. (Abstr) *Journal of Andrology*, 9: P-36.