TESTOSTERONE TRADE-OFFS AND PARTNERING IN WOMEN AND MEN

by

Sari van Anders
Hons. B.A., The University of Western Ontario, 2001
M.A., The University of Western Ontario, 2003

DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

In the
Department
of
Psychology

SIMON FRASER UNIVERSITY

Summer 2007

APPROVAL

Name:	Sari van Anders
Degree:	Doctor of Philosophy (Department of Psychology)
Title of Thesis:	Testosterone Trade-Offs and Partnering in Women and Men
Chair:	Dr. Barry Beyerstein Professor
	Dr. Neil Watson Senior Supervisor Professor
	Dr. Ralph Mistlberger Supervisor Professor
	Dr. Mario Liotti Supervisor Associate Professor
Internal Examiner:	Dr. Charles Crawford Professor
External Examiner:	Dr. Rui Oliveira Associate Professor Instituto Superior de Psicologia Aplicada
Date Approved :	May 23, 2007

STATEMENT OF ETHICS APPROVAL

The author, whose name appears on the title page of this work, has obtained, for the research described in this work, either:

(a) Human research ethics approval from the Simon Fraser University Office of Research Ethics,

or

(b) Advance approval of the animal care protocol from the University Animal Care Committee of Simon Fraser University;

or has conducted the research

(c) as a co-investigator, in a research project approved in advance,

or

(d) as a member of a course approved in advance for minimal risk human research, by the Office of Research Ethics.

A copy of the approval letter has been filed at the Theses Office of the University Library at the time of submission of this thesis or project.

The original application for approval and letter of approval are filed with the relevant offices. Inquiries may be directed to those authorities.

Simon Fraser University Library
Burnaby, BC, Canada

ABSTRACT

Previous research has shown that partnered heterosexual men have lower testosterone than single heterosexual men. Whether this pattern is apparent beyond heterosexual men has not been examined, and there is, as of yet, little empirical basis for directional interpretations. To address these issues, three studies were conducted in which the partnering-testosterone link was examined in diverse samples of North American men and women. In the first study, cross-sectional results showed that testosterone and partnering were associated in heterosexual men and non-heterosexual women, as partnered individuals in these groups exhibited lower testosterone than their unpartnered counterparts. No significant difference in testosterone by partnered status was found in heterosexual women or non-heterosexual men. Longitudinal results showed that lower testosterone predicted entering relationships, and there was no evidence that changes in relationship status influenced testosterone. In the second study, findings indicated that physical partner presence was associated with lower testosterone for women, but not men. In the third study, polyamory (having multiple, committed relationships) was associated with higher testosterone for both men and women. Neither sexual desire nor sociosexual orientation (willingness to engage in sexual contact outside a committed relationship) explained these associations. These studies are discussed within a framework of testosterone trade-offs between high testosterone and 'competitive' (resource acquisition/defence) behaviours versus low testosterone and 'bond-maintenance' (intimacy) behaviours. Interpretations of results from these studies point

more strongly towards a trait effect (such that testosterone affects partnering, or 'relationship orientation') than a state effect (such that partnering would affect testosterone, or 'relationship status').

Keywords: testosterone; gender; relationships; sex; affiliation; pair bond

Subject Terms: Hormones Psychological Aspects; Psychoneuroendocrinology; Hormones, Sex; Testosterone, Social Aspects; Social Behavior in Animals

DEDICATION

To all the folks who left mittens and boots and portable heaters to help me keep moving in this chilly climate. I've left some scarves for those to come.

ACKNOWLEDGEMENTS

Firstly, a very special thanks to the wonderful administrators in psychology at SFU, especially Bev Davino and Deb Jopling for being excellent sources of help and advice, and for stepping in to solve seemingly intractable problems.

Neil Watson, my Ph.D. supervisor, provided the crucial opportunity for me to develop into an independent investigator, helped me develop important academic skills, and offered enthusiastic encouragement. My defense committee, especially Rui Oliveira, asked many interesting and thought-provoking questions. Tony Vernon and Scott MacDougall-Shackleton provided excellent encouragement and guidance, stemming from a seemingly unending and cheerful willingness to provide prompt, comprehensive, and thoughtful responses to any and all of my varied questions. My sincere thanks to all.

Various wonderful lab volunteers worked and laughed with me during my doctorate: Lisa Dawn Hamilton, Janine Farrell, Nataiya Macdonald, Stephanie Orford, Giselle Panduri, Raquel Park, Mark Pillay, Mariam Safi, Nicole Schmidt, Camille Viray, and Emily Wagner. I won't miss the crammed confines of our lab meetings (thanks to everyone for taking a turn on the filing cabinet!), but I will miss all of you.

Reviewers provided important and helpful feedback on the articles that in part make up this dissertation, and I would especially like to thank Peter Ellison, Peter Gray, Ben Jones, and Greg van Anders (who also read a draft of this dissertation – thanks!). Thanks to Mark Schaller at UBC for lending us space for data collection and to the Vancouver Pride Parade for allowing researchers to book booths. A very sincere thank-

you to all the participants, especially to the polyamory groups in Canada and the U.S. who allowed us to attend meetings for data collection or held saliva samples for us. Posters based on some of these data were presented at the annual meetings of the Society for Behavioral Neuroendocrinology in Lisbon, 2004, the Human Behavior and Evolution Society in Berlin, 2004, the International Association of Sex Research in Ottawa, 2005, and the Kinsey Conference on Research Innovations in Bloomington, 2007. The Endocrine Core Assay Lab at Yerkes Primate Research Center, Emory University, conducted salivary assays and I am appreciative of the helpful staff members there. I would especially like to send a big thank-you to Susie Lackey for her ever-cheerful help and willingness to respond to my many questions.

Without financial support, completing this dissertation might have been impossible, and certainly would have been more difficult. I would therefore like to extend my most sincere gratitude to the following sources for allowing me to concentrate on conducting and disseminating my research: the Natural Sciences and Engineering Research Council of Canada (NSERC) for postgraduate scholarship (PGS-B) support, the 'For Women in Science' Program from L'Oreal-UNESCO-NSERC for a PGS Supplement, SFU for a CD Nelson and other scholarships, IODE for an IODE War Memorial Scholarship, and SBN for a student travel award. This research was supported by NSERC Discovery Grant 0194522 to my supervisor, Neil Watson. Though I was fortunate to be supported through various agencies, I was also fortunate to know that – should this support cease – my parents were happy (and able, luckily) to offer me financial support; thanks to them for providing a very well appreciated safety net.

Three hundred million thanks to Greg, who puts the van in my van Anders.

TABLE OF CONTENTS

LIST OF FIGURES AND TABLES

LIST OF ACRONYMS

Het = heterosexual.
Non-het = non-heterosexual.
SOI = sociosexual orientation inventory.

1 GENERAL INTRODUCTION

Note: This section is based in part on the following article, with permission: van Anders, S. M. & Watson, N. V. (2006b). Social neuroendocrinology: Effects of social contexts and behaviors on sex steroids in humans. *Human Nature*, *17,* 212-237.

1.1 Social Neuroendocrinology

Behavioural neuroendocrinology has generally focused on how hormones can affect behaviour and sexual differentiation, and this has produced promising results in most species. Although mammalian sex determination is genomic (dependent on the expression of the Y-chromosome's *sry* gene), subsequent sexual differentiation of the nervous system and behaviour is largely mediated by sex hormones (but see Gatewood et al., 2006, for a discussion on chromosomal plus hormonal influences). In typical mammalian fetal development, possession of a Y chromosome leads to *sry* protein secretion, which induces the bipotential gonads of the fetus to develop into secretory testes. Testicular androgens (either directly, or after conversion to estrogens or dihydrotestosterone) masculinise the developing fetus leading to sexual dimorphism in subsequent life (for an overview, see Nelson, 2000). In the absence of an *sry* gene, the mammalian fetus develops into a phenotypic female (although the dogma of 'female as default' is probably an oversimplification, e.g. Hughes, 2004). Historically, the bulk of human behavioural endocrinology research has adopted a causal perspective mirroring the unidirectional relationship between hormone secretion and fetal sexual differentiation. Specifically, most studies focus on the effects of hormones on somatic or behavioural

measures, because hormones have significant effects on the nervous system throughout life.

In addition to examining the effects of hormones on behaviour, researchers have extended or reversed this scope to examine how behaviour may influence hormone secretions. Studies have shown, for example, that exposure to novel females increases the gonadotropin luteinizing hormone (LH) in males (Coquelin and Bronson, 1979). In humans, these efforts to examine the influences of behaviours on hormonal levels have been undertaken in various lines of research. For example, researchers have examined the effects of psychological stressors on the hypothalamic-pituitary-adrenal (HPA) axis, and downstream hormones like cortisol (e.g. Kudielka, Schommer, Hellhammer, and Kirschbaum, 2004; for a review, see Dickerson and Kemeny, 2004). Another line of research entails studying the effects of exercise on both the HPA and hypothalamic-pituitary-gonadal (HPG) axis (e.g. Aizawa et al., 2006; Izquierdo et al., 2006). More relevant to this dissertation is the body of research examining the effects of social behaviours on androgens in humans (for reviews, see Archer, 2006; van Anders and Watson, 2006b). This small but growing body of research grew mostly out of animal research (especially birds and fish), and Hirschenhauser and Oliveira (2006) provide a comprehensive review of how social behaviours affect androgen levels in males of various species.

In this dissertation, I address behavioural neuroendocrine questions using bidirectional approaches, i.e., how behavioural contexts might affect hormones and how hormones might affect behavioural contexts. Specifically addressed are social behavioural contexts, which are important to study because human behaviour (like the

behaviour of other social animals) is enacted within existing social systems. Moreover, these social systems can directly impact human evolutionary fitness, or the success at reproducing over generations. The influence of social systems on fitness can stem from various sources, including (perhaps most obviously) the social constraint or facilitation of access to potential sexual partners. For example, female and male athletes report more sexual partners than non-athletes and better athletic performance is correlated with more partners (Faurie, Pontier, and Raymond, 2004). It is possible that access to partners may be enhanced by successful participation in sport (though third variables may account for both). In another example, Wallen (2001) describes how social rank can affect female rhesus monkeys' access to prime reproductive partners, and how hormones can influence risk-taking (e.g. willingness to risk hostility from other females) to gain reproductive opportunities at times of peak fertility. This example illustrates how social systems can influence female proceptive (mate-seeking) behaviour, and thus fitness, and how hormone-behaviour associations can be moderated by social dynamics. Because of the influences of social systems on fitness, social contexts and behaviours can be especially relevant to evolutionary considerations. Androgens show heritability estimates of 40% (Meikle, Stringham, Bishop, and West, 1988) to 70% (Hong et al., 2001), which is consistent with evidence of selective pressures, but also with room for environmental (e.g. social) influences. I focus on relationships (i.e. partnering) and testosterone because partnering-hormone links should be sensitive to, and reflective of, evolutionary influences. In many species, mating systems are linked to androgens (Hirschenhauser and Oliveira, 2006), and evidence reviewed in Section Two highlights previous research on pair bonding, partnering and hormones.

The convergence of studies of social behaviours and behavioural neuroendocrinology makes sense in light of the influences hormones may have on factors critical to engaging with a social system, including perceptions (e.g. heightened sensitivity to facial expressions of danger when progesterone levels are high: Conway et al., 2007), cognitive performance on tests (e.g. improved visuospatial ability following testosterone administration: Aleman, Bronk, Kessels, Koppeschaar, & van Honk, 2004), and behaviours (e.g. fewer signs of facial mimicry or empathetic behaviour following testosterone administration: Hermans, Putman, and van Honk, 2006). As such, hormones can potentially affect social decision-making. This convergence makes sense in light of the central role the human nervous system (including endocrine axes) plays in assessing social situations and behaviours.

1.2 The 'Challenge Hypothesis'

The most prominent and relevant theoretical framework for conceptualising androgens and social behaviours of evolutionary significance is the 'challenge hypothesis' (Wingfield, Hegner, Dufty, and Ball, 1990), related to life history approaches (e.g. Ketterson and Nolan, 1992). Wingfield et al. posit in the challenge hypothesis, originally based on avian research, that androgens should be high around times of social challenges, either to facilitate or in response to male-male competition or mating needs. The challenge hypothesis largely concerns seasonal fluctuations in both androgens and mating behaviours, and a main focus is on trade-offs between high testosterone in relation to challenges associated with mating (e.g. during the mating season) and low testosterone in relation to parenting. In addition, the challenge hypothesis holds that the pattern of seasonal fluctuations in androgens and androgenic responses to challenges differs

depending on a given species' pattern of aggressive, mating, or parental behaviour. For example, androgens are more responsive to social challenges in avian species with monogamous males than species with polygynous males (Wingfield et al., 2000; Hirschenhauser, Winkler, and Oliveira, 2003).

The majority of evidence supporting various tenets of the challenge hypothesis comes from avian research (for a review, see Oliveira, 2004), including some of the following examples. In the red-wing blackbird, testosterone was significantly correlated with various measures of aggression, increased in response to receptive females, and showed seasonal increases in conjunction with the mating season (Johnsen, 1998). Also, males in higher-density areas (thus with increased likelihood of social challenges) exhibited higher testosterone (Beletsky, Orians, and Wingfield, 1992). Testosterone levels were also significantly correlated with mating success in black grouse males, largely because the most central territories were held by high testosterone individuals (Alatalo, Höglund, Lundberg, Rintamäki, and Silverin, 1996). In dark-eyed juncos, testosterone administration increased the frequency of extrapair copulations (Raouf, Parker, Ketterson, Nolan, and Ziegenfus, 1997), the frequency of singing (which can attract females), and decreased paternal behaviours (Ketterson, Nolan, and Sandell, 1992). In male house sparrows, testosterone administration has been shown to inhibit parental behaviours like feeding (Hegner and Wingfield, 1987). Interestingly, antiandrogens did not inhibit sexual behaviour, supporting predictions of the challenge hypothesis that androgen levels above baseline levels are likely more important for non-sexual reproductive social behaviours like aggression or parenting. Testosterone administration has been shown to inhibit feeding behaviours in male house finches

(Stoehr and Hill, 2000). Androgens have been shown to increase following the introduction of females into territories in European starlings (Gwinner, Van't Hof, and Zeman, 2002) and unpaired flycatchers (who also showed increased androgen levels after attacks of decoys, Silverin, 1993). Testosterone implants have been shown to induce polygyny in avian species regularly showing monogamous mating patterns (Wingfield, 1984; De Ridder, Pinxten, and Eens, 2000). Evidence from various avian species thus provides large-scale, intra-, and inter-specific support for various tenets of the challenge hypothesis.

Though the challenge hypothesis is grounded largely in avian male behaviour, the authors explicitly note that it should and could be relevant to males and females of other species, and a large body of research exists for teleost fish (for a review, see Oliveira, Hirschenhauser, Carneiro, and Canário, 2002). For example, multiple cichlid fish species showed elevated 11-ketotestosterone (a potent androgen in fish species) following territorial challenges (Hirschenhauser, Taborsky, Oliveira, Canário, and Oliveira, 2004). In demoiselles *Chromis dispilus*, androgen levels were increased during spawning phases and decreased during nesting phases (Pankhurst and Barnett, 1993). In cichlid fish, rank and androgen levels were correlated after but not before group formation, suggesting that the behaviours needed to achieve higher rank (or correlates of higher rank itself) increased androgens instead of androgen levels determining rank (Oliveira, Almada, and Canário, 1996). In the rock blenny, males who had been administered 11-ketotestosterone showed more aggression and developed larger home territories than untreated males (Ros, Bruintjes, Santos, Canário, and Oliveira, 2004). Other findings show that, in Saint Peter's Fish, polygyny is correlated with 11-ketotestosterone. Experimental increases in

11-ketotestosterone did not lead to increased polygyny however; instead, polygynous behaviours appeared to increase 11-ketotestosterone (Oliveira, Ros, Hirschenhauser, and Canário, 2001). Counter to some predictions that stem from the challenge hypothesis, treated males did not show inhibited parental behaviour.

Evidence from mammals and primates has also provided support for the challenge hypothesis (for a review of the challenge hypothesis in male vertebrates, see Hirschenhauser and Oliveira, 2006). In wild chimpanzees, Muller and Wrangham (2004) found that testosterone levels were high during competition for mating opportunities; additionally, testosterone levels in the alpha male were significantly higher than other males, and testosterone levels in all males was correlated with dominance. Moreover, testosterone levels were higher in males with exposure to fertile females. Similarly, rhesus monkeys showed increased testosterone following introduction to females (Bernstein, Rose, and Gordon, 1977). In a study of ringtailed lemurs, Cavigelli and Pereira (2000) found that testosterone and aggression was correlated only in the mating season; in other seasons, no relationship between testosterone and aggression were found, supporting seasonality considerations of the challenge hypothesis. Higley et al. (1996) found that testosterone (measured from cerebrospinal fluid) was significantly correlated with aggressive behaviours in rhesus monkeys, though age accounted for much of this variation. Male spotted hyenas who were defending females at time of hormone sampling exhibited higher androgens than hyenas not defending females (Goymann, East, and Hofer, 2003). In naked mole rats, higher androgens were associated with higher rank for males (Clarke and Faulkes, 1998). In hamsters, who have high paternal behaviour, androgens increased before birth (likely for mate guarding behaviours) and decreased

after birth (Reburn and Wynne-Edwards, 1999). In olive baboons, aggressiveness was correlated with testosterone levels (Sapolsky, 1982). Evidence from primates and other mammals thus shows broad support for various predictions from the challenge hypothesis.

Supporting evidence for the challenge hypothesis in females is limited, largely because studies with females are limited and not necessarily because of null findings. Some (e.g. Moore, in press) have called for more research with females to provide more general advances in detailing broad understandings of the challenge hypothesis. Though research with females is limited, some researchers have addressed the issue of sex, including research with avian females (Ketterson and Nolan, 1992). Ketterson and Nolan's (1992) findings and theoretical positionings have led them to question whether testosterone-behaviour associations in females are related to selection pressures based on female reproductive ecology or are secondary to selection pressures for male development; their evidence supports both trajectories of androgen and behaviour-related selection in females. Research with females does show some support for evidence of the challenge hypothesis in females. Exogenous testosterone has been shown to induce aggressive behaviours in adult female zebra finches (Adkins-Regan, 1999), and increase dominance rank in adult female rhesus monkeys (Cochran and Perachio, 1977). Prenatal testosterone administration has sometimes led to increased dominance behaviours for female rhesus monkeys (Joslyn, 1973). Female dunnocks showed elevated androgens during periods of unrest (Langmore, Cockrem, and Candy, 2002), and higher androgens during periods of social instability are a key prediction of the challenge hypothesis. Colonially breeding female birds (who have high aggression) have been shown to exhibit

higher testosterone than solitarily breeding females (Møller, Garamszegi, Gil, Hurtrez-Boussès, and Eens, 2005). However, in dark-eyed juncos, testosterone does not appear to increase following aggression nor is it related to dominance rank (Jawor, Young, and Ketterson, 2006). In contrast to possible (but by no means definite) benefits of higher androgens for male fitness, exogenous testosterone can delay or inhibit fertility or reproductive events in females in various avian species (e.g. Clotfelter et al., 2004), and testosterone is negatively correlated with regular menstruation in women (van Anders and Watson, 2006c). Thus, some evidence supports the challenge hypothesis in women, though there are null effects throughout the literature, and sex-specific fitness should be considered. If findings with females are to become consistent with predictions from the challenge hypothesis, it is far from clear whether these associations (e.g. testosterone and dominance) would result in enhanced female fertility. Thus, whether selection acts to promote female reproductive fitness or male reproductive fitness with byproduct effects on females (Ketterson and Nolan, 1992) is not yet clear in general or for specific species. Some evidence, for example greater variance in testosterone levels of females versus males in avian species (Møller et al., 2005), can be taken as suggestive that male testosterone levels are subject to stricter selection pressures than female testosterone levels. Additionally, female and male peak testosterone levels are highly correlated (in birds: Møller et al., 2005; in some fish species: Menk, 2007), suggesting coupling in evolutionary development. And, statistical modeling is indicative of evolution of male testosterone followed by evolution of female testosterone (Møller et al., 2005).

Though evidence often supports the challenge hypothesis, there have been some caveats and null results as briefly indicated above. For example, dwarf mongooses

showed no increase in androgens during phases of reproductive-related aggression or activity, and androgens were not correlated with aggressive behaviours, outcomes of aggressive interactions, or reproductive rates (Creel, Wildt, and Monfort, 1993). In muriquis (woolly spider monkeys), which do not show competition for reproductive access, testosterone levels were not higher during the mating season (Strier, Ziegler, and Wittwer, 1999). This does not necessarily contradict the challenge hypothesis, because higher testosterone might not be expected in the mating season if the mating season does not entail challenges and competitions. Accordingly, Strier et al. (1999) note that there is an absence of overt aggression over access to females in the muriquis. Still, some null findings, especially in mammals and especially related to parental behaviours, have led to adjustments or questions for the challenge hypothesis.

1.3 The Testosterone Trade-Off Framework

I situate my research within a testosterone trade-off framework (van Anders and Watson, 2006b), which is grounded in theoretical approaches like the Challenge Hypothesis, but varies from these approaches. The testosterone trade-off hypothesis posits a trade-off between (1) higher testosterone and competitive behaviours/states (i.e. aimed at or entailing competition for or defence of resources, including partners, offspring, status, etc.), versus (2) lower testosterone and bond-maintenance behaviours/states (i.e. aimed at or entailing promotion and development of intimate and caring bonds with a partner, offspring, or others). In the following paragraphs, I highlight how the testosterone trade-off framework differs from existing frameworks (like the Challenge Hypothesis), but first I discuss the evidence linking high testosterone and

competitive behaviours/states, and low testosterone and bond-maintenance behaviours/states.

1.3.1 Competitive Behaviours/States and Higher Testosterone

Various pieces of evidence suggest that competitive behaviours/states are associated with higher testosterone in humans. For example, androgens have been positively correlated with self-reported status (Cashdan, 1995), dominance (Christiansen and Knussmann, 1987), confidence (Baucom, Besch, and Callahan, 1985), aggressive behaviours (Susman et al., 1987) aggressive responses to provocation (Olweus, Mattsson, Schalling, and Löw, 1988), and aggressive characteristics (in men, but not women: Gladue, 1991). Athletic competition can lead to increased testosterone, as evidenced in male wrestlers (Passelergue and Lac, 1999), male and female soccer players (Edwards, Wetzel, and Wyner, 2006), and athletes in other sports (for reviews, see Archer, 2006; van Anders and Watson, 2006b). Complicating this relationship (i.e. between sports and testosterone increases), however, is that physical competition of a strenuous and sustained nature can decrease testosterone levels (e.g. Maestu, Jurimae, and Jurimae, 2005), likely in relation to the inhibiting effects of prolonged stress on the HPG axis (for a review, see Maztorakos, Pavlatou, and Mizamtsidi, 2006). In part related to this, non-athletic competitive encounters have also been studied, and increased androgens have been found following a lottery competition (Gladue, Coechler, and McCaul, 1989), chess (Mazur, Booth, and Dabbs, 1992), and a coin toss competition (McCaul, Gladue, and Joppa, 1992), though these studies have generally found increases after wins only.

The phenomenon of higher testosterone following wins relative to post-loss levels is known by various terms, including the 'competition effect'. Despite being named, the

competition effect is not well explicated, though there are findings from non-human species. For example, male golden hamsters showed decreased testosterone levels and increased submissive behaviours following defeat (Huhman, Moore, Ferris, Mougey, and Meyerhoff, 1991). Rhesus monkeys also showed decreased androgens and rank after losses, and increased androgens and rank following victories (Bernstein, Rose, and Gordon, 1974; Rose, Holaday, and Bernstein, 1971; Rose, Bernstein, and Gordon, 1975). Male olive baboons that were increasingly successful in contests showed increasing levels of testosterone (Sapolsky, 1982). Additionally, male chimpanzees higher in rank exhibited higher testosterone levels (Muller and Wrangham, 2004). Evolutionarily, it is not difficult to see how increased androgens following wins but not losses might be beneficial, e.g. reinforcing the behaviours that led to the win (as androgens have mildly reinforcing effects: Wood, 2004), influencing further development of male secondary sexual characteristics, or facilitating sperm production (McLachlan, Wreford, O'Donnell, de Kreser, and Robertson, 1996). Oliveira (2004) describes how wins in many species lead to increased probabilities of future wins in subsequent competitions (a process known as the 'winner/loser effect'), and that increased androgens may be involved in mediating the winner/loser effect. If testosterone levels are increased following wins and losses, but higher following a win than a loss, then the competition effect literature is consistent or reconcilable with predictions made by the challenge hypothesis. But, if testosterone is selectively increased following success, and shows no increase (or even a decrease) after failure, this would diverge from the challenge hypothesis. In this case, the relevant predictions from the competition effect (higher testosterone after wins relative to losses) and the challenge hypothesis (higher testosterone after social challenge) are not

immediately reconcilable, since the challenge hypothesis does not make a case for differentiated androgen-challenge associations by challenge outcome, or androgen decreases following poor outcome from a social challenge. Far from a theoretical quibble, decreased androgens following losses in humans (e.g. van Anders and Watson, 2007a) or unsuccessful competition in other species like baboons (Sapolsky, 1982) have been found. Obviously, more research is needed to reconcile findings and evidence for the competition effect and the challenge hypothesis.

Behavioural engagement in competitions is not necessarily a prerequisite for increased testosterone with social challenges in some species, as viewing competitions has led to increased testosterone in men (Bernhardt, Dabbs, Fielden, and Lutter, 1998; though in winners only) and cichlid fish (Oliveira, Lopes, Carneiro, and Canário, 2004). Curiously, cichlid fish did not appear to show an androgen response to 'tied' fights, in which they attacked an image of themselves in a mirror (Oliveira, Carneiro, and Canário, 2005). Oliveira et al. (2005) suggest that information about outcome is necessary to trigger androgenic responses. However, in humans, anticipating physical competition (and thus having no information about competition outcome) has been shown to increase testosterone in male hockey players (Carre, Muir, Belanger, and Putnam, 2006) and soccer players (Salvador, Suay, Gonzalez-Bono, and Serrano, 2003). Additionally, testosterone levels are also correlated with the degree of self-reported competitiveness in women (Cashdan, 1995) and the competitive nature of occupations in men (Dabbs, de La Rue, and Williams, 1990) and women (Bancroft, Sanders, Davidson, and Warner, 1983; Purifoy and Koopmans, 1979). This evidence suggests that facets of competition itself that might not be associated with outcome, per se, are associated with androgens – at

least in humans. In either case, anticipation or post-interaction, competition-modulated androgen levels may potentially have the function of affecting subsequent interactions.

Engaging in sexual activity, which could be seen as an ultimate resource acquisition behaviour, appears to increase testosterone as well. Viewing sexually explicit movies increased testosterone levels compared to viewing neutral films in men (Hellhammer, Hubert, and Schürmeyer, 1985; Pirke, Kockott, and Dittmar, 1974; Stoleru, Ennaji, Cournot, and Spira, 1993; cf. Carani et al., 1990; Rowland et al., 1987). Similarly, engaging in sexual activity generally appears to produce an increase in testosterone, though not as consistently. Masturbation led to increases in testosterone relative to pre-masturbation levels in men (Purvis, Landgren, Cekan, and Diczfalusy, 1976; c.f. Kruger et al., 1998) and women (Exton et al., 1999). And, some studies have found an effect of intercourse on testosterone in men (Dabbs & Mohammed, 1992; Hirschenhauser, Frigerio, Grammer, and Magnusson, 2002; Kraemer et al., 1976; c.f. Fox, Ismail, Love, Kirkham, and Loraine, 1972; Lee, Jaffe, and Midgley, 1974; Stearns, Winter, and Faiman, 1973) and women (van Anders, Hamilton, Schmidt, and Watson, in press). Anticipation of sexual activity itself seems to be associated with increased androgenic activity in men (or, one man; e.g. beard growth: Anonymous, 1970) and women (e.g. testosterone measures: van Anders et al., in press).

Thus, various pieces of evidence link competitive behaviours/states (e.g. competition itself, dominance, aggression, sexual activity, etc.) and higher testosterone, though more evidence is needed to provide a more comprehensive understanding of this relationship and to determine how these associations occur.

1.3.2 Bond-Maintenance Behaviours/States and Lower Testosterone

Evidence also supports an association between bond-maintenance behaviours and lower testosterone. For example, women with lower testosterone were judged by their peers as more caring and exhibiting more social smiles (Cashdan, 1995), and self-reported a 'more caring' attitude on personality questionnaires (Baucom, Besch, and Callahan, 1985). Similarly, men with lower testosterone exhibited more 'eye crinkling' with smiles (Dabbs, 1997), and reported more marital satisfaction and better father-child relationships (Julian and McKenry, 1989).

Lower testosterone has also been associated with parental behaviour, particularly paternal behaviour and responses (where more research on testosterone and parenting has been conducted relative to testosterone and maternal parenting). Storey, Walsh, Quinton, and Wynne-Edwards (2000) found that men with more symptoms of couvade (sympathetic pregnancy) during the prenatal period of their partners' pregnancy showed a greater decrease in testosterone following exposure to infant cues. Men's testosterone also decreased from the late prenatal period to the early postnatal period (Storey et al., 2000). Men with lower testosterone in the prenatal period held test dolls longer than men with higher levels, and testosterone was inversely associated with responsivity to infant cues (Storey et al., 2000). Fleming, Corter, Stallings, and Steiner (2002) found that fathers and non-fathers with lower baseline levels of testosterone exhibited higher objective (e.g. heart rate) and subjective (e.g. negative affect, sympathy) responses to baby cry stimuli, and suggested that lower testosterone may be reflective of a more nurturant disposition. Wynne-Edwards (2001), in a comprehensive review of hormonal changes in mammalian fathers, suggested that paternal and maternal behaviour are homologous at a neural and endocrine level. She noted that in species with extensive

paternal care, new fathers show decreased testosterone, expectant fathers have lower testosterone than controls, and testosterone levels are lower closely before, around, and closely after birth. Wynne-Edwards suggested the lower testosterone might be functional, in terms of reduced likelihood of aggression towards infants or distraction by courtship and mating, or facilitation of paternal care or social bonding with the infant. For example, antiandrogens increased parental behaviours in male house sparrows (Hegner and Wingfield, 1987). Some research has found that human fathers exhibit lower testosterone than non-fathers (Burnham et al., 2003; Gray, Yang, and Pope, 2006), though some research has not found this difference (Gray, Kahlenberg, Barrett, Lipson, and Ellison 2002; Gray, Campbell, Marlowe, Lipson, and Ellison, 2004a), pointing perhaps no long-term or permanent decrease in testosterone associated with fatherhood, or broad behavioural expectations of fatherhood that may differ between samples. Seemingly paradoxically, some infant cues like crying can increase testosterone in new fathers (Storey et al., 2000), but it is possible that infant cues like crying can be interpreted differently compared to cues like smiles. For example, crying might be interpreted as a problem (or stressful) cue, and not as a bond-maintenance cue, especially by new parents.

As with all the social behaviours described in this dissertation, other hormones have been implicated in parenting and bond-maintenance behaviours and contexts. In contrast to competitive behaviours and contexts, however, other hormones like prolactin have been more widely studied in parenting contexts and more strongly related to parenting than androgens have. Prolactin is generally elevated during paternal behaviours in males from various species, including birds, primates, and rodents (Ziegler, 2000) as well as after birth (e.g. in marmoset males, Schradin and Anzenberger, 2004). Prolactin

appears to have a specific role in the initiation of parental behaviours in many avian species (Storey, Delahunty, McKay, Walsh, and Wilhelm, 2006), and showed increases response to infant stimuli in new human mothers (Delahunty, McKay, Noseworthy, and Storey, 2007). Ziegler (2000) notes that testosterone and prolactin appear to be inversely related, at least in rodents, suggesting a further role for high testosterone in the inhibition of bond-maintenance behaviours – indirectly through prolactin. Other hormones fundamentally involved in parental behaviour include oxytocin, which has been shown to facilitate maternal nurturance in rodents (e.g. Kendrick, Keverne, and Baldwin, 1987; McCarthy, 1990; Pedersen, Ascher, Monroe, and Prange, 1982; see Lim and Young, 2006, for a review).

1.3.3 Testosterone Trade-Offs and Related Schemata

The testosterone trade-off framework differs from the following schemata, which are significant theoretical frameworks. It complements them by hypothesizing how relevant behaviours may be associated with androgens.

1.3.3.1 Parenting vs. Mating Effort, and the Challenge Hypothesis

In the challenge hypothesis (Wingfield et al., 1990), and contrasts between parenting and mating effort, a distinction between behaviours and contexts is based on behavioural targets. Mating effort is thus directed towards competitors; it is oriented towards successfully attracting a mate, which means that the behaviours are directed towards competitors for potential mates, for territory, for nesting resources, and for rank. Parenting effort is directed towards offspring; it is oriented towards successfully hatching

and/or rearing newborns, which means that behaviours are directed towards offspring for feeding, protecting, and nurturance.

Though the testosterone trade-off framework is largely grounded in the challenge hypothesis, a key distinction between the two lies in the issue of directed behaviour. In the testosterone trade-off framework, the key contrast is between competitive and bond-maintenance behaviours/contexts; these are not target-directed and each can occur with partners/mates, competitors, offspring, etc. Bond-maintenance behaviours, for example, could be directed towards various individuals, unlike parenting behaviours. Infant protection is an example of parental effort in the challenge hypothesis because it is offspring-directed (Wingfield et al., 1990). However, in the testosterone trade-off framework, infant defence would be a competitive behaviour because it entails defence of a resource. As such, the testosterone trade-off framework holds that it is not the behavioural target that determines the categorization of the behaviour (as it would in the challenge hypothesis), but the aim and type of behaviour.

Further, in the challenge hypothesis, infant defence is considered a 'low parental effort behaviour' (Wingfield et al., 1990), since infant defense is generally associated with higher testosterone (unlike many other behaviours that are 'high' parental effort behaviours and associated with low testosterone). However, a more parsimonious position might be to divest infant defence of its 'parental behaviour' status and reconceptualise it as a competitive behaviour (as per the testosterone trade-off framework). Oliveira (2004) notes that lower testosterone and parental behaviour (not just infant defence) are not always associated. The testosterone trade-off framework explicitly acknowledges that not all parental behaviours should be associated with

testosterone, and attempts to account for this. Parental behaviours/contexts may be subdivided into bond-maintenance (e.g. caring one-on-one behaviours) and competitive (e.g. competitive food gathering, infant or nest defence involving competitions). Only bond-maintenance parental behaviours/contexts should be associated with lower testosterone. This provides a clearer, more parsimonious, and more conceptually consistent behavioural distinction.

A primary challenge, therefore, is to determine which behaviours/contexts fall into bond-maintenance or competitive categorizations within species (as this may differ by species) in an a priori fashion to predict associations with testosterone. The testosterone trade-off framework represents, in some ways, a subtle distinction from the challenge hypothesis, with considerable overlap between hormone-behaviour relations. But, there is also overt divergence between the two theoretical approaches, because the breakdown of behaviours related to high or low testosterone is conceptually very different via targeting (is the recipient of the behaviour relevant or not?) and 'aim' (is the intended goal relevant or not?). In addition, the testosterone trade-off framework is less situated in seasonal fluctuations and breeding seasons, perhaps rendering it more suited to investigations with humans and others with non-seasonal reproductive patterns. Though humans appear to show seasonal patterns in androgen levels (see Section 1.5.5), there is no consistent evidence of seasonal reproductive patterns, and certainly no strong linkage between seasonality and fertility. The issue of aim (including possible explorations of intent) may also make the testosterone trade-off framework more amenable to human theorizing and experimentation.

1.3.3.2 Hormones and Implicit Motives: Power and Affiliation

Though the challenge hypothesis and life history approaches remain the theoretical frameworks most strongly related to the testosterone trade-off framework, there are additional approaches that should be noted. A small body of research examines associations between hormones and implicit motives, which Schultheiss, Dargel, and Rohde (2003, p. 293) define as "...enduring preferences for affectively charged incentives..." 'Implicit affiliation motivation' refers to a motivation towards close, intimate contact with others, and is hypothesised by Schultheiss and colleagues to be associated with higher progesterone. 'Implicit power motivation' refers to a trait orientation towards dominance, and is hypothesised to be associated with higher testosterone. These implicit motives are generally assessed via coding of Picture Story Exercise (PSE) tasks (e.g. Schultheiss, Wirth, and Stanton, 2004).

The body of evidence is small, and findings are mixed. For example, one study found associations between testosterone and implicit power motivation in men and single, but not partnered, women (Schultheiss et al., 2003). Another study reported a negative association between progesterone and affiliation motivation in men, but null or marginal results in women (Schultheiss et al., 2003). A different study examined endocrine responses to movies selected with the goal of stimulating power and affiliation motives; men and women with increased affiliation (as measured via the PSE task) showed increased progesterone, but no such change was apparent for testosterone (Schultheiss et al., 2004). And, only individuals who showed measurable increases in implicit motives showed increased progesterone; individuals who viewed the affective stimuli but did not show these measurable changes in implicit motives did not show increases in

progesterone. In one other study, Schultheiss and Rohde (2002) found that changes in men's testosterone levels from before to after a competition were correlated with high implicit power motivation, but only in individuals with low activity inhibition (which represented a measure of impulse control).

Power motivation could be conceptualised as similar to a competitive trait, and affiliation motivation to a bond-maintenance trait. However, the implicit motivation framework differs from testosterone trade-offs in that no associations between testosterone and affiliation motivation are hypothesised. In addition, these implicit motivations can only be measured via PSE tasks, and not via behaviours or contexts. Thus, an individual should not show increases in progesterone with a situation primed and expected to increase affiliation motivations unless an individual's level of affiliation motivation changes (e.g. Schultheiss et al., 2004).

The prime difference, of course, between implicit motivations and testosterone trade-offs is that implicit motivations do not theorise about trade-offs. There is no expectation that power motivation and affiliation motivation should necessarily be at odds. That is, there is no continuum along which to conceptualise high versus low testosterone and related behavioural contexts.

1.3.3.3 Appetitive vs. Consummatory Behaviours

Here, the primary contrast is between trying to acquire a resource versus 'having' the resource, or a pre- versus peri-resource state. One key difference between this and the testosterone trade-off framework is that though competitive behaviours can be aimed at acquiring a resource like appetitive behaviours, they can also be aimed at defending a resource or preventing another individual from accessing that resource. Thus, there is no

contrast between pre- and peri-resource states in the testosterone trade-off framework, since competition can occur over resources that individuals would like to acquire or already possess.

1.3.3.4 Mate Acquisition vs. Mate Retention

Similar to the appetitive versus consummatory distinction, mate acquisition versus mate retention contrasts a pre- and post-mate state (see, e.g., Schmitt and Buss, 2001). In contrast, the testosterone trade-off hypothesis contrasts behaviours intended to attract, acquire, and secure a mate (competitive) with those intended to develop social bonds with the mate (bond-maintenance). For example, mate-guarding would be a mate-retention tactic in the above framework but a competitive behaviour in the testosterone trade-off framework because it would be inspired by real or imagined challenges to the legitimacy of the partnership, and not aimed at promoting the affiliative bond itself with the partner.

1.3.4 Testosterone Trade-Offs and Directionality

A pivotal challenge is to discover whether testosterone trade-offs are: (1) state-level effects (i.e. varying within-individuals) such that testosterone rises in a person engaging in competitive behaviours and decreases when they engage in bond-maintenance behaviours; (2) trait-level (i.e. varying between-individuals) such that stably high testosterone and more competitive behaviours are found in some people while stably low testosterone and more bond-maintenance behaviours are linked in other groups; or (3) both trait- and state-level such that, for example, people exhibit both high testosterone and competitive behaviours, but testosterone still decreases with bond-maintenance behaviours. Fortunately, this theoretical orientation yields testable hypotheses; with the

accrual of enough research and data, the state/trait association with testosterone trade-offs should be come clearer, though interesting complexities that take a long time to disentangle are likely.

1.4 Summary of Dissertation Goals

The goals of the dissertation are to (1) establish how partnering affects and/or is affected by testosterone in humans; (2) examine gender/sex similarities and differences in these effects; (3) examine the possible evolutionary significance of these effects. Specific hypotheses being tested are located in each section.

1.5 Testosterone and General Methodological Issues

1.5.1 Sex Steroids and Testosterone

Androgens, estrogens, and progesterone are commonly referred to as 'sex steroids'. In humans, estrogens include estradiol (which is generally found in higher concentrations than other estrogens), estriol (a weaker estrogen: Beyer, Morali, and Vargas, 1971), and estrone (which is higher than other estrogens after menopause: Vermeulen, 1976). Androgens include testosterone (the most common androgen), dehydroepiandrosterone and its sulphate (weaker androgens released from the adrenal gland), androstenedione (an androgen precursor), and dihydrotestosterone (a testosterone metabolite and a potent androgen especially important for genital virilization, among other things) (Becker, Breedlove, Crews, and McCarthy, 2002).

There are sex differences in hormone concentrations, with higher levels of androgens in men, and higher levels of estrogens in women. Still, both classes of hormones are represented in women and men, and play significant roles in the physiology

of both men and women. Androgens are released largely via the HPG axis, but also via the HPA axis in smaller quantities (adrenal androgens are a higher percentage of overall androgen levels in females since the testes release large quantities of androgens relative to the ovaries). Steroids move through blood via sex-hormone binding globulin, and act by binding to nuclear receptors and exerting genomic effects (e.g. affecting transcription), or, as has been more recently been found, through membrane-bound receptors to exert non-genomic effects (Losel et al., 2003) possibly on axons (DonCarlos et al., 2006).

Release of sex steroids from the HPG axis is stimulated by gonadotropin-releasing hormone (GnRH) in the hypothalamus. GnRH then stimulates the anterior pituitary gland to release both luteinizing hormone (LH) and follicle-stimulating hormone (FSH). LH stimulates the Leydig cells of the testes and the thecal cells of the ovaries to release sex steroids. Sex steroids are also produced by conversion in peripheral adipose tissue from precursor hormones. The HPG axis generally functions through negative feedback (i.e. higher sex steroids lead to the downregulation of gonadotropins, leading to the lower gonadal steroid release), but sometimes positive feedback can occur as happens, for example, with the pre-ovulatory surge of estradiol during the menstrual cycle or with increasing levels of progesterone over pregnancy. Additionally, GnRH appears to be influenced by other hormones in both a stimulatory (by kisspeptin) and inhibitory (by gonadotropin inhibitory hormone, GnIH) fashion (for a review, see Kriegsfeld, 2006).

Sex steroids are all derived from a common pathway starting at cholesterol, from the common hormone precursor pregnenolone. Estradiol and dihydrotestosterone are derived from testosterone, which itself can be derived from dehydroepiandrosterone (an

androgen precursor) or progesterone pathways (Chung and Hu, 2002). Testosterone can be 'aromatised' (i.e. converted through the enzyme aromatase) to estradiol, and can be converted to dihydrotestosterone through the enzymatic activity of 5-alpha-reductase; these conversions (testosterone to dihydrotestosterone; testosterone to estradiol) are thought to be unidirectional. Steroids bind to hormone class-specific receptors, i.e. androgen receptors (AR), estrogen receptors (ER), and progesterone receptors. Receptors are present in multiple isoforms intracellularly, e.g. ERα and Erβ, and potentially in a different membrane-bound morph.

1.5.2 Serum and Saliva Measures of Testosterone

Serum measures of testosterone generally result in measures of total testosterone and sometimes free testosterone (which is an estimate based on quantities of total testosterone relative to quantities of sex-hormone binding globulin). Free testosterone is thought to be the bioactive portion of testosterone (and therefore relevant to questions in behavioural neuroscience), as it should represent the unbound portion available to travel throughout the blood to receptors; it may include the weakly-bound (i.e. albumin-bound) portion of testosterone.

Similarly, salivary measures of testosterone are often referred to as bioavailable testosterone, because the portion of testosterone that can be accessed through salivary measures is the unbound or very weakly bound (to, e.g. albumin) fraction that can travel to receptors (and thus potentially exert androgenic effects) (Quissell, 1993). Salivary measures of testosterone have been validated for clinical use (e.g. hypogonadism in men: Morley, Perry, Patrick, Dollbaum, and Kells, 2006; hyperandrogenism in women: Baxendale, Jacobs, and James, 1982) and are widely used in research. Anecdotally, there

appears to be a split in preferences for serum or saliva measures of testosterone, with biomedical researchers favouring blood and behavioural researchers preferring saliva. The preference for saliva among behavioural researchers stems from various methodological considerations that make saliva a choice measure for psychologists, anthropologists, human neuroscientists (etc.), including the ease of collection and storage and shipment, non- (or decreased) implication of biohazard regulations, the low level of invasiveness, compliance by participants (e.g. less fear of needles), and the ability for participants to easily self-collect and store samples. All of these considerations are important for studies of hormone-behaviour relationships; the use of salivary measures has allowed human biologists to address questions that would have been impossible at worst, or extremely difficult at best, to study in the past.

Salivary testosterone measures have shown high internal validity (e.g. Dabbs, 1990b; Granger, Schwartz, Booth and Arentz, 1999) and correlate well with free testosterone in men (Goncharov et al., 2006; Granger, Shirtcliff, Booth, Kivlighan, and Schwartz, 2004; Johnson, Joplin, and Burrin, 1987; Khan-Dawood, Choe, and Dawood, 1984; Shirtcliff, Granger, and Likos, 2002; Walker, Wilson, Read, and Riad-Fahmy, 1980; Wang, Plymate, Nieschlag, and Paulsen, 1981). In women, some studies have reported that free and salivary testosterone levels show good correlations (Khan-Dawood et al., 1984; Granger et al., 2004; Magrini, Chiodoni, Rey, and Felber, 1986; Swinkels, Meulenberg, Ross, and Benraad, 1988). However, there are studies that have found lower (including nonsignificant) correlations between salivary testosterone and free testosterone (Granger et al., 2004; Shirtcliff et al., 2002; Swinkels, Meulenberg, Ross, and Benraad, 1988), though Granger et al. (2004) and Shirtcliff et al. (2002) did find high and

significant correlations between salivary and total testosterone. Granger (2004) and Shirtcliff et al. (2002) report that the use of salivary testosterone measures in tests of hormone-behaviour relationships is likely to lead to an underestimation of effects in women. However, Taieb et al. (2003) reported that there may be problems with *serum* assays of testosterone in women, so low serum-saliva correlations in women may actually represent less accurate serum and more accurate saliva measures. Studies using salivary testosterone have generally shown evidence for hormone-behaviour relationships (the majority of research detailed in the above sections in women was conducted with salivary samples), and generally any potential (though still not well established) costs of salivary samples are outweighed by the many and serious benefits, especially if used with sufficiently large samples of women.

1.5.3 Diurnal Rhythms in Testosterone Secretion

Androgen release shows a diurnal pattern, with higher levels in the morning after waking, decreasing levels throughout the day, and increasing levels during sleep (Boyar et al., 1974; Piro, Fraioli, Sciarra, and Conti, 1973). Though this pattern is diurnal, testosterone release appears to be more closely tied to zeitgebers related to sleep rather than daylight, as testosterone shows increases during daytime sleep (Axelsson, Ingre, Skerstedt, and Holmback, 2005) as it does over night-time sleep. As well, disturbances in sleep patterns can change the pattern of testosterone release over the day and night (Luboshitzky, Zabari, Shen-Orr, Herer, and Lavie, 2001), suggesting that testosterone increases are fundamentally linked to sleep. Still, there does appear to be some non-sleep related circadian rhythmicity, as the specific patterns of testosterone secretion differ between daytime and nighttime sleep (Axelsson et al., 2005). Studies on diurnal

rhythmicity and testosterone have mainly been conducted with men, though women show the same pattern of high morning and low evening testosterone (e.g. Dabbs, 1990b; van Anders and Hampson, 2005). The diurnal pattern of testosterone release appears to be moderated by age, as younger and middle-aged men differ in patterns of release (Luboshitzky, Shen-Orr, and Herer, 2003).

1.5.4 Menstrual Cycles and Testosterone Variation

In additional to diurnal rhythmicity, testosterone shows a pattern of variation over the menstrual cycle. Changes in hormones over the menstrual cycle are fundamental to ovulation; estradiol, progesterone, LH, and FSH show important patterns of fluctuations over the cycle to stimulate development of the uterine lining, follicles, ova release, etc. Testosterone shows a less remarkable pattern of release over the menstrual cycle relative to these other hormones; levels rise gradually until they reach a peak evident at ovulation (Dabbs and de La Rue, 1991), and then decline until onset of menses. Studies attempting to show how menstrual cycle phase may moderate hormone-behaviour associations must estimate or determine phase of cycle (e.g. Bancroft et al., 1983). However, research has shown that unless menstrual phase is a key part of the research design, it need not be explicitly controlled for, as individual differences will cancel out (Dabbs and de La Rue, 1991).

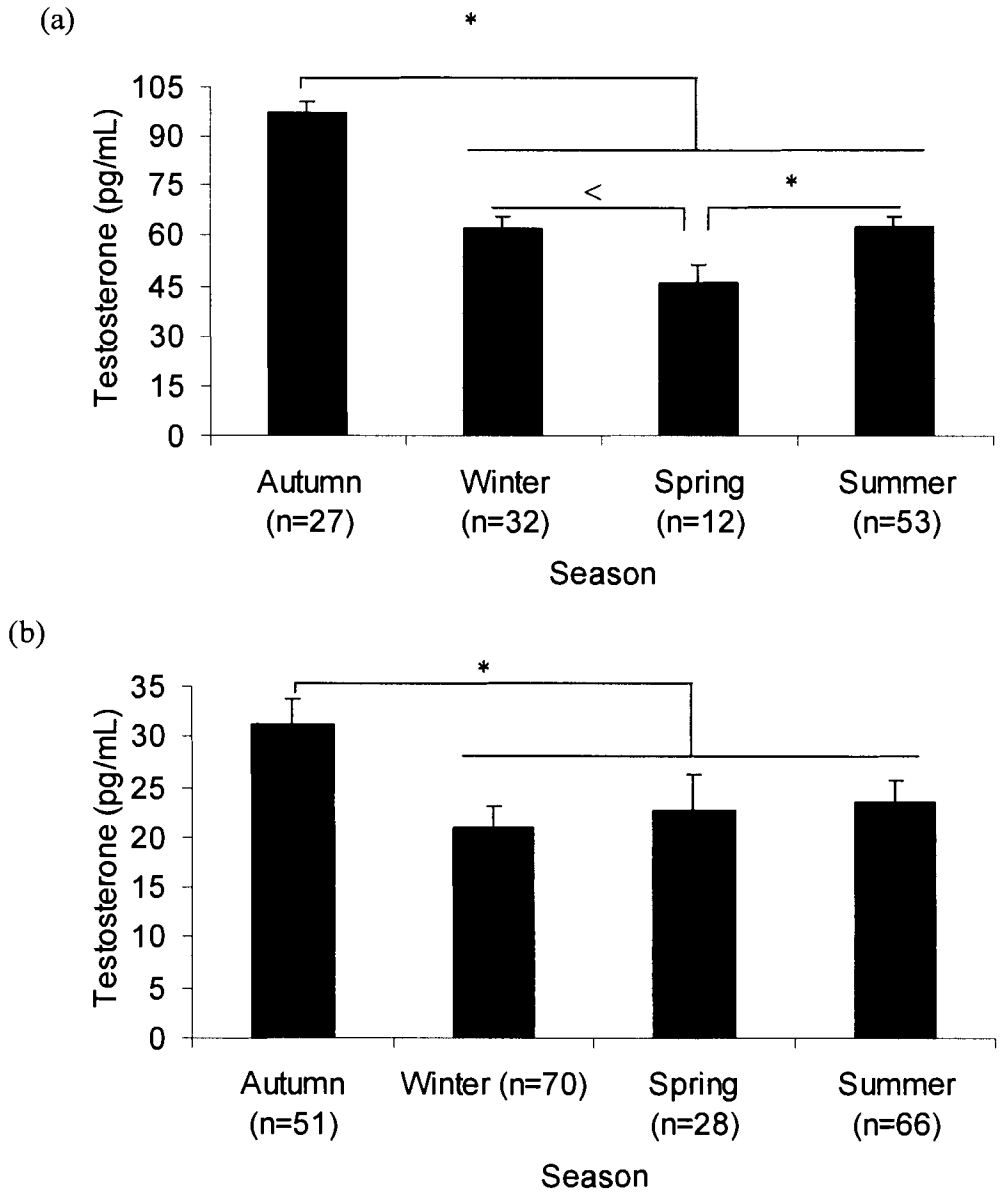
1.5.5 Seasonal Rhythms in Testosterone Secretion

> Note: This section is based in part on the following article, with permission: van Anders, S. M., Hampson, E., & Watson, N. V. (2006). Seasonality, month, and testosterone in a North American sample of women and men. *Psychoneuroendocrinology, 31,* 895 – 899.

In addition to diurnal and menstrual rhythmicity in testosterone, humans show seasonal variation in androgens. Various non-human species show seasonal patterns in testosterone production that are associated with fertility, behaviour, cognition, and morphology (for a review, see Nelson, 2000). Evidence for the nature of the human seasonal variation in testosterone has been less clear than patterns of seasonality in many other species. Higher levels of testosterone have been reported for men in most months and seasons, including May (Valero-Politi and Fuentes-Arderiu, 1998), the autumn months (Dabbs, 1990a; Moffat and Hampson, 2000; Svartberg, Jorde, Sundsfjord, Bonaa, and Barrett-Connor, 2003), and late winter months (Perry, Miller, Patrick, and Morley, 2000). Few studies have investigated women, but peaks have been reported in the fall (Wisniewski and Nelson, 2000) and July-September (Garde, Hansen, Skovgaard, and Christensen, 2000).

Research (van Anders, Hampson, and Watson, 2006) stemming in part from data collected for this dissertation showed that a similar pattern of seasonal testosterone release may be present in both women and men (see Figure 1). These data show that testosterone is highest during the autumn in men as well as women, and that men, but not women, show a decline in testosterone in the spring relative to winter and summer levels. Participants were students as well as community members, limiting the applicability of school year-related explanations. Interestingly, recent research (Muroyama, Shimizu, and Sugiura, 2007) on male Japanese macaques found that testosterone levels were also highest during the autumn, and specifically during the same months (October and November) as people exhibited in van Anders et al. (2006). Previous research also identifies October and November as high testosterone periods for male rhesus monkeys

Figure 1. Mean testosterone with standard error bars by season for (a) men and (b) women.



Note: '*' indicates a significant difference at $\alpha < .05$, and '<' indicates a trend towards a significant difference at $\alpha < .10$.
Source: van Anders, Hampson, and Watson (2006), by permission.

(Gordon, Bernstein, and Rose, 1978), and especially so when the males were housed in living conditions with exposure to females. Controlling for seasonality is generally

important, either through statistical means like inclusion of seasonality as a covariate or through sampling dates.

1.5.6 Exogenous Hormones, Aging, and Testosterone

Endocrine studies with humans must generally attend to the widespread use of medications that alter endogenous endocrine profiles. Large numbers of women use hormonal contraceptives, which alter androgen levels along with estrogens and progesterone. Women using hormonal contraceptives exhibit lower testosterone than women not using hormonal contraceptives (e.g. Bancroft, Sherwin, Alexander, Davidson, and Walker, 1991; van Anders and Watson, 2006c). This association has been shown to be causal, in that hormonal contraceptives can decrease testosterone in women, though not all women show this reduction (Graham, Bancroft, Doll, Greco, and Tanner, 2007). Additionally, the use of various medications including hormone replacement therapies may change circulating concentrations of sex steroids. Thus, human behavioural neuroendocrine research must generally limit usage or avoid inclusion of participants using hormone-altering medications, including hormonal contraceptives.

In Western populations, testosterone shows an age-related decline in both men and women, though more studies have used cross-sectional than longitudinal approaches. In women, ovarian androgen output appears to decrease with increasing age (Bachmann, 2002; Burger, Dudley, Cui, Dennerstein, & Hopper, 2000; Davis, 1999), but there is no specific decrease in testosterone levels or other androgens associated with menopausal transitions. In men, there generally appears to be a similar gradual decline in testosterone, (Ferrini and Barrett-Connor, 1998; Gray, Berlin, McKinlay, and Longcope, 1991; Morley et al., 1997; Nahoul & Roger, 1990; Ellison et al., 2002).

2 INTRODUCTION TO PARTNERING AND HORMONES

2.1 Pair Bonding and Hormones

Lim and Young (2006, p. 506) note that "Relationships among spouses, family, and friends are universally important across all human societies, yet little is known about the neurobiological mechanisms underlying the development and maintenance of such human relationships." In spite of this, or maybe because of the opportunity afforded by such a wide-open area, researchers have begun to examine associations between neurobiology and partnering, pair bonding, and other social attachments. Behavioural neuroendocrine foci have included androgens (further described in Section 2.2) and manipulations in animal models with peptide hormones like oxytocin, vasopressin, and corticosterone (briefly covered in this section).

2.1.1 Animal Models of Pair Bonding

Oxytocin and vasopressin, as well as corticoids, have been implicated in pair bonding, especially using vole models of pair bonding. Closely related species of voles demonstrate markedly different patterns of adult affiliation, allowing for comparisons between species. Prairie and pine voles show monogamous mating styles, and the behaviour and neurobiology of these species can be contrasted with montane and meadow voles, which mate non-monogamously (Young and Wang, 2004).

Administration of oxytocin and vasopressin has been shown to facilitate pair bonding in female and male prairie voles, and administration of oxytocin and vasopressin

receptor blockers has also been shown to inhibit pair bonding (Cho, DeVries, Williams, and Carter, 1999; Williams, Carter, and Insel, 1992; Williams, Insel, Carter, and Harbaugh, 1994; Winslow, Hastings, Carter, Harbaugh, and Insel, 1993; Young, Murphy Young, and Hammock, 2005). In addition, species comparisons have shown that oxytocin and vasopressin receptor density differ between monogamous and non-monogamous species (e.g. Insel and Shapiro, 1994). Meadow voles, who are non-monogamous, exhibit lower receptor density in areas like the nucleus accumbens and ventral pallidum than prairie voles, who are monogamous (reviewed in Lim and Young, 2006). Experimental increases in vasopressin receptor density in these areas facilitated partner preference in meadow voles, who usually do not show evidence of partner preference (Lim, Wang, et al., 2004).

The HPA axis has also been implicated in pair bonding using the monogamous/non-monogamous vole model (e.g. DeVries, Guptaa, Cardillo, Cho, and Carter, 2002). Studies have found that male prairie voles showed enhanced pair bond formation following corticosterone treatment (DeVries, DeVries, Taymans, and Carter, 1996; DeVries et al., 2002), and impaired or eliminated partner preference following corticosterone receptor blocker administration (DeVries et al., 2002). In addition, and similarly to oxytocin and vasopressin receptors, the distribution and density of corticosterone receptors differs by vole species depending on mating type, with lower density in the nucleus accumbens of monogamous species (Lim, Nair, and Young, 2005; Lim, Tsivkovskaia, Bai, Young, and Ryabinin, 2006). Lim, Liu, Ryabinin, Bai, Wang, and Young (in press) found that administration of corticotropin-releasing hormone

facilitated partner preference in prairie but not meadow voles, when injected into the nucleus accumbens.

Thus, research supports a role for oxytocin, vasopressin, and the HPA axis in pair bond formation and development in voles.

2.1.2 Pair Bonding and Neurobiology in Humans

A very small body of research has examined how neurobiology and pair bonding might be associated in humans. These studies have generally examined neural responses to 'love stimuli', like images of a person with whom another person is in love ('beloveds') relative to acquaintances.

A study of neural activation measured via fMRI in men and women newly in love (averaging about 7 months) showed increased neural activation in response to images of beloveds in areas like the ventral tegmental area, caudate nucleus, and putamen (Aron et al., 2005), which have been implicated in reward pathways (e.g. Martin-Soelch et al., 2001; Schultz, 2006). Studies of women and men in late stage and less intense love showed activation in the same areas (Bartels and Zeki, 2000; 2004). One study of women and men in states of unrequited love showed activation in the same areas (Fisher, Aron, and Brown, 2005), though one other study of women showed no such effects (Najib, Lorberbaum, Kose, Bohning, and George, 2004). Fisher, Aron, and Brown (2006) stated that the areas showing activation in response to love stimuli overlap (e.g. ventral pallidum) with neural structures in prairie voles shown to be high in oxytocin and/or vasopressin receptor density and related to pair bonding (Fisher, Aron, and Brown, 2006).

2.2 Partnering and Testosterone in Humans

Note: This section is based in part on the following article, with permission: van Anders, S. M. & Watson, N. V. (2006b). Social neuroendocrinology: Effects of social contexts and behaviors on sex steroids in humans. *Human Nature, 17,* 212-237.

Previous endocrine research on long-term committed partnering in humans has mainly focused on androgens, probably because of the inability to measure peptide hormones from saliva. Studies have also focused exclusively on men, probably stemming from theoretical considerations. For example, Mazur and Booth (1998), in a widely cited review article, linked testosterone with status (i.e. one's place in a social hierarchy), as opposed to aggression or other variables widely thought to be associated with testosterone but little supported by empirical evidence. The authors' conclusion was that this link between testosterone and status did exist in men but not women, notably on the basis of a very few studies showing null effects with women. In commentary, other authors critiqued this conclusion as a premature assessment of an understudied phenomenon. Other theoretical considerations have also entailed focusing largely on males, including the Challenge Hypothesis with its focus on androgens and male mating effort (Wingfield et al., 1990). Interestingly, researchers have begun to include females and make theoretical cases for the inclusion of females (e.g. Moore, in press), and the original authors (Wingfield et al., 1990) stated that there may be reason to include females in studies relating to the Challenge Hypothesis.

Endocrine perspectives on partnering have generally contrasted single with partnered individuals, sometimes attending to accompanying contextual variables (e.g. parenthood status). Other lines of research have examined how testosterone may be associated with courtship and early stage love as well as measures of marital quality, and marital dissolution, which are examined in this next section.

2.2.1 Courtship, Early-Stage Love, and Androgens

Two studies have investigated how the early stages of relationships might be associated with androgens. One focus has been on the intense period of early stage love, and how it might be associated with androgens. The other focus has been on how possible flirtations or even conversations might be associated with androgens, which could be considered the initial stages of relationship formation.

In a study examining the effects of brief conversations with women on men's testosterone, Roney, Mahler, and Maestripieri (2003) found that men's testosterone was higher following brief conversations with women, but not other men. This increase in testosterone appeared to occur mainly in men with prior sexual experience, suggesting either an effect of sexual experience on subsequent physiological responses or a trait association whereby men who have testosterone increases in response to women are also more likely to engage in sexual activity. Additionally, the change in men's testosterone was correlated with their display or 'show-off' behaviours during the conversations.

The experience of falling in love is also associated with androgens as well as other hormones. Marazziti and Canale (2004) examined men and women who had recently fallen in love compared to controls who were either in no relationship or in a longer relationship. Though the authors found no differences between people who had

recently fallen in love and controls in some hormones (i.e. LH, estradiol, progesterone, dehydroepiandrosterone, androstenedione), other hormones did show differences. Specifically, men who had recently fallen in love had lower testosterone, lower FSH, and higher cortisol than controls. Women who had recently fallen in love had higher cortisol and higher testosterone than controls. Marazziti and Canale followed their participants, and at 12-18 months after falling in love, the participants from the 'in love' group who were still in relationships showed similar endocrine parameters to controls. The authors suggested that the initially altered endocrine states of the experimental group had returned to normative levels. Early-stage love may thus be associated with lower HPG axis activity and higher cortisol in men, and high testosterone and cortisol for women. The elevated cortisol might be reflective of the stress inherent to the intensity of early love, as stress has been implicated in pair bonding (described above in Section 2.1.1.; also see Carter et al., 1995). One problem with interpreting the testosterone findings is the constitution of the control group, which included both single and partnered individuals. As discussed in the following sections, testosterone levels differ between people who are single or partnered. It is therefore unclear whether gender differences in relative testosterone levels and early stage love are truly gender differences, or reflect different make-up of each control group (since the ratio of singles to partnereds is not reported).

Preliminary evidence thus supports associations between androgens and early stage love, as well as flirtation or courtship. There are also studies that have examined marriage or longer relationships, and how testosterone might be associated with these.

This next section focuses on the associations between hormones and long-term marital-like relationships, and factors that may contribute to relationship longevity and success.

2.2.2 Hormones, 'Marital Quality', and Divorce.

Evidence suggests that higher testosterone may be associated with less successful long-term relationships, as would be expected if higher testosterone is negatively associated with bond-maintenance behaviours. For example, divorce appears to be associated with higher testosterone: using a large sample of about 4,000 male Vietnam army veterans, Booth and Dabbs (1993) found that higher testosterone was associated with increased incidence of divorce. With a similar large sample of about 2,100 male air force veterans, Mazur and Michalek (1998) conducted a longitudinal study and found that men who remained wed had consistently lower testosterone than men who remained single or men who had divorced at some point. Higher testosterone appeared to be associated with an increased likelihood of future divorce, and testosterone was transiently elevated around divorce.

Why should higher testosterone be associated with divorce? Some authors (Booth and Dabbs, 1993; Mazur and Michalek, 1998) have suggested that higher testosterone may be associated with qualities that undermine successful committed long-term relationships (described below). As would be expected from the testosterone trade-off framework where lower testosterone should be associated with bond-maintenance behaviours, higher testosterone appears to be negatively associated with some traits and behaviours that could contribute to marital quality in Western cultures. For example, Julian and McKenry (1989) found that higher testosterone was negatively associated with marital happiness and father-child relationships in middle-aged men. Booth and Dabbs

(1993) found that variables like extra-marital sex and physical abuse within a marriage were positively associated with testosterone, while quality of marital interaction was negatively associated with testosterone. This association was not linear, however; men with low testosterone reported the highest marital quality, and men with high testosterone reported lower marital quality, but men with mid-range levels of testosterone reported the lowest marital quality. The implications of this nonlinearity have not been followed up, are not well understood, and have not placed in a theoretical framework. Additional evidence links past physical and verbal abuse with higher testosterone in a sample of men at high risk for HIV/AIDS who were recruited from social services organizations (Soler, Vinayak, and Quadagno, 2000). Tellingly, high testosterone is correlated with lower prevalence of empathetic behaviours, but also causally linked: one study has found that administrations of testosterone led to reductions in empathetic behaviours (Hermans, Putnam, and van Honk 2006). Since empathetic behaviours are an important contributor to marital satisfaction (Waldinger et al., 2004), it may be that it is variations in empathy that mediate a link between high testosterone and lower marital success.

Some evidence thus appears to support an association between higher testosterone and behaviours or traits that contribute to less successful long-term relationships. As lower marital quality is associated with higher testosterone, the link between divorce and high testosterone appears to be mediated by lower marital quality. However, how testosterone may directly contribute to lower marital quality (e.g. via empathy; extra-marital sex, etc.), and how this may be associated with cultural and contextual variables is not clear at present.

Some research has examined married couples as a context for associations between testosterone and marital quality, including both spouses as part of a dynamic system. This moves beyond the (possibly unstated) assumption that there is an influence of one person's testosterone on partnering, regardless of the other person's testosterone levels or the concordance between the two partners. Cohan, Booth, and Granger (2003), in a complex series of analyses examining 92 newlywed couples, examined how marital quality and testosterone were associated, when testosterone levels of wives and husbands were considered as well as the match between couples' testosterone levels. This approach has proven enlightening, though findings are far from clear. Cohan et al. (2003) found that wives with higher testosterone relative to other wives had less positive conversations with their husbands when these conversations were initiated by wives. They also found that husbands were more negative, less positive, and provided less social support when they had lower testosterone relative to other husbands than their wives testosterone levels relative to other wives. Thus, the authors suggest that concordance between couples' testosterone levels may be associated with more positive relations, and husbands may behave more negatively when their wives have higher testosterone relative to other wives. These results are complex and beg further study, since a man or woman's testosterone levels relative to other same-sex individuals, *and* relative to their spouse's relative testosterone levels, were important to consider. Thus, this approach recognises the importance of examining the interactions between partners, their testosterone, and their testosterone relative to others, to contextualise any findings or theorizing about the associations between testosterone and relationships. One other study has found that

spouses' testosterone levels were positively correlated, though this study included only spouses who had children (Hong et al., 2001).

So, higher testosterone can be associated with lower marital quality, but this depends on gender, concordance between partners, and also on the target individual (e.g. hormone levels in a partner can affect an individual's behaviours). Interestingly, men's testosterone has been shown to correlate with their female partners' monthly endocrine patterns, but only in men who wanted to have children with their partners (Hirschenhauser et al., 2002), further suggesting that similarities between partners' testosterone are likely to be reflective of context. Thus, higher testosterone appears to be associated with lower marital satisfaction and success, likely mediated through intervening variables and contextual factors. Androgens have also been associated with partnering and relationships in another way. A small but growing body of research concerns how partner status itself might be associated with androgens, and this literature is reviewed in the following section.

2.2.3 Partner Status and Androgens

Some research has examined marital interactions and quality, and other studies have focused on how relationship status might be associated with androgens in humans. Previous studies have compared mostly single and partnered heterosexual men both in North America and in international contexts. Researchers have begun attending to how cultural contexts may affect how partnering is associated with testosterone, and examining how and why partnering and testosterone may be associated.

The earliest studies in this line of research were conducted under the aegis of determining if testosterone was negatively associated with marital quality (as per above), and so authors were interested both in relationship status and indicators of marital quality, whether divorce or other measures. In the first cross-sectional study, Booth and Dabbs (1993) found that men who were unwed had higher testosterone than married men, using a large sample of army veterans. Following this, Mazur and Michalek's (1998) longitudinal study with another large sample of air force veterans found that men who were consistently wed had lower testosterone than men who were consistently single or who had divorced at some point.

More recent research has provided additional data on testosterone and partnering, focusing more on ecological context and questions than earlier research with its focus on testosterone and maladaptive psychological traits. This is, in part, likely due to differing perspectives and backgrounds of the cohorts of researchers. Recently published research has thus shown that North American single men have higher testosterone than married men (Gray et al., 2002; Gray et al., 2004a) or men who are in committed romantic relationships but not married (Burnham et al., 2003; Gray et al., 2004b). Gray and colleagues point out that these findings of higher testosterone in single men and lower testosterone in partnered men are consistent with theoretical predictions grounded in male mating effort that testosterone should be lower in individuals who do not need to compete for partners, i.e. those who engage in lower levels of male-male competition for female mates.

The majority of this research has been conducted with North American populations (who are, of course, internally diverse in terms of culture and ethnicity), but

studies have also included international populations. This has been extremely important in furthering our understanding of testosterone-partnering associations, because researchers can utilise these findings to identify some of the ecological contexts that might predicate these associations. This international research highlights that cultural considerations must be taken into account when examining testosterone-partnering associations, and this can help inform us of what aspects of being partnered are associated with lower testosterone.

For example, Gray et al. (2006), in research undertaken in Beijing with Chinese participants, found that parental as opposed to partner status appears to be more strongly related to testosterone. As such, they found that married fathers exhibited lower testosterone than single men or married non-fathers. In a study undertaken in Japan, Sakaguchi, Oki, Honma, and Hasegawa (2006) found that though testosterone tended to be lower in paired men compared to unpaired men, this association only reached the levels of a statistical trend and not significance, suggesting a possibly weaker overall association. These findings point to the need for contextualised considerations of pair bonding. Gray et al. (2006) suggest that fathers in Beijing may be more committed to their relationships or families, while single men and married non-fathers may similarly be interested in finding new partners. In support of this interpretation, Gray et al. (2006) report that married men in the Beijing China sample engaged in high levels of extra-pair sexual encounters relative to North American married men. Generally, understanding local conceptualisations of pairing, partnering, and marriage, and their accompanying expectations and normative behaviours and cognitions, is likely to be crucial in understanding when and why partnering and testosterone are associated in both North

American and international locales. If partnering is conceived as a way to have children, but not a way to limit one's sexual or romantic encounters, than being in a long-term relationship may not be associated with lower testosterone, and future research should be able to clarify this. Researchers note that marriage in China has been historically oriented to some extent toward the purposes of having children, as opposed to romantic connection, though this pattern has been changing to standards of companionate marriage (Pimental, 2000). It may also be that the lower testosterone in fathers relative to single men and married non-fathers reflects only heightened stress or less sleep in the fathers, and is not associated with commitment at all. Pimental (2000) reports that Chinese fathers actually perceived lower marital quality than married non-fathers, suggesting that higher marital commitment in the fathers might not be a factor in their lower testosterone.

In additional international research, the study of cultures that include the option of polygynous marriage has provided the opportunity to examine questions related to testosterone trade-offs. The possibility of additional marital partners might be associated with higher testosterone, because finding new partners would entail competitive behaviours or mindsets. Or, having multiple partners might be associated with lower testosterone, because an individual might be engaging in more overall bond-maintenance behaviours. This likely depends on whether the polygyny of a culture entails multiple sexual contacts and/or bond-maintenance contacts between one individual and others.

Gray (2003) examined polygynously married men, monogamous men, and single men in a group of Kenyan Swahili men where polygynous marriage is one marital option. He found that polygynously married men had higher testosterone than the other men, but that monogamously married men did not have lower testosterone than the single men (as

had been found in the North American populations). Gray (2003) noted that the characteristics of these men differ markedly from the Harvard-based men in earlier studies (of partnering and testosterone in North American contexts) for many reasons including the possibility of obtaining multiple wives for the Kenyan men. As well, many of the 'single' Kenyan men had been married previously and/or were fathers, whereas the single Harvard men had no children and had never been married. Obviously, one additional factor relates to socioeconomic status (SES), with Harvard men likely representing a very selected group. Additionally, SES is likely to be a factor in studies of polygyny in international populations, because many proscriptions for multiple marriages include adequate resources for supporting multiple wives.

Though not examined by Gray (2003), it may be that men who have multiple wives represent a subset of married men who are more inclined to look for more wives or attract their attention (i.e. more involved in competitive than bond-maintenance activities). It is also possible that Kenyan men with one wife differ from those with multiple wives in terms of desire or willingness to compete for more wives or women's attention. This fits the testosterone trade-off framework, where the possibility of additional wives or partners in polygynous approaches to marriage should be associated with higher testosterone. It may also be that societies with polygynous marriage have a conceptualisation of marriage such that men are not engaging in many bond-maintenance behaviours with their wives or offspring; this remains to be seen.

International contexts are thus enlightening, and it should not be surprising that attending to diversity in North America might be similarly so (van Anders, under review). In North America, partnering is not limited to monogamous couples or even two

individuals. 'Cheating' occurs when an individual seeks extra-partner sexual/romantic encounters in the context of a relationship with another person who assumes fidelity, and research has found that individuals who report more extra-pair sexual encounters have higher testosterone (Booth and Dabbs, 1993) as is found in other species through paternity testing (Garamszegi, Eens, Hurtrez-Boussès, and Møller, 2005). In North America, polygamy is practiced generally within religious strictures and mainly consists of multiple marriages between one man and multiple women. Swinging is another approach to relationships that could provide insights into testosterone trade-offs and partnering-testosterone associations. It generally consists of a committed pair who encourage or allow each other the opportunity to seek extra-pair sexual relationships. No research has examined testosterone and partnering in either of these contexts, but these paradigms would be likely to provide important insights.

Interestingly, some research (for reviews, see van Anders and Watson, 2006b; van Anders and Gray, under review) points to perhaps even lower testosterone in married fathers than in married non-fathers (Burnham et al., 2003; Gray et al., 2006). However, null findings have also been published (Gray et al., 2002; Gray et al., 2004a) suggesting that fatherhood and testosterone, if associated, may only weakly be so. Men show transient decreases in testosterone around birth of their offspring (Storey et al., 2000) like many other paternally investing species (Wynne-Edwards, 2001), and it may be possible that sampling fathers sometimes includes men with this transient decrease (leading to interpretations of overall lower testosterone). Gray and colleagues generally interpret the decreased testosterone in fathers as a possible state effect writ large, i.e. fatherhood decreases testosterone in a long-term way. It remains possible, however, that fathers

represent those men who are more likely to engage in bond-maintenance behaviours or who are already more bond-maintenance-oriented and have lower testosterone. Lower testosterone in men has been shown to be associated with higher physiological and behavioural responses to baby cues, suggesting that men with lower testosterone may be more nurturant or prepared for the father role (Fleming et al., 2002). It seems possible that men who marry and have children represent a group of men more committed to relationships and parenting than men who marry and do not have children. Thus, it is entirely possible that the lower testosterone found in married fathers compared to married non-fathers is not an effect of fatherhood on testosterone, but an effect of testosterone on the likelihood of fathering. No research has pointed specifically to state or trait associations, and either or both remain possible.

2.2.4 The State/Trait Issue: Relationship Status or Orientation

Originally, researchers like Booth and Dabbs (1993) and Mazur and Michalek (1998) interpreted their findings of higher testosterone and remaining unwed (etc.) as evidence for effects of testosterone on relationships. Specifically, they viewed higher testosterone as negatively contributing to relationship success or the likelihood of developing long-term relationships. More recently, Gray and colleagues have interpreted their data as evidence for effects of relationships on testosterone (and fathering on testosterone). In an earlier interpretation of past research, theoretical reasons prompted the consideration of the possibility of effects of relationships on testosterone (van Anders and Watson, 2006b), though acknowledgements were made that evidence was weak in support of either direction. This issue of testosterone being associated with relationship

status versus orientation is important, however, in determining future directions, possible mechanisms, and interpretations.

Analyses of this literature and the partnering-testosterone literature suggest that there are at least three possibilities for conceptualising the directionality of partnering-testosterone associations. I will refer to the first of these as 'relationship status'. A relationship status association with testosterone is a state association, such that entering bond-maintenance-type relationships leads to lower testosterone. This may occur upon entering the relationship, or after a latency associated with increased bond-maintenance behaviours/contexts. The second of these possibilities can be termed 'relationship orientation'. A relationship orientation association with testosterone is a trait association, such that lower testosterone levels predispose individuals to enter bond-maintenance-type relationships. This could mean that higher testosterone is associated with a competitive relationship orientation, and that lower testosterone is associated with a bond-maintenance relationship orientation. The third possibility is that there is an interaction effect, such that, e.g., lower testosterone predicts entering bond-maintenance-type relationships and entering these relationships further decreases testosterone. Thus, the debate need not be constructed as dichotomous with mutually exclusive alternatives, as both relationship status and relationship orientation interpretations could receive empirical support.

An association between relationship orientation and testosterone should not be interpreted as stemming from 'innate' causal mechanisms without relevant evidence, though. For example, it could be that stable and characteristic ways of behaving in the world lead to stable and characteristic levels of testosterone, and that levels of

testosterone therefore "predict" stable and characteristic ways of future behaviour. Thus, influences on trait testosterone may be behavioural, as trait testosterone has an associated developmental trajectory.

In support of a relationship orientation interpretation, Booth and Dabbs (1993) have found that men with higher testosterone were less likely to be married and more likely to have divorced than lower testosterone men. Additionally, Gray et al. (2004a) have found that evening testosterone did not differ in men between days spent at work and days spent with their wives (as might be expected if state behaviours related to partnering decreased testosterone). As well, Mazur and Michalek (1998) reported that testosterone was lower in stably married men compared to stably unmarried men. They also suggested that divorce was associated with increased testosterone as their evidence showed transient effects of divorce on testosterone, implicating state effects of divorce on testosterone. However, after a duration, divorced men's testosterone declined to pre-divorce (and married) levels, suggesting that the change to singlehood was not associated with a change to lower testosterone levels, but that instead divorce was associated with higher testosterone. In other words, changes in relationship status, per se, were not associated with changes in testosterone; otherwise, testosterone would have remained elevated during singlehood relative to pre-divorce marital levels. Interestingly, though, the testosterone levels of men who divorced or had been divorced were still higher than consistently married men's testosterone. And, they noted that testosterone levels in unwed men were not much different from those of men who changed marital status. Thus, men who were more likely to be single (at some point) exhibited higher testosterone. Similarly, early stage love was associated with changes in androgens, but

this change appeared to be transient (Marazziti and Canale, 2004). Still, there are reasons to expect factors related to partnering to affect testosterone levels, since many social behaviours can affect testosterone in humans (for reviews, see Archer, 2006; van Anders and Watson, 2006b) and other species (e.g. birds, Wingfield et al., 1990). As noted, divorce appears to elevate testosterone in men (Mazur and Michalek, 1998), as do brief conversations and/or flirtations with women (Roney et al., 2003). Early stage love appears to be related to increased testosterone in women and decreased testosterone in men (Marazziti and Canale, 2004).

In the following sections, three studies are detailed that closely examine associations between partnering and testosterone. This includes the use of cross-sectional and longitudinal approaches, and the inclusion of broader populations and diverse relationship types. In the last section of this dissertation, conclusions and implications of this research for our understanding of partnering and hormones are discussed, with attention to how the research detailed within this dissertation have contributed to the literature on partnering and testosterone.

3 STUDY 1: PARTNERING AND TESTOSTERONE IN HETEROSEXUAL AND NON-HETEROSEXUAL WOMEN AND MEN

Note: This section is based on the following article, with permission: van Anders, S. M. & Watson, N. V. (2006a). Relationship status and testosterone in North American men and women of diverse orientations: Cross-sectional and longitudinal data. *Psychoneuroendocrinology, 31*, 715-723.

3.1 Introduction to Study 1

As noted above, previous research has established that North American heterosexual partnered men exhibit lower testosterone than heterosexual single men (Booth and Dabbs, 1993; Mazur and Michalek, 1998; Burnham et al., 2003; Gray et al., 2002; Gray et al., 2004a; Gray et al., 2004b). This association has generally been interpreted as causal, first as an effect of testosterone on relationships, and more recently such that entering relationships decreases testosterone. However, little research has examined the issue of directionality empirically.

Time of day at which testing occurs appears to be an important variable: where associations between testosterone and partnering are found, they occur more frequently in studies with afternoon and evening hormone sampling rather than morning sampling. Testosterone does show a diurnal rhythm with a decrease during waking hours (Axelsson et al., 2005), so it is plausible that behavioural or cognitive factors over the course of the day could affect the rate of decline in testosterone. However, one study examining effects of days spent with wives and children (e.g. bond-maintenance days) versus days spent

with work partners resulted in no difference in evening testosterone levels (Gray et al., 2004a). Thus, evidence is not necessarily consistent with a relationship status interpretation, and the question of directionality is open.

One notable limitation of previous studies is that they have sampled only heterosexual men. There is no reason to suppose that the association between partnered status and testosterone levels is limited to a particular sex or sexual orientation, and a broader sample would permit a more comprehensive understanding of the population pattern and might point to possible mechanisms (e.g. physiological cues from partners, psychological states, etc.). For example, if all partnered individuals, regardless of sex or sexual orientation, exhibit lower testosterone than unpartnered individuals, that might suggest that the effect is mediated by partnered status alone and is unrelated to individual or partner sex.

Another impediment to generating hypotheses about causality or mechanisms is the cross-sectional nature of previous research. Although Mazur and Michalek (1998) reported longitudinal data, they unfortunately lacked men who were single and then wed. The study described in this section was designed to attempt to address these limitations, by incorporating a longitudinal subsample. Further, the testosterone trade-off framework (competitive versus bond-maintenance behaviours) posits that it is not being single per se that is associated with higher testosterone, but partner-seeking competitive behaviours or orientations. Competitive behaviours or orientations should characterise single people, of course, but also people in non-committed, non-monogamous, polyamorous (multiple or simultaneous loving relationships), or 'open' relationships. Previous research has supported this notion: polygynous married men exhibited higher testosterone than

monogamous married men (Gray, 2003). Therefore, partnered people were contrasted with non-partnered (i.e. not-monogamously partnered and single) individuals, instead of with people who were single only.

3.2 Goals and Hypothesis

Goals included the following. (1) To assess the testosterone-partnering association in a broader segment of the population, as previous research included only heterosexual men. (2) To use a longitudinal approach to address directionality and see if changes in partnered status result in changes in testosterone. (3) To examine associations between partnering and testosterone using the testosterone trade-off framework as a source for hypothesis generation.

I hypothesised that unpartnered individuals would exhibit higher testosterone than partnered individuals, perhaps independent of sex or sexual orientation.

3.3 Methods

3.3.1 Participants

Participants were recruited in three ways: (1) From the SFU psychology undergraduate participant pool, where they were prescreened for exogenous hormone use; (2) from the university community through posters; (3) from the Vancouver Pride Parade and the university community on-site at testing stations. Participants from the psychology pool received course credit for participation, and the others received small payments for participation.

Of the 293 participants initially involved in the study, 33 participants were excluded due to use of exogenous hormones (e.g. hormonal contraceptives, hormonal

treatments, drugs that affect endocrine systems), and two were excluded due to pregnancy, leaving 258 participants (127 male; 131 female) in the sample. Participants completed questions regarding sexual experience and fantasy on sexual orientation (Kinsey Pomeroy, and Martin, 1948). Based on these responses, participants were dichotomised such that those scoring two or higher on either of the scales were categorised as non-heterosexual (Non-Het) (n = 106), while those scoring one or lower were categorised as Het (n = 151), and one person did not respond. This categorization (Het and Non-Het) was used based on previous usage (e.g. van Anders and Hampson, 2005) and theoretical considerations regarding group composition. These include the relatively small numbers of exclusively same-sex oriented individuals in the population (and the sample), as well as difficulties with cell sample sizes if various groupings are used (e.g. heterosexual, bisexual, gay/lesbian). Also, because there are social constraints on individuals indicating any degree of same-sex sexual fantasy, desire, or behaviour, categorizing all individuals who report at least moderate levels of same-sex sexuality together may provide for a more meaningful grouping of individuals if sexual orientation has biological influences, as some evidence suggests. There were 55 Non-Het women (mean age = 28.20 yrs), 75 Het women (mean age = 23.84 yrs), 51 Non-Het men (mean age = 34.25), and 76 Het men (mean age = 24.80 yrs). In terms of education, the majority of participants had one year of undergraduate education (n = 112), followed by college/university graduates (n = 57), high school graduates (n = 45), advanced degree holders (n = 27), one year of advanced degree (n = 14), some high school (n = 2), and grade 7-9 (n = 1). It is possible that, since the sample is biased towards those with more extensive education, education levels may restrict the generalizability of the results.

Participants indicated whether they were single, dating, in a long-term monogamous relationship but not living with their partner (paired), in a long-term monogamous committed relationship and living with their partner (established paired: married, common-law, cohabiting), in a non-monogamous relationship, and/or divorced/widowed. A dichotomy was then imposed such that paired and established paired individuals were classified as partnered, while those who were single, dating, or in non-monogamous relationships were classified as unpartnered.

3.3.2 Materials and Procedure

All participants were tested between 1300 and 1800 hours to control for diurnal rhythms in testosterone. At each session, participants provided a saliva sample and completed a brief questionnaire concerning their demographics and relationship status. Information about menstrual cycle was collected, but was not controlled for; previous research has shown that cycle effects are small (though consistent) and do not need to be controlled unless cycle is a variable of interest (Dabbs and de La Rue, 1991).

The first 100 participants were subsequently contacted monthly by email in order to track their relationship status. Participants were contacted about follow-up sessions at least six months after their baseline testing (and longer for participants tested earlier). Of the 100, the final longitudinal sample consisted of 48 participants, after six participants were excluded for exogenous hormone use. Participants were not retested for the following reasons: a few requested an end to emails during the monthly contacts; some email addresses were no longer viable; some did not respond; some were away from the city during follow-up testing; some had scheduling conflicts. Follow-up testing involved the same procedures as baseline testing.

Saliva samples were collected in polystyrene tubes that had been pretreated with sodium azide, and frozen after collection at -20°C until assay. Saliva was stimulated with the use of an inert gum (sugar-free cherry Trident). The samples were assayed for testosterone using radioimmunoassay in three batches at the Endocrine Core Lab at Yerkes National Primate Research Center, Emory University, all in duplicate, using a modified kit from Diagnostic Systems Laboratories (Webster, TX). The sensitivity was 2-500 pg/mL per 200 μL dose, and the interassay coefficient of variation was 8.77% at .65 ng/mL and 6.88% at 5.06 ng/mL. The intra-assay coefficient of variation was 6.54% at 98.82 pg/mL.

Analyses were conducted with the Statistical Package for the Social Sciences (SPSS), v. 13.0. Three participants did not provide saliva samples, one male participant had testosterone levels that were so high (2073.27 pg/mL) that they must have reflected unreported exogenous hormone usage or blood contamination or error, and one male had testosterone that was three standard deviations over the mean; all were excluded from the analyses. Main effects were evaluated using the LSD (Least Significant Difference) test after significant omnibus analyses.

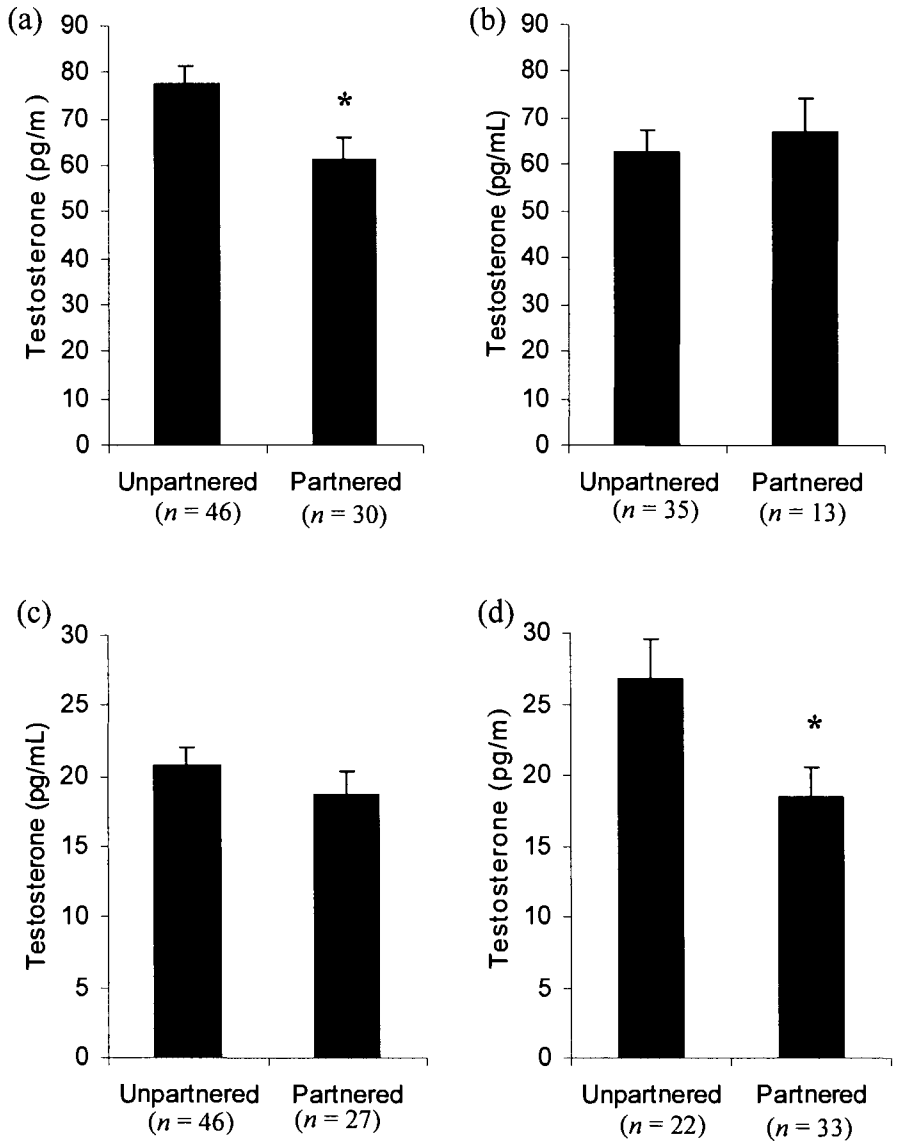
3.4 Results

3.4.1 Cross-Sectional Analyses (Baseline)

An omnibus analysis of covariance (ANCOVA) was conducted to control for error rate inflation due to multiple comparisons; this holds the family-wise error rate constant over derivative comparisons. Sex, sexual orientation, and partnered status were entered as independent variables, age and month as covariates, and baseline testosterone

as the dependent variable. There was a significant three-way interaction, $F(1,242) = 4.31$, $p = .039$. Age was included as a covariate only when it accounted for a significant proportion of the variance.

Figure 2. Mean baseline testosterone with standard error bars of in partnered and unpartnered individuals, by gender/sex and sexual orientation.



Note: (a) heterosexual men; (b) non-heterosexual men; (c) heterosexual women; (d) non-heterosexual women. '*' indicates a significant difference at $p < .05$.
Source: van Anders and Watson (2006a), by permission.

The pattern of results is as follows: (1) Het unpartnered men had significantly higher testosterone than Het partnered men, $F(1,73) = 6.48$, $p = .013$. (2) Testosterone in Non-Het men did not differ significantly by partnered status, $F(1,45) = .21$, $p = .652$. (3) Testosterone in Het women did not differ significantly by partnered status, $F(1,70) = .88$, $p = .351$ (4) Non-Het unpartnered women had significantly higher testosterone than Non-Het partnered women, $F(1,52) = 5.54$, $p = .022$. Please see Figure 2 for means and standard errors. Thus, partnered individuals had lower baseline testosterone than unpartnered individuals, but only if they were Het men and Non-Het women.

Participants were already coded as being in one of five relationship statuses (single, dating, paired, established paired, polyamorous), so how these were associated with testosterone could be examined. To do this, baseline testosterone was correlated with relationship status in terms of implicit commitment (single < dating < paired < established paired), excluding polyamory because it did not fit conceptually in this ladder. Increasing implicit commitment was significantly correlated with testosterone, $r(241) = -.14$, $p = .036$. With the effects of month and age partialled out, the correlation was slightly stronger, *partial* $r(236) = -.19$, $p = .003$. Thus, higher levels of implicit commitment were associated with lower testosterone.

An ANCOVA was then conducted with age and month entered as covariates when significant, relationship status (five categories), sex, and sexual orientation as the independent variables, and baseline testosterone as the dependent variable. There was a significant overall three-way interaction, $F(4,229) = 2.56$, $p = .039$. It should be noted that with a breakdown by sex and sexual orientation some cell sizes were small (see Table 1), with an associated decrease in statistical power. Nonetheless, several patterns

emerged. (1) There was a significant difference in testosterone depending on relationship status in Het men, $F(4,70) = 2.73$, $p = .036$. Men in established paired relationships had lower testosterone than singles, $p = .006$, or polyamorous individuals, $p = .032$. (2) There was no significant overall difference in testosterone by relationship status in Non-Het men, $F(4,41) = .93$, $p = .459$. (3) There was no significant overall difference in testosterone by relationship status in Het women, $F(4, 67) = 1.47$, $p = .222$. (4) Despite the smallest sample size, there was a trend for a significant difference in testosterone by on relationship status in Non-Het women, $F(4, 49) = 2.35$, $p = .067$. Comparisons showed that singles had higher testosterone than paired, $p = .026$, established paired, $p = .008$, and polyamorous women, $p = .032$. Thus, testosterone and relationship status was associated in the same groups in which the association was found with partnered status,

Table 1. Mean baseline testosterone and cell numbers (with standard errors in brackets) for heterosexual and non-heterosexual women and men by relationship status

	Single	Dating	Paired	Established Paired	Polyamorous
Men					
Heterosexual	77.88 (4.45) $n = 35$	66.22 (7.79) $n = 11$	69.65 (5.86) $n = 20$	49.73 (8.87) $n = 9$	109.28 (-) $n = 1$
Non-Heterosexual	63.77 (5.34) $n = 26$	59.08 (15.74) $n = 3$	50.36 (13.64) $n = 4$	76.45 (9.11) $n = 9$	53.50 (12.27) $n = 5$
Women					
Heterosexual	20.84 (1.54) $n = 36$	21.37 (2.79) $n = 11$	18.49 (2.31) $n = 16$	15.64 (3.10) $n = 9$	35.93 (-) $n = 1$
Non-Heterosexual	30.62 (3.42) $n = 14$	24.74 (6.72) $n = 4$	18.78 (3.79) $n = 11$	18.26 (2.77) $n = 21$	15.73 (5.68) $n = 5$

Note: van Anders and Watson (2006a), by permission.

as would be expected. Interestingly, in these groups (Het men; Non-Het women), dating individuals did not differ from any other groups, and paired (Non-Het women) and

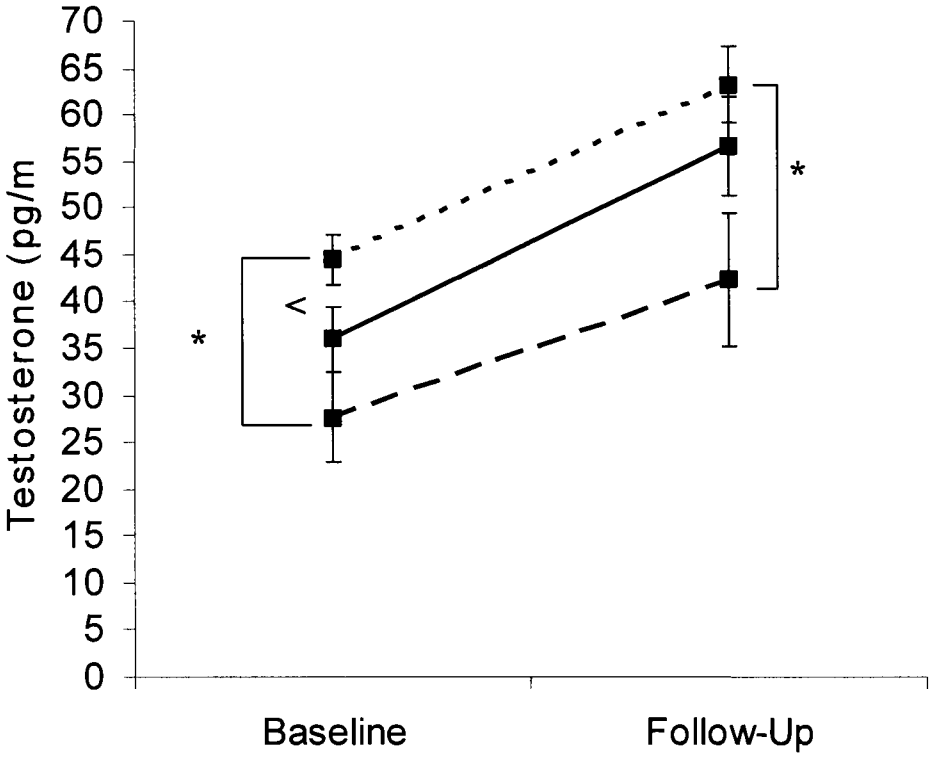
established paired (Non-Het women and Het men) had lower testosterone than singles. The *n*'s for polyamorous individuals were particularly small, limiting interpretability, but this group looks promising for future research.

3.4.2 Longitudinal Analyses

As described above, follow-up data were collected from 48 participants, to see if partnered status over time and testosterone were associated. Partnered status over time was encoded into four groups: stably partnered individuals (men: $n = 8$; women: $n = 6$); individuals who transitioned from partnered to unpartnered (no men; women: $n = 3$); individuals who transitioned from unpartnered to partnered (men: $n = 3$; women: $n = 5$); and stably unpartnered individuals (men: $n = 10$; women: $n = 14$). A repeated-measures ANOVA was conducted with status pattern and sex as the independent variables, and testosterone at baseline and follow-up (date) as the repeated measures. Neither baseline nor follow-up month of testing, nor age, were significant covariates, and so were not included in the analyses as covariates.

There was a significant main effect of date, $F(1,42) = 16.83$, $p < .001$, such that testosterone at follow-up was significantly higher than at baseline, $p < .001$. There was also a significant interaction between date and sex, $F(1,42) = 12.09$, $p = .001$, such that both sexes showed the same pattern (i.e. follow-up > baseline), but men exhibited a larger increase over time than women. There were no significant interactions between date and status pattern, $F(3,42) = .114$, $p = .951$, or date, sex, and status pattern, $F(2,42) = .27$, $p = .764$. Please see Figure 3 for means and standard errors. Thus, there was no evidence that changes in partnered status led to changes in testosterone.

Figure 3. Mean testosterone at baseline and follow-up with standard error bars in participants by their pattern of partneredness over time.



Note: '*' indicates a significant difference at $p < .05$; '<' indicates a trend towards significance at $p < .10$. The solid line indicates stably partnered individuals, the long-dashed line indicates unpartnered-to-partnered individuals, and the short-dashed line indicates stably unpartnered individuals. Data are collapsed for men and women since the pattern was the same, and there was no significant interaction with gender and status pattern.
Source: van Anders and Watson (2006a), by permission

The main effect of date was likely an artefact of month of testing. Though month of testing was not a significant covariate, a paired-t test revealed a significant difference between season of testing at baseline and follow-up, $t(49) = -5.07$, $p < .001$. Post hoc inspection revealed that no participants received baseline testing during the months of peak testosterone secretion (October, November), but 40% of follow-up sessions occurred during this time. In addition, many participants were tested during the spring and summer at baseline when testosterone was low, while none were at follow-up. So, the

effect of date likely reflects seasonality of testing (see van Anders et al., 2006 for further discussion).

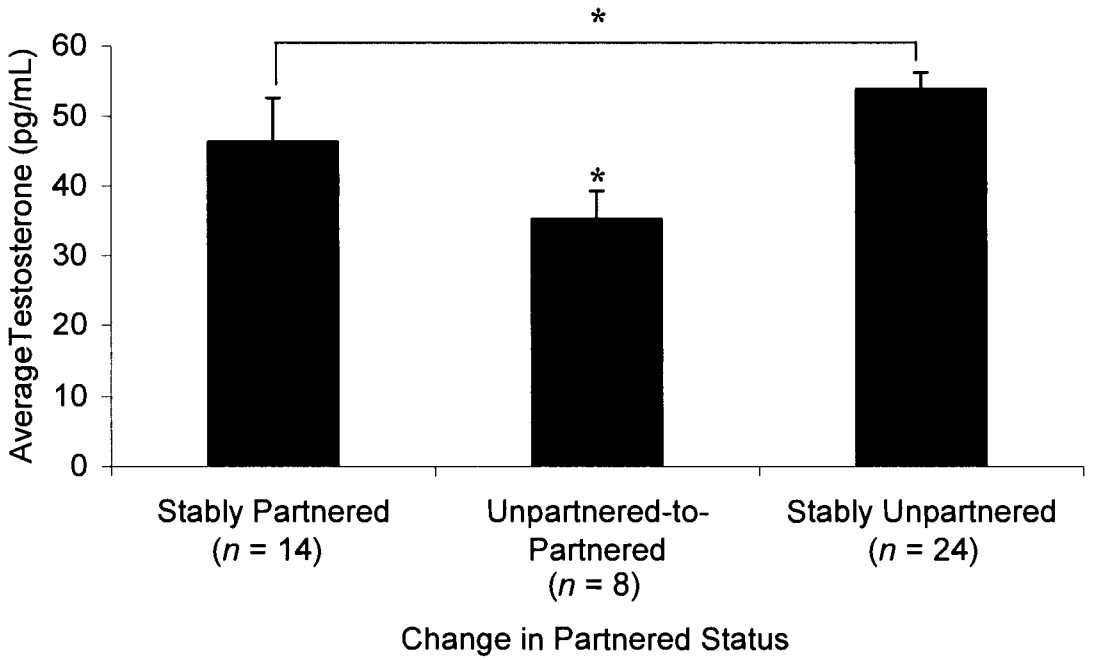
3.4.2.1 Between-Participant Effects

There was a significant main effect of sex, $F(1,42) = 180.27$, $p < .001$, as well as a significant main effect of longitudinal partner status pattern, $F(3,42) = 6.26$, $p = .001$. The effect of status pattern was surprisingly large, $\eta^2 = .309$, accounting for nearly 10% of the variance in testosterone. The interaction between sex and status pattern approached significance, $F(2,42) = 2.55$, $p = .090$, which likely was a reflection of the absence of men in one of the levels of change, since women and men showed the same pattern of testosterone in the other three levels. Examination of the main effect of status pattern on average testosterone showed that average testosterone levels in all patterns differed significantly from each other (all p's $< .05$; Figure 4), though partnered-to-unpartnered is not included here due to the lack of men. Individuals who were unpartnered at baseline but partnered at follow-up had significantly lower testosterone on average than stably unpartnered individuals. This suggests that, at any one point, unpartnered individuals represent a heterogeneous group. Stably partnered individuals had significantly higher testosterone than stably unpartnered individuals and significantly lower testosterone than unpartnered-to-partnered individuals.

3.4.2.2 Baseline Testosterone and Change in Partnered Status

To see if baseline testosterone was associated with partnered status over time, an ANOVA was conducted with baseline testosterone as the dependent variable, and sex and status pattern as the independent variables. Though testosterone and partnered status are

Figure 4. Mean average testosterone (over baseline and follow-up) with standard error bars in participants by their pattern of partneredness over time.



Note: '*' indicates a significant difference at $p < .05$. Data from women and men are collapsed because they showed the same pattern, and there was no significant interaction with gender.
Source: van Anders and Watson (2006a), by permission

conceptually reversed here (as the question was whether baseline testosterone predicted future partnership status), this analysis was useful for statistical purposes. There was a significant main effect of sex, $F(1,44) = 66.48$, $p < .001$, and of status pattern, $F(3,44) = 4.07$, $p = .012$, and no significant interaction, $F(2,44) = 1.22$, $p = .306$. Those who were stably unpartnered had significantly higher baseline testosterone than unpartnered to partnered individuals, $p = .003$, and marginally higher baseline testosterone than stably partnered individuals, $p = .078$. Unpartnered-to- partnered individuals and stably partnered individuals did not significantly differ in baseline testosterone, $p = .102$. Please see Figure 3 for means and standard errors. Overall, therefore, high testosterone at baseline was associated with remaining unpartnered, regardless of sex.

To confirm this with a more conceptually accurate analysis (in terms of independent versus dependent variables), a median split was also calculated in baseline testosterone by sex, to look at individuals who were unpartnered at baseline in a univariate ANOVA with status pattern as the dependent variable and high/low baseline testosterone and sex as the independent variables. There was no significant main effect of sex, $F(1,28) = .691$, $p = .413$, nor was there a significant interaction, $F(1,28) = .372$, $p = .120$. There was, however, a significant main effect of high/low testosterone, $F(1,28) = 13.08$, $p = .001$, such that the unpartnered individuals with the high testosterone were significantly more likely to stay unpartnered (i.e. be stably unpartnered) than the unpartnered individuals with the low testosterone, mirroring the above analyses.

3.4.2.3 Follow-Up Testosterone and Change in Relationship Status

To see if status pattern was associated with follow-up testosterone, an ANOVA was conducted with follow-up testosterone as the dependent variable, and sex and status pattern as the independent variables. The partnered-to-unpartnered category was not included (the category with no men). There was a significant main effect of sex, $F(1,40) = 90.04$, $p < .001$, and the main effect for status pattern approached significance, $F(2,40) = 3.12$, $p = .055$. The interaction was not significant, $F(2,40) = 1.25$, $p = .298$. Stably unpartnered participants had significantly higher follow-up testosterone than unpartnered individuals who became partnered, $p = .017$. Please see Figure 3 for means and standard errors. The differences between the other groups did not approach significance.

3.5 Discussion of Study 1

In this study, the association between testosterone levels and partnered status in non-heterosexual (Non-Het) and heterosexual (Het) women and men was examined. As in previous studies (Burnham et al., 2003; Gray et al., 2002; Gray et al., 2004a; Gray et al., 2004b), the results showed that partnered Het men have lower testosterone than unpartnered Het men. However, this was not specific to Het men: partnered Non-Het women have lower testosterone than unpartnered Non-Het women. This effect is not apparent in Het women or Non-Het men. This suggests that the relationship between testosterone and partner status may be only seen in individuals who are interested in, and partner with, women.

The longitudinal results do not support an effect of partnering on testosterone despite the expectation that partnering would lead to decreased testosterone (c.f. van Anders and Watson, 2006b), however results should be interpreted with caution in light of the small longitudinal sample size. In contrast with Mazur and Michalek (1998) who found an increase in testosterone upon marriage dissolution, the present study provided no evidence for an effect of change in partnered status on testosterone. The designs differed in that the present study did not examine divorce or marriage nor did it have men who became unpartnered as a possible comparison group. Still, results suggest that becoming partnered did not lead to decreased testosterone. Another difference exists in that the longitudinal time period was much shorter (< 1 yr) than Mazur and Michalek (1998) (10 yrs), so it is possible that longer time periods would reveal an effect. Furthermore, Mazur and Michalek (1998) reported that testosterone increased around divorce, then decreased to pre-divorce levels; this might indicate that divorce does not

have a permanent effect on trait levels of testosterone. And, since divorce generally represents a major life change that is often accompanied by debilitating consequences rather than just a change in partnered status; it may be an extreme period of stress. Gray et al. (2002) did find a negative correlation between spousal investment and evening testosterone; however, an alternative (and parsimonious) interpretation is that those with lower testosterone invest more. Gray et al. (2004a) found that men's testosterone did not differ depending on days spent with their partner and children compared to those spent without their family, providing no evidence of an effect of bond-maintenance activities or partnering on testosterone.

One limitation of the present study is the relatively small size of the longitudinal sample, though it was comparable to previous studies on relationship status and testosterone. A replication would have a larger sample and a group of partnered individuals who become unpartnered. Conducting baseline and follow-up testing in the same season would be beneficial, since there is a large effect of seasonality on testosterone (van Anders, Hampson and Watson, 2006).

Instead of an effect of partnering on testosterone, these results support an influence of testosterone on partnering. Unpartnered individuals with lower testosterone were more likely to become partnered than unpartnered individuals with higher testosterone, regardless of sex. Also, this pattern of testosterone remained stable over time. Thus, it appears that the association between testosterone and partnered status might be unidirectional and trait-level: lower testosterone individuals are more likely to become and stay partnered. That the baseline population effect (partnered < unpartnered) appears to occur only in those who partner with women (i.e. Het men and Non-Het women) has

various possible explanations. It might be advantageous for women (since they give birth), to select low testosterone partners since low testosterone in men is associated with greater parental responsiveness (Storey et al., 2000) and better father-child relationships (Julian and McKenry, 1989). This remains speculative for female co-partners since testosterone and parenting in this group has received no empirical attention, though humans and other species show partnering and parenting within long-term same-sex pair bonds (Bagemihl, 1999).

It is unclear why higher testosterone individuals are less likely to be partnered, but speculations can be put forth for future study. Female mate choice may play a role, i.e. women may view higher testosterone individuals as less attractive or desirable as long-term partners for reasons noted above, but potentially more attractive for short-term relationships. Thus higher testosterone would not necessarily diminish reproductive opportunities even though it is associated with a decreased likelihood of partneredness. Higher testosterone individuals may be less interested in longer-term relationships as a reproductive strategy. Higher testosterone is associated with decreased need for long-term commitment in women (Cashdan, 1995), as well as a higher probability of extra-marital sex (Booth and Dabbs, 1993) and increased number of sexual partners in men (Bogaert and Fisher, 1995) and women (Cashdan, 1995). In other mammalian taxa, such as voles, species that form pair bonds and engage in parental behaviour have lower testosterone than those that compete for different mates (e.g. Klein and Nelson, 1997).

It is important to note that 'unpartnered' individuals form a heterogeneous category, as the testosterone levels of the unpartnered participants at baseline could be differentiated on the basis of future behaviour. Previous studies support this interpretation

of subgroups embedded within the larger category of unpartnered individuals. Gray et al. (2004b) found that unpartnered men with prior relationship experience had higher testosterone than unpartnered men without such experience. Conjecturally, this might be expected if the 'experienced' unpartnered group contains an over-representation of men who have serial short relationships and thus continue to be unpartnered, in contrast to 'inexperienced' unpartnered men who are unlikely to move from partner to partner.

It may be that the evolutionary trade-off between competitive and bond-maintenance behaviours within individuals is also apparent between individuals (as per a relationship status association with testosterone), and data from the present study support this interpretation. Results from the present study show that lower trait levels of testosterone are associated with increased likelihood of becoming partnered, and others have found that lower testosterone is associated with greater parental responsiveness (Storey et al., 2000). However, changes in state levels of testosterone can still occur regardless of one's trait level of testosterone. In men, testosterone dips when their partners giving birth (Storey et al., 2000), and increases in response to infant stimuli (Fleming et al., 2002) perhaps in preparation for infant protection. Fathers also may have lower testosterone than non-fathers (Burnham et al., 2003; Gray et al., 2006; c.f. Gray et al., 2002; Gray et al., 2004a), which could be interpreted that becoming a father decreases testosterone. This may be conflated with infant age, and may represent a change in state testosterone in response to birth. In addition, it may be that those who become co-parents had lower trait testosterone than those who do not, even before the birth. The most parsimonious explanation, taking into account the results and the literature, is that

evolutionarily influenced trade-offs occur in state levels of testosterone within individuals and trait levels of testosterone between individuals.

In summary, these findings show that the pattern of lower testosterone in partnered individuals reported in Het men extends to Non-Het women, and is not apparent in Non-Het men or Het women. In addition, there was no evidence that partnering modulates testosterone levels, and it is possible that the reverse relationship holds: i.e., testosterone levels may affect the likelihood of partnering.

4 STUDY 2: LONG-DISTANCE VS. SAME-CITY PARTNERING AND TESTOSTERONE

Note: This section is based on the following article, with permission: van Anders, S.M. & Watson, N.V. (2007b). Testosterone levels in women and men who are single, in long-distance relationships, or same-city relationships. *Hormones and Behavior, 51,* 286-291.

Section 3 presented research that examined associations between testosterone and partnering in heterosexual and non-heterosexual men and women with a cross-sectional and a longitudinal approach. These findings pointed towards a possible association between relationship orientation and testosterone. In this section, one of the follow-up studies is described that further examined some of the important questions and issues raised in Section 3.

4.1 Introduction to Study 2

As described in Sections 2 and 3, research has established that heterosexual partnered men exhibit lower testosterone than heterosexual single men (Booth and Dabbs, 1993; Burnham et al., 2003; Gray et al., 2002; Gray et al., 2004a; 2004b; Mazur and Michalek, 1998). Research described in Section 3 (i.e. van Anders and Watson, 2006a) has shown that this can be replicated using a comparison derived from the testosterone trade-off framework, in which partnered and unpartnered individuals are contrasted. The pattern has been extended to non-heterosexual women (i.e. higher testosterone in unpartnered non-heterosexual women compared to partnered non-heterosexual women), but not to Het women or non-Het men. As well, evidence showed that lower testosterone

predicted entering a relationship, but did not support testosterone changes upon entering a relationship. However, since there was a small sample of participants who changed relationships in Section 3, future evidence is needed to state conclusively that relationship status does affect testosterone.

Behavioural neuroendocrine research has long relied upon the diversity apparent in both animal and human phenotypes to conduct research into questions of typical and atypical endocrine development. This naturally-occurring diversity has been important, since causal hormone-behaviour relationships are not frequently amenable to experimental testing in humans (i.e., we can rarely administer hormones for non-clinical purposes to look for endocrine effects on behaviour), so research has often focused on people with clinical conditions. This has allowed investigators to develop a more comprehensive understanding of how the presence or absence of hormones and/or receptors may affect development, as when prenatal androgen levels are higher than typical in congenital adrenal hyperplasia (CAH). Another approach is to look to the diversity in human behaviours and strategies (van Anders, under review). For example, though we cannot assign individuals to certain relationship categories, some people have already chosen to have specific types of relationships.

The present study taps into this diversity in relationship types, by examining women and men who were single, in long-distance relationships, or in same-city relationships. If relationship *orientation* is associated with testosterone, then individuals in long-distance and same-city relationships should display similar levels of testosterone, and levels that are lower than single individuals. That is, if lower testosterone is associated with a bond-maintenance relationship orientation, then physical partner

presence should not affect the partnering-testosterone association. Or, put another way, there should be no state effect of partnering on testosterone. If relationship *status* is associated with testosterone, then individuals who are in long-distance relationships should display higher testosterone than individuals in same-city relationships, and comparable levels (perhaps) to single individuals. That is, if the lower testosterone found in partnered individuals is associated with their daily behaviours or partner cues, then physical partner presence should affect this partnering-testosterone association.

4.2 Goals and Hypotheses

The following were goals of this study: (1) To further address questions of directionality by taking empirical advantage of already existing and relevant partnering diversity; (2) To further address how sex may be associated with partnering.

I tested two competing (but not necessarily exclusive) hypotheses: (1) relationship orientation: testosterone should be higher in single people compared to people who are partnered, regardless of partner presence; and (2) relationship status: testosterone should be highest in single people and lowest in same-city partnered people.

4.3 Methods

4.3.1 Participants

Participants were recruited through the undergraduate psychology participant pool, where they were prescreened for exogenous hormone use and from the larger community through poster advertisements. Participants from the community received small reimbursements and participants from the psychology pool received course credit for participation. Participants included 72 women (mean age = 20.79 yrs; min = 17 yrs,

max = 32 yrs) and 49 men (mean age = 21.47 yrs, min = 17 yrs, max = 40 yrs). Five women were using hormonal contraceptives, and one man was using medications that affect sex steroids. These participants were excluded, leaving 67 women and 48 men in the analyses.

Participants identified their sexual orientation via self-report and the Kinsey questions of sex-directed fantasy and behaviour (Kinsey et al., 1948). Dichotomous labels were imposed such that participants who scored 0 or 1 on both measures were categorised as heterosexual and individuals who scored 2 or more on one or both measures were categorised as non-heterosexual (van Anders and Watson, 2006a; van Anders and Hampson, 2005). This categorization resulted in 43 heterosexual women, 24 non-heterosexual women, 28 heterosexual men, and 10 non-heterosexual men. This provided a very liberal estimate of non-heterosexual participants: using self-identification, there were two gay men, three queer women, and four bisexual/bicurious women.

Participants had all graduated from high school, and 61 had at least one year of university or college (or similar), 10 were college/university graduates, two had at least one year in graduate or professional school, and three had a graduate degree. The majority (n = 112) of participants were currently students, but many of them (n = 51) were employed in diverse occupations. Participants were diverse ethnically: they self-identified their ethnicity and these were their responses with n's in brackets: Chinese (30), Caucasian (29), Korean (6), Canadian (4), Anglo/Latin (1), Asian (11), and one each for Black, British/Canadian, Chinese/Italian, Croatian/Chinese, Dutch/First Nations, East Asian, East Indian, Egyptian, Hindi, Mexico, Indian, Jewish, Métis, Middle Eastern, Persian, Punjabi (Sikh), Sinhalese, Turkish, and Vietnamese.

Participants self-identified their relationship status, and long distance status was further determined by asking whether their partners lived in the same city as them. The breakdown of participants was as follows: single and not currently seeing people (28 women; 21 men), same-city partnered (15 women; 12 men), or long-distance partnered (17 women; 11 men). Though recruitment was specifically directed towards people who were single or in long-term relationships (same-city or long-distance), seven women and four men who were dating participated, and they were excluded from subsequent analyses.

4.3.2 Materials and Procedure

The procedures were subject to prior approval by the SFU Research Ethics Board. Participants were tested between 1200 and 1800 hours to control for diurnal rhythms in testosterone (except one participant at 23:30 and one at 11:15). Participants provided a saliva sample and completed a brief questionnaire about their demographics, health and background, and relationship status. Menstrual cycle phase was not controlled as previous research has shown that these consistent but small effects do not need to be controlled unless menstrual cycle is of interest (Dabbs and de La Rue, 1991); information about menstrual cycles was collected, however, as a potential control measure.

The questionnaire included questions about demographic variables (as per above), sleep-wake variables, weight and height to compute BMI (body mass index, a measure of weight corrected for height) and relationship variables: whether participants considered their partners to be partners for the long-term (yes, no); whether participants had sexual/romantic contact with non-partners during the relationship (no, once, rarely, sometimes, often, regularly); whether participants were sexually active with their partners

(no, once/month, 2-3 times/month, once/week, 2-3 times/week, once/day, more than once/day); level of commitment to the relationship (Likert-type scale from 1 = extremely to 7 = not at all); likelihood of being together with partner 'forever' (same Likert-type scale); level of sexual attraction to partner over the past month (same Likert-type scale). People in long-distance relationships also indicated how often on average they saw their partners and estimated how long during each year they saw their partners in person; these measures were converted into days.

Saliva samples were collected in polystyrene tubes that had been pretreated with sodium azide, and frozen after collection at -20°C until assay. Saliva was stimulated with the use of an inert gum (Trident cherry sugar-free). The samples were assayed in two batches for testosterone using radioimmunoassay at the Endocrine Core Lab at Yerkes National Primate Research Center, Emory University, all in triplicate, using a modified kit from Diagnostic Systems Laboratories (Webster, TX). The sensitivity was 2-500 pg/mL at a 200 μL dose. The interassay coefficients of variation were 19.16% at 5.03 pg/mL, 15.08% at 170.81 pg/mL, and 16.40% at 25.31 pg/mL. The intra-assay coefficient of variation was 3.41% at 26.89 pg/mL.

Analyses were conducted with the Statistical Package for the Social Sciences (SPSS), v. 13.0. Overall effects were tested using analyses of variance (ANOVA) or covariance (ANCOVA), or independent *t*-tests when appropriate. Group differences were evaluated using the LSD (Least Significant Difference) test after significant omnibus analyses. Correlations were evaluated using Pearson's Product Moment Correlations.

4.4 Results

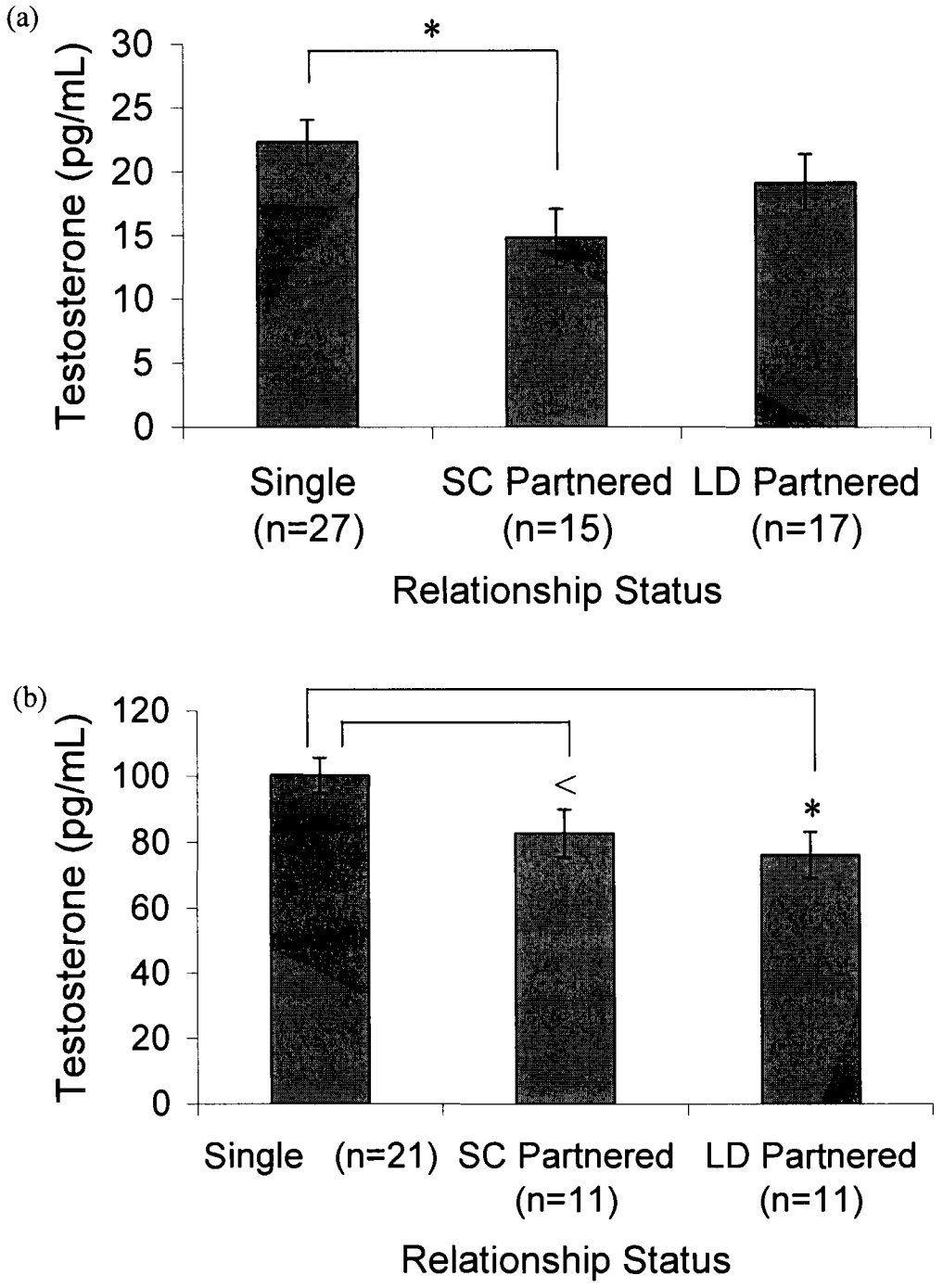
Participants in long-distance relationships spent an average of 70 days per year together, and participants in same-city relationships spent an average of 243 days per year together, and this was significantly different, $t(37) = 5.01$, $p < .001$.

4.4.1 Women

To see if women's testosterone differed as a function of relationship status (single, same-city partnered, long-distance partnered), an ANCOVA was conducted with age as a covariate. There was a significant overall difference in women's testosterone, $F(2,55) = 3.28$, $p = .045$, partial $\eta^2 = .107$ (see Figure 5a). Women in long-distance relationships did not have significantly different testosterone than women in same-city relationships, $p = .166$, or women who were single, $p = .287$. However, women in same-city relationships did have significantly lower testosterone than single women, $p = .013$.

To ensure that these findings were not the result of other variables or confounds, additional variables were controlled to see if the pattern of results changed. Because women in these various types of relationships might show different sleep-wake patterns (e.g. late night contacts with long-distance partners) and sleep patterns are associated with testosterone (Axelsson et al., 2005), an additional ANCOVA was conducted controlling for time of waking, but this did not change the pattern of significant results. Previous research has also shown that women's sexual orientation may moderate associations between partnering and testosterone (van Anders and Watson, 2006a), but controlling for sexual orientation in an additional ANCOVA did not change the pattern of significant results either, likely because there was only a small number of self-identified

Figure 5. Mean testosterone with standard error bars by relationship status and gender/sex.



Note: (a) Women, adjusted for age; (b) men, adjusted for age and time-of-waking. 'SC' indicates 'same-city'; 'LD' indicates long-distance'; '*' indicates a significant difference at $p < .05$; '<' indicates a trend at $p < .10$.
Source: van Anders and Watson (2007b), by permission

non-heterosexuals in the study. There was no significant difference between long-distance and same-city partnered women's BMI, $t(30) = -.10$, $p = .918$.

To see if there were differences in relationship variables between women in long-distance and same-city relationships that could explain the pattern of findings, the following were analysed using independent *t*-tests. There were no significant differences (or trends) between women in same-city or long-distance relationships in whether the women considered their partner for the long-term (statistic could not be calculated because *SD*s = 0 in both groups), sexual contact with non-relationship partners, $t(29) = .20$, $p = .846$, commitment to relationship, $t(30) = .94$, $p = .354$, the reported likelihood that the women and their partners will be together 'forever', $t(30) = -.45$, $p = .654$, level of sexual attraction to their partner over the past month, $t(30) = .15$, $p = .886$, or length of relationship, $t(30) = .24$, $p = .809$. Correlations between testosterone and number of days spent together in the past year were not significant in all partnered women, $r(22) = -.15$, $p = .474$, in long-distance partnered women alone, $r(13) = -.11$, $p = .697$, or same-city partnered women alone, $r(7) = .41$, $p = .271$. The correlations did not become larger when age was controlled in partial correlations.

4.4.2 Men

To see if men's testosterone differed as a function of their relationship status, an ANCOVA was conducted with age as the covariate. There was a trend towards a significant overall effect, $F(2, 39) = 3.08$, $p = .057$. Time of waking was then entered as a covariate (see above discussion), and the ANCOVA showed a significant overall effect, $F(2, 38) = 3.78$, $p = .032$, partial $\eta^2 = .166$, so all further values are adjusted for age and time of waking (see Figure 5b). Testosterone levels in single men were significantly

higher than long-distance partnered men, $p = .012$, and showed a trend towards being significant higher than same-city partnered men, $p = .072$. There was no significant difference between same-city partnered men or long-distance partnered men, $p = .505$.

As with women, additional variables were controlled to see if other variables accounted for the pattern of results in men. There was no significant difference between long-distance and same-city partnered men's BMI, $t(20) = -.14$, $p = .894$. Entering sexual orientation as a covariate did not change the pattern of significant results, again likely because there was only a small sample of self-identified non-heterosexual participants.

To see if there were differences in relationship variables between men in long-distance and same-city relationships that could explain the pattern of findings, the following were analyzed using independent *t*-tests. There were no significant differences (or trends) between men in same-city or long-distance relationships in whether the men considered their partner for the long-term, $t(10) = -1.49$, $p = .167$, sexual contact with non-relationship partners, $t(10) = -1.15$, $p = .274$, commitment to relationship, $t(21) = .34$, $p = .738$, the reported likelihood that the men and their partners will be together 'forever', $t(21) = 1.53$, $p = .142$, or length of relationship, $t(21) = .41$, $p = .688$. However, there was a significant difference in men's sexual attraction to their partners over the past month, $t(21) = 2.11$, $p = .047$, such that same-city partnered men reported significantly less sexual attraction to their partners than long-distance partnered men. Correlations between testosterone and number of days spent together in the past year were not significant in all partnered men, $r(18) = .27$, $p = .258$, in long-distance partnered men alone, $r(7) = -.10$, $p = .803$, or same-city partnered men alone, $r(9) = .37$, $p = .266$. The correlations did not become larger when age was controlled in partial correlations.

4.4.3 Multiple Partners

There was a small number of individuals (n = 6) in relationships who had additional casual or long-term relationships. These included five individuals in long-distance relationships (three men; two women), and one woman in a same-city relationship. Excluding these participants did not change the pattern of results, except to change the overall ANCOVA in the women to a trend.

4.5 Discussion of Study 2

The present study examined testosterone levels in women and men who were single, in long-distance relationships, or in same-city relationships. Two hypotheses were tested: (1) relationship *orientation*: testosterone should be similar in partnered individuals (regardless of physical partner presence) and lower than testosterone levels in single people; (2) relationship *status:* testosterone should be lower in same-city partnered individuals than single or long-distance partnered individuals. Though the results do not directly answer the question of causality, they do shed light on the issue. It should be noted that relationship orientation may reflect individual propensities towards entering relationships and/or individual attractiveness for relationships, and the present study does not address this.

Results showed that partnered men displayed lower testosterone than single men, and this was true for men with same-city relationships or long-distance relationships. This was true despite same-city partnered men reporting less sexual attraction to their partners than long-distance partnered men, and that long-distance partnered men must have inevitably had less (or no) sexual contact with their partners, which are interesting findings in themselves, and suggest that differences in sexual activity or attraction are not

associated with differences in testosterone levels. There were no other differences between the men in relationships, including current/long-term commitment and length of relationship. One caveat is the sample size of 11 men in each partnered group. However, mean testosterone was nonsignificantly lower in long-distance partnered men suggesting that a larger sample size would not lead to higher testosterone in long-distance partnered men. The data are in accord with previous findings that are suggestive of an association between testosterone and relationship orientation. For example, van Anders and Watson (2006a) found that testosterone levels predicted entering relationships but no evidence that entering a relationship decreased testosterone, Booth and Dabbs (1993) found that testosterone levels predicted divorce and singlehood, and Mazur and Michalek (1998) also found that testosterone levels predicted divorce.

There is one finding that suggests that changes in relationship status cause changes in testosterone, which is that testosterone is increased around divorce (Mazur and Michalek, 1998). These authors note that testosterone in unwed men is similar to men who change marital status, which arguably supports a relationship orientation interpretation. Additionally, testosterone levels do not differ in heterosexual men between days spent with partners versus days spent at work (Gray et al., 2004), which suggests that partner directed behaviours do not lead to lower testosterone over the day. McIntyre et al. (2006) have shown that partnered but not single men with a less restricted SOI (sociosexual orientation: a measure of reported willingness to engage in sex outside of a committed, emotionally involved relationship, Simpson and Gangestad, 1991) exhibit higher testosterone, which is suggestive that relationship orientation, regardless of relationship status, is associated with testosterone. The suggestion that evidence points to

an association between relationship orientation and testosterone does not negate the idea that behaviours related to partnering affect men's testosterone. It has been elsewhere posited that they should (e.g. van Anders and Watson, 2006b), and there is evidence that they do (e.g. Roney et al., 2003). It is possible that relationship status does affect testosterone, and studies that address relevant cues other than long-term physical partner presence, short-term partner-directed behaviours, or relationship commitment (which has not been found to be correlated with testosterone in any studies) should prove instructive. One possibility is that behaviours directed at attracting non-partner individuals increase testosterone and account for higher testosterone in single men (van Anders and Watson, 2006b), as Roney et al. report that 'show-off' behaviours increase testosterone.

Results showed that same-city partnered women display lower testosterone than long-distance partnered or single women, despite no differences in parameters like current/long-term commitment, sexual attraction, or length of relationship. This was surprising, since the one previous study including women found an effect only in non-heterosexual women (van Anders and Watson, 2006a); however, the finding from the present data did not disappear when sexual orientation was controlled, suggesting that partnering and testosterone may be associated across women. In the previous study, heterosexual women's means were in the expected direction but did not significantly differ. It remains possible that the previous study included long-distance partnered women in the partnered category (potentially inflating their testosterone levels), obscuring any association between testosterone and partnering. This is speculative, and further study including women is clearly warranted. The data suggest that physical partner presence is associated with decreased testosterone, which supports a relationship

status interpretation in women. One interesting possibility is that long-distance partnered women's higher testosterone may be associated with increased frequency of masturbation, as research has found preliminary evidence of an association between masturbation-induced orgasms and higher testosterone (van Anders et al., in press). Replication and further empirical data are needed before possible explanations are proposed for sex differences in testosterone-partnering associations.

The issue of physical partner presence is promising for future study. Most same-city partnered participants did not live with their partners, and previous studies have not identified whether partners were live-in or not. Apparently, live-in partners are not necessary for partnered men to display lower testosterone than single men, since the long-distance partnered men had lower testosterone than single men. However, this may be a mediating factor for women, as same-city partnered women exhibited lower testosterone than single or long-distance partnered women. There was only a small sample of same-city partnered women with live-in partners, but their testosterone levels appeared to be lower than same-city partnered women who did not live with their partners (15.33 vs. 18.57 pg/mL), though not significantly so. However, the estimated number of days spent with partners did not correlate with testosterone in partnered women or by relationship type, though numbers were small for correlational analyses. It would be interesting to further examine the issue by comparing testosterone in women with live-in and non-live in (but same-city) partners of similar relationship lengths, commitment, and ages.

Evidence from various sources suggest that sexual experience may sensitise or organise the endocrine system of human and non-human males in terms of future endocrine or behavioural responses to reproductive/sexual opportunities (e.g. Clancy,

Singer, Macrides, Bronson, and Agosta, 1988; Domjan, Akins, and Vandergriff, 1992; Pfeiffer and Johnston, 1994; Roney et al., 2003). Is this true for pair bonding experience? And, exposure to female cues often is associated with increased testosterone in males (humans: Roney et al., 2003; hamsters: Pfeiffer and Johnston, 1992), but testosterone is lower in partnered men; do cues need to be from unfamiliar partners in humans and other species? Counter to the present findings, male golden hamsters housed with or without females show no difference in baseline androgens (Pfeiffer and Johnston, 1992). So, research with pair bonding species may provide insights as to how testosterone is associated with partnering in males and potentially partner presence in females.

Findings from the present study suggest that physical partner cues – salient signals of relationship status – do not affect the partnering-testosterone association in men. In conjunction with previous evidence, this is suggestive of an association between relationship orientation and testosterone. Do men with lower testosterone display more of a bond-maintenance relationship orientation than their higher testosterone counterparts? Are these men more likely to be selected for long-term relationships? In women, the findings suggest that physical partner cues are associated with reduced testosterone, which is suggestive of an association between relationship status and testosterone. Do women with live-in partners have lower testosterone than women with partners who live in the same city but not the same residence? How and why these sex differences occur remains to be seen, and studies of within-sex associations between testosterone and partnering will likely be suggestive.

5 STUDY 3: POLYAMORY AND TESTOSTERONE

Note: This section is based on the following article, with permission: van Anders, S. M., Hamilton, L. D., & Watson, N. V. (2007). Multiple partners are associated with higher testosterone in North American men and women. *Hormones and Behavior, 51,* 454-459.

Section 4 described research that examined testosterone levels in men and women who are single, in long-distance relationships, or same-city relationships to try and further understand partnering-testosterone associations, and to address issues of directionality. Section 3 reported on contrasts between partnered and unpartnered individuals. Some of these unpartnered individuals were 'polyamorous', and there were indications, despite the small sample size, that these individuals may have higher testosterone than other participants. The following section describes follow-up research that examines testosterone levels in single, polyamorous, and monoamorous women and men.

5.1 Introduction to Study 3

As noted, research has established that unpartnered heterosexual men exhibit higher testosterone than partnered heterosexual men (Booth and Dabbs, 1993; Burnham et al., 2003; Gray et al., 2002; Gray et al., 2004a; 2004b; Mazur and Michalek, 1998; van Anders and Watson, 2006a; 2007b). In addition, studies suggest that this effect may occur in heterosexual but not non-heterosexual men, and may be more apparent in non-heterosexual women (van Anders and Watson, 2006a). One study with a population (i.e. Kenyan Swahili men) where monoamorous relationships like marriage are not the only

long-term relationship possibility found that polygynously married men exhibited higher testosterone than monogamously married men (Gray, 2003).

Of course, monoamorous relationships are not the only long-term relationship possibility in North American cultures either, and one additional relationship type is polyamory. Polyamory is not as widely known as other relationship types, and though there are various definitions, it generally refers to the "...philosophy and practice of loving multiple people simultaneously" (Introduction to Polyamory). Polyamory is a specific approach to relationships that includes nonpossessiveness, honesty, and openness (and thus differs from 'cheating' or adultery). Polyamory differs from North American polygyny in many ways; e.g. it is not regulated through religious strictures and/or communities, it is not focused on multiple marriages between one man and many women, and it is associated with values related to freedom to pursue emotional and sexual intimacy and expression. Polyamory also differs from swinging or open relationships (though not all agree on this distinction), especially with polyamory's focus on love (*poly amor* = many loves) and emotional connections in multiple romantic/sexual relationships.

It has been posited that being in a monoamorous committed relationship might be associated with lower testosterone because this is a bond-maintenance context in the testosterone trade-off framework (van Anders, under review; van Anders and Gray, under review). In this framework (described further earlier), low testosterone is associated with bond-maintenance behaviours, contexts, or orientations (aimed at promoting intimate caring bonds with others), and high testosterone is associated with competitive behaviours, contexts, or orientations (aimed at acquiring or defending resources, including partners and offspring). If looking for additional partners, or the possibility of

additional partners, is a competitive situation, then polyamory might be associated with higher testosterone. Though people in monoamorous relationships often seek sexual/romantic encounters beyond their relationship, on average this should occur less frequently than in individuals with a lifestyle approach that makes this possibility explicit.

Included as a related part of the study were both sociosexual orientation (SOI: Simpson and Gangestad, 1991) scores and sexual desire. SOI scores might be associated with the testosterone-partnering association, since SOI is a measure of self-reported willingness to engage in sexual activity outside of committed, emotional contexts. Because of this, however, it is therefore unclear whether monoamorously partnered individuals should differ from polyamorous individuals in SOI scores; should they be less restricted (i.e. more willing), more restricted (i.e. less willing), or similar because of polyamory's focus on multiple but committed relationships? Similarly, sexual desire was included because it might be associated with relationship status and the link between partnering and testosterone.

5.2 Goals and Hypotheses

The following were goals for this study: (1) To determine how polyamory might be associated with testosterone in North American populations; (2) To examine how gender/sex might factor into any partnering-testosterone associations; (3) To study whether sexual desire or SOI scores might mediate any partnering-testosterone associations.

I hypothesised that polyamorous individuals might exhibit higher testosterone than monoamorously partnered individuals. I also hypothesised that polyamorous individuals might exhibit higher testosterone than single individuals, because their lifestyle is explicitly oriented toward the possibility and likelihood of new partners in a way that being single is not. An interesting alternative possibility is that polyamorous individuals might exhibit lower testosterone than single individuals because they are engaged in more bond-maintenance behaviours or are more bond-maintenance-oriented, and exhibit similar testosterone levels to monoamorously partnered individuals because these groups may be similarly oriented towards long-term relationships.

5.3 Methods

5.3.1 Participants

Participants were recruited through advertisements in the community or through listservs (email discussion groups), and received small payments for their involvement and time. Participants self-identified their sex, and there were 59 women, 47 men, two male-to-female trans-identified individuals, and one bi-gendered identified individual. Participants who were using medications that affected gonadal steroids (including hormonal contraceptives) were excluded from the study, leaving 48 women (mean age = 31.48 yrs; min = 18 yrs, max = 60 yrs) and 47 men (mean age = 31.98 yrs, min = 19 yrs, max = 54 yrs). Participants were diverse in their ethnicity, occupation, and education, though all participants but two were high school graduates.

For sexual orientation, participants self-identified and also responded to the Kinsey questions of sex-directed fantasy and behaviour (Kinsey et al., 1948). From the

responses to the Kinsey questions, participants were divided into heterosexual (exclusive or near exclusive opposite-sex fantasy and behaviour) and non-heterosexual (some to exclusive same-sex fantasy or behaviour). This resulted in 36 heterosexual men, 10 non-heterosexual men, 26 heterosexual women, and 22 non-heterosexual women. One man did not respond to the Kinsey questions. Because of a close match between sexual orientation by self-identification and the Kinsey questions, and because the Kinsey questions have been used in the past (e.g. van Anders and Watson, 2006a; 2007b), sexual orientation as per the Kinsey questions was used in the subsequent analyses.

Recruitment was directed toward participants who were single or in relationships, but two dating participants (one man and one woman) volunteered for the study and were excluded from subsequent analyses. Participants indicated their relationship status and their number of partners, and individuals were grouped into single (11 men; 13 women), partnered (11 men; 6 women), polyamorous with current multiple partners (12 men; 17 women), and polyamorous lifestyle (poly lifestyle) but not with current multiple partners (6 men; 4 women). The following criteria were used for the purposes of classifying and grouping participants. Single participants identified themselves as 'single' and responded to questions for people with no current partners. Partnered people responded to questions for people with one current partner and identified as being in a long-term relationship.

Polyamorous individuals used various terms to identify that they were in relationships that were or were not exclusive, with or without one primary partner, serious or casual, etc. Polyamorous participants were mostly (but not exclusively) recruited from polyamory groups and responded to questions for people with two or more current partners. There was one participant included in this category who responded to

questions for people with one partner but identified as 'married and dating' and was recruited through the polyamory groups. Poly lifestyle participants responded to questions for people with no or one current partner, but were categorised as poly lifestyle instead of single, dating, or partnered because they either were recruited through poly networks or groups and/or identified their relationship status using words that indicated they were not currently having multiple committed relationships.

The plurality of polyamorous women had two partners (n = 6), followed by three partners (n = 5), four partners (n = 3), and one each for five and six partners (with three non-responders). The majority of polyamorous men also had two partners (n = 6), followed by four partners (n = 3) and then one each for three and five partners (with five non-responders). The majority of polyamorous participants reported having a primary partner (10 of 16 women, 8 of 11 men). All women reported that all their partners were aware of them having multiple partners, as did all men but one.

5.3.2 Materials and Procedure

This study was subject to prior approval by the SFU Research Ethics Board, and all participants completed informed consent forms. Participants were tested mainly between 1300 and 2100 hours to control for diurnal rhythms in testosterone, except six who were tested outside this timeframe because of methodological constraints (time of sampling was controlled in analyses). Participants were tested in the lab, in their homes, or at public testing sites. Many of the polyamorous participants were tested at one of two meetings of regional polyamory groups (month of sampling was also controlled in analyses because of this and seasonal patterns in testosterone: van Anders et al., 2006). At one of these groups, participants were given an abbreviated version of the

questionnaire because of time constraints. Participants provided a saliva sample and completed a brief questionnaire about their demographics, health and background, and relationship status.

This questionnaire included the SOI (Simpson and Gangestad, 1991) and the Sexual Desire Inventory (SDI: Spector, Carey, and Steinberg, 1996) because both constructs are likely to be, or may be, associated with relationship type. The SDI provides three scales: solitary SDI, dyadic SDI, and total SDI. Information about menstrual cycle status was collected but was not used for statistical control of menstrual phase. Though studies have shown that variables related to partnering or sexuality can shift over the menstrual cycle (e.g. Gangestad, Simpson, Cousins, Garver-Apgar, and Christensen, 2004; Jones et al., 2005), research has found that these menstrual phase does not need to be controlled unless cycle phase is of interest (Dabbs and de La Rue, 1991).

Saliva samples were collected in polystyrene tubes pretreated with sodium azide, and frozen after collection at -20°C until assay. Saliva was stimulated with the use of an inert gum (Trident cherry sugar-free). The samples were assayed for testosterone using radioimmunoassay in one batch at the Endocrine Core Lab at Yerkes National Primate Research Center, Emory University, all in triplicate, using a modified kit from Diagnostic Systems Laboratories (Webster, TX). The sensitivity was 2-500 pg/mL per 200 uL dose, and the interassay coefficient of variation was 8.77% at .65 ng/mL and 6.88% at 5.06 ng/mL. The intra-assay coefficient of variation was 6.54% at 98.82 pg/mL.

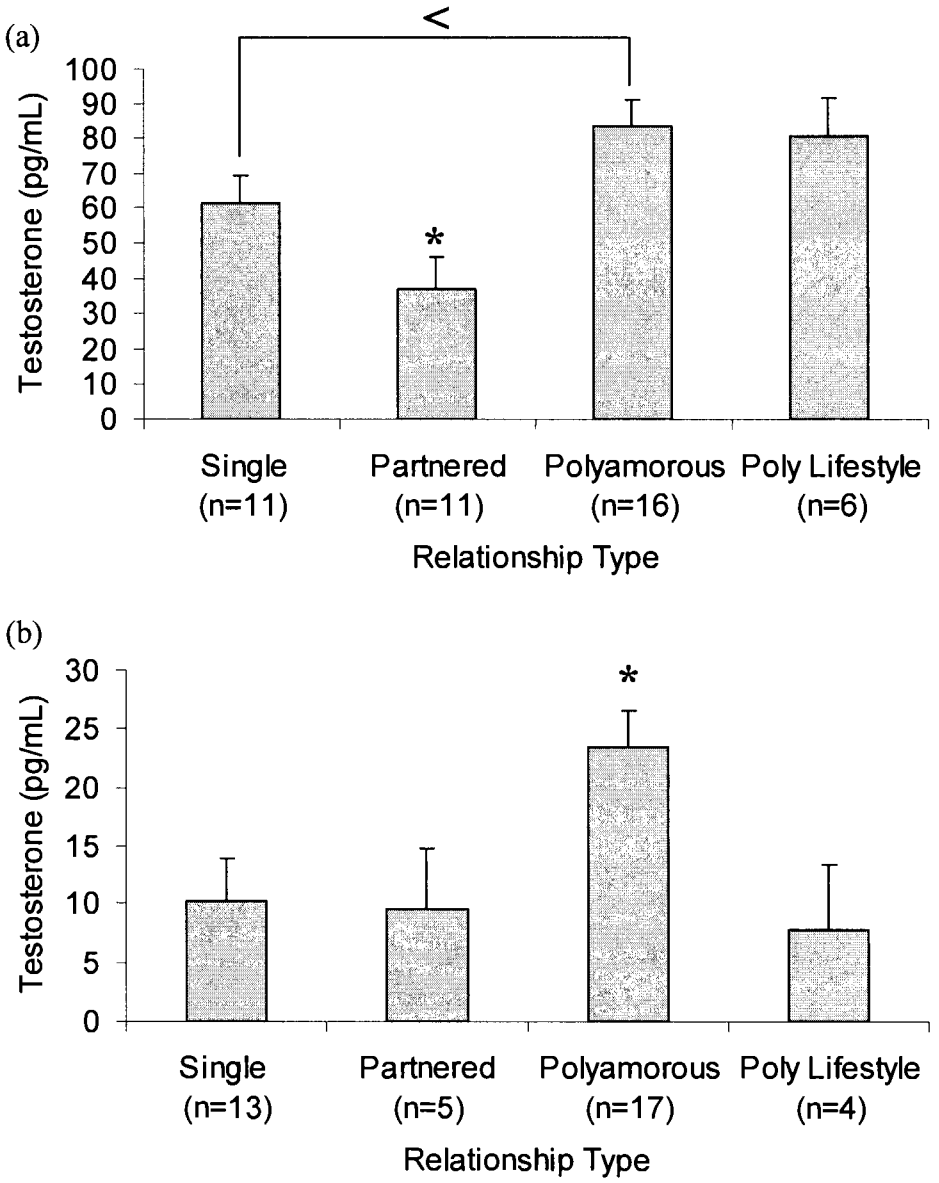
5.4 Results

Analyses were conducted with the Statistical Package for the Social Sciences (SPSS), v. 13.0. Group differences were analysed with analyses of covariance (ANCOVA) separately for sex. Main effects of relationship type were evaluated with the LSD (Least Significant Difference) test after significant omnibus analyses. Covariates for analyses with testosterone included age, sampling time, and sampling month, since all are associated with testosterone and may be confounded with relationship status as per testing times. Correlations were conducted with Pearson Product Moment Correlations and partialled the effects of age. Poly lifestyle women ($n = 4$) and men ($n = 6$) were included in analyses for exploratory purposes, since there were not specific relevant hypotheses but they constituted a group of interest for future study.

5.4.1 Relationship Type and Testosterone in Men

To see if men's testosterone differed as a function of relationship type, a univariate ANCOVA was conducted. There was a significant overall effect, $F(3,37) = 4.33$, $p = .010$, partial $\eta^2 = .260$ (see Figure 6a). Partnered men had significantly lower testosterone than single men, $p = .033$, polyamorous men, $p = .001$, and poly lifestyle men, $p = .005$. There was a trend for polyamorous men to have significantly higher testosterone than single men, $p = .073$. Controlling for BMI (body mass index: a measure of weight corrected for height) only increased the effect size (partial $\eta^2 = .293$) and resulted in the same pattern of significant results. Controlling for sexual orientation did not change the pattern of significant results. The association between testosterone and relationship type was not dependent on SOI, since controlling for SOI did not change the pattern of significant results.

Figure 6. Mean testosterone with standard error bars by relationship type and gender/sex, adjusted for age, sampling month, and sampling time.



Note: (a) Men; (b) Women; 'Poly Lifestyle' indicates participants not currently with multiple partners but identifying as having a poly approach to relationships. '*' indicates a significant difference from all other means at $p < .05$; '<' indicates a trend towards a significant difference from other means at $p < .10$.
Source: van Anders et al. (2007), by permission

5.4.2 Relationship Type and Testosterone in Women

There was one outlier who exhibited a testosterone value that was over eight

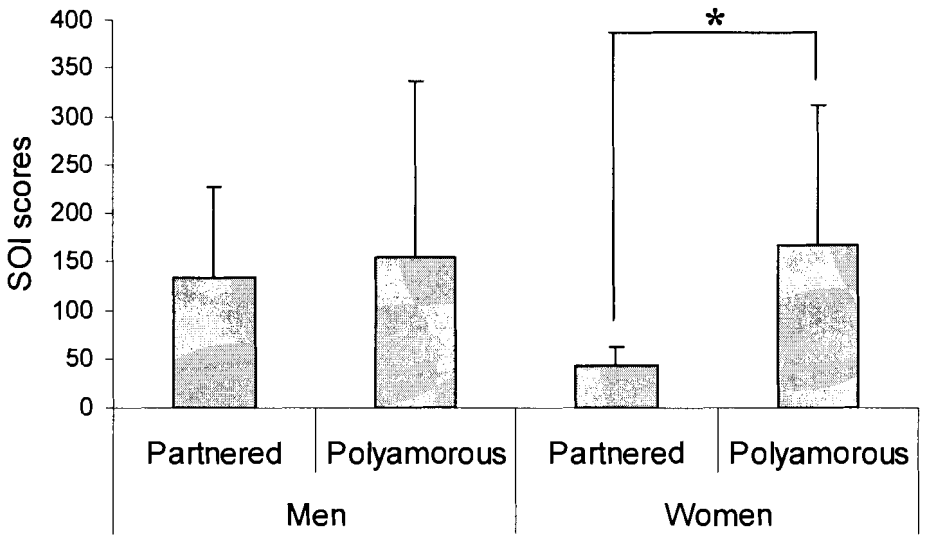
standard deviations away from the mean, which may have reflected blood contamination of the saliva sample; this participant was excluded from the endocrine assays and this reduced the number of partnered women to five. To see if women's testosterone differed as a function of relationship type, a univariate ANCOVA was conducted. There was a significant overall effect, $F(3,32) = 3.83$, $p = .019$, partial $\eta^2 = .264$ (please see Figure 6b). Polyamorous women had significantly higher testosterone than single women, $p = .020$, partnered women, $p = .020$, and poly lifestyle women, $p = .023$. Controlling for BMI or sexual orientation did not change the overall pattern of significant results. As in men, the association between testosterone and relationship type was not dependent on SOI, since controlling for SOI did not change the pattern of significant results.

5.4.3 Sociosexual Orientation Scores and Sexual Desire by Relationship Type

Polyamory relates to multiple relationships, but also commitment within these, so it is unclear whether SOI scores should differ between polyamorous and partnered individuals. An independent *t*-test was conducted to see if SOI scores differed as a function of relationship type (partnered vs. polyamorous) (see Figure 7). Polyamorous women did have significantly less restricted SOI scores than partnered women, $t(17) = -3.31$, $p = .004$. One man from the polyamory group was excluded who had an SOI score over 17 standard deviations away from the mean. There was no significant difference in SOI scores between partnered and polyamorous men, $t(19) = .121$, $p = .732$.

To determine whether sexual desire differed by relationship type, separate ANCOVAs by sex were conducted with the three SDI measures (solitary, dyadic, total) as the dependent measures and relationship status as the independent measure, and age as the covariate (because sexual desire tends to decrease with age). In men, there were no

Figure 7. Mean SOI scores (sociosexual orientation inventory) with standard deviation bars by gender/sex and relationship type.



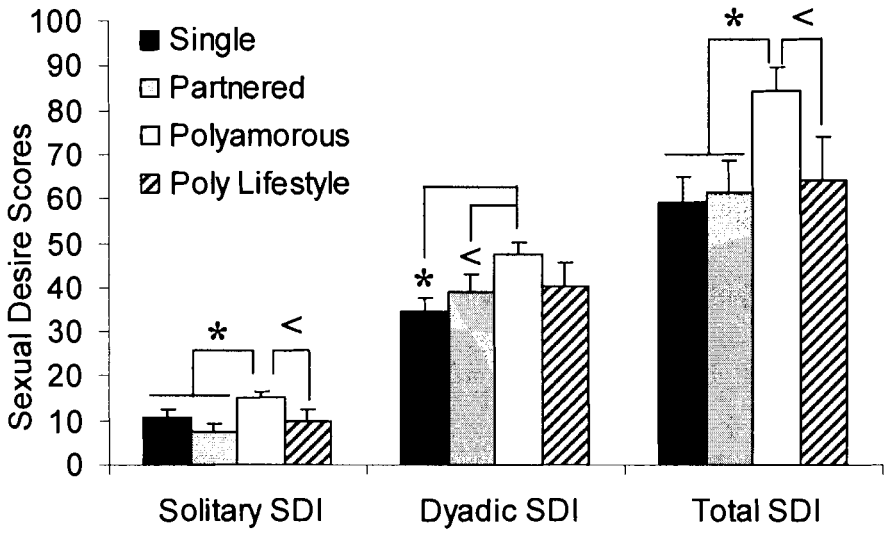
Note: Higher scores represent a less restricted sociosexual orientation. '*' indicates a significant difference from other means at $p < .05$.
Source: van Anders et al. (2007), by permission

significant overall effects of relationship type on solitary SDI, $F(3,35) = .62$, $p = .606$, dyadic SDI, $F(3,35) = .20$, $p = .897$, or total SDI, $F(3,35) = .10$, $p = .99$.

For women, however, there were significant overall effects for solitary SDI, $F(3,35) = 4.24$, $p = .012$, dyadic SDI, $F(3,35) = 2.89$, $p = .049$, and total SDI, $F(3,35) = 4.19$, $p = .012$. Post hoc analyses (see Figure 8) revealed that polyamorous women had significantly higher solitary SDI than single women, $p = .040$, partnered women, $p = .002$, and nearly so compared to poly lifestyle women, $p =. 058$. Similarly, polyamorous women had significantly higher dyadic SDI than single women, $p = .007$, and nearly so compared to partnered women, $p = .092$. Also similarly, polyamorous women had significantly higher total SDI than single women, $p = .004$, partnered women, $p = .014$, and nearly so compared to poly lifestyle women, $p = .073$.

Thus, polyamorous women had significantly less restricted SOI scores than partnered women. And, polyamorous women had significantly higher sexual desire than other women. These differences were not apparent in men.

Figure 8. Women's mean sexual desire (SDI scores) with standard error bars by relationship type.



Note: '*' indicates a significant difference at $p < .05$; '<' indicates a trend at $p < .10$.
Source: van Anders et al. (2007), by permission

5.4.4 Interrelations among SOI, Sexual Desire, and Testosterone

In men, SOI was not significantly correlated with SDI: solitary SDI, *partial* $r(31) = -.16$, $p = .362$, dyadic SDI, $r(31) = -.16$, $p = .362$, or total SDI, $r(31) = .06$, $p = .740$. SOI and testosterone were not significantly correlated, *partial* $r(31) = .08$, $p = .631$. There were no significant correlations between testosterone and any of the individual SOI questions. Testosterone was not significantly correlated with SDI scores with age controlled: solitary SDI, *partial* $r(35) = .07$, $p = .677$, dyadic SDI, *partial* $r(35) = -.05$, $p = .753$, total SDI, *partial* $r(35) = -.01$, $p = .933$.

In women, SOI was not significantly correlated with SDI scores: solitary SDI, *partial* $r(33) = .24$, $p = .146$, dyadic SDI, *partial* $r(33) = .20$, $p = .235$, or total SDI, *partial* $r(32) = .23$, $p = .172$. SOI and testosterone were not significantly correlated, *partial* $r(29) = -.04$, $p = .840$. However, testosterone was significantly correlated with two of the behavioural SOI questions: number of partners in the previous year, *partial* $r(31) = .44$, $p = .008$, and number of different sexual partners expected for the next five years, *partial* $r(30) = .45$, $p = .007$. This is likely explained by the association between multiple partners and higher testosterone. Testosterone was not significantly correlated with dyadic SDI, *partial* $r(31) = .22$, $p = .200$, or total SDI, *partial* $r(30) = .27$, $p = .130$, but there was a trend for solitary SDI, *partial* $r(31) = .33$, $p = .053$.

5.5 Discussion

The present study examined testosterone (T) levels in women and men who were single, in monoamorous relationships (partnered), in polyamorous relationships, or in a polyamorous lifestyle. Results showed that testosterone was lower in partnered men than in single, polyamorous, or poly lifestyle men. This replicates previous findings showing that testosterone is higher in unpartnered than partnered men (e.g. Booth and Dabbs, 1993; Mazur and Michalek, 1998; Gray et al., 2002; van Anders and Watson, 2006a). This study is the first to report that testosterone is higher in polyamorous than partnered men using a sufficient sample size, supporting the first hypothesis. Presumably, polyamorous individuals have a higher likelihood of additional partners (as this is explicitly part of their approach to relationships), which fits a competitive-type situation and should be associated with higher testosterone under the testosterone trade-off framework (van Anders and Watson, 2006b). There was also a trend for polyamorous

men to exhibit higher testosterone than single men. This supports (partially) the hypothesis that polyamorous men would display higher testosterone than single men, because polyamory is explicitly oriented toward the likelihood of new partners in a way that being single is not.

The men's data suggest that having a partner, per se, is not associated with lower testosterone, since polyamorous men who had multiple partners exhibited higher testosterone than monoamorously partnered men. This is similar to Gray (2003), where polygynously married men had higher testosterone than monogamously married men. Though sample sizes were comparable to similar studies, replication with larger *n*'s is still warranted. Still, previous studies have shown that higher testosterone is associated with a competitive relationship orientation (propensity to enter relationships), including more sexual partners (Bogaert and Fisher, 1995; Cashdan, 1995), more extra-marital sex (Booth and Dabbs, 1993), less need for long-term commitment (Cashdan, 1995), and less relationship commitment (in partnered men: McIntyre et al., 2006). And, longitudinal studies have shown that testosterone is higher in consistently single men and in men who divorce than in consistently wed men (Mazur and Michalek, 1998), and that higher testosterone predicts staying unpartnered (van Anders and Watson, 2006a).

These findings suggest that the testosterone-partnering link in men is not driven by sexual desire or SOI, which did not differ significantly by relationship type, or even sexual activity, which likely did differ between single and polyamorous men. SOI, it should be noted, is a measure of willingness to engage in sexual activities outside of an exclusive pair bond, and as such does not address multiple partners of a sexual *and* romantic nature. An interesting aspect of polyamory is its focus on emotional

commitment with multiple partners. Thus, men who were mono- or polyamorously partnered may have been similarly oriented toward bond-maintenance behaviours. It would thus be interesting to include men in multiple but not committed relationships in the future.

The results from women show that polyamorous women have higher testosterone than other women who are single, partnered, or in a poly lifestyle. These results support the first hypothesis that polyamorous women would have higher testosterone than partnered women, and support the second hypothesis that polyamorous women would have higher testosterone than single women. These hypotheses, again, were based on the notion that polyamory would be a competitive-type context and thus associated with higher testosterone in the testosterone trade-off framework (van Anders and Watson, 2006b). There was an implicit hypothesis, however, that was unsupported: that single women would have higher testosterone than partnered women. This too was based on the testosterone trade-off framework, as well as past research. These results should be cautiously interpreted in light of the small sample of partnered women, and further replication is warranted. One previous study has found that partnered women have lower testosterone than unpartnered women, though this only reached significance in non-heterosexual women (van Anders and Watson, 2006a). The only other study that has examined partnering and testosterone in women found that physical partner presence is associated with lower testosterone (van Anders and Watson, 2007b). Similar to the present study, these results were still apparent when analyses controlled for sexual orientation. Thus, though the findings from women in the present study confirmed the explicit hypotheses, they are not entirely consistent with expectations.

The finding of higher sexual desire and SOI scores in polyamorous women may reflect trait and/or state associations. Accordingly, women may be more likely to be polyamorous because of higher sexual desire (or less restricted sociosexuality), or having more partners may increase women's sexual desire (or lead to less restricted sociosexuality). The present study did not have a longitudinal component, so the former cannot be addressed. However, the finding that polyamorous women had a trend towards higher sexual desire than poly lifestyle women supports the latter. Since women who were oriented towards multiple partners (i.e. poly lifestyle) had lower sexual desire than women who currently had multiple partners (i.e. polyamorous women), the interpretation that multiple partners might increase sexual desire could be supported. Would imagining other sexual partners be similarly associated with higher sexual desire? If so, would there be a causal direction to this? The association between multiple partners and higher sexual desire is interesting and, with additional research, may prove to be informative and useful to researchers in the field of sexual desire (including low sexual desire).

Replications and extensions with both men and women are warranted because of both the smaller sample sizes (especially in monoamorously partnered women) and recruitment. The majority of the polyamorous individuals were recruited from polyamory group meetings or listservs with a minority through advertisements, whereas the majority of non-polyamorous participants were recruited through advertisements or general listservs. It is possible, then, that the polyamorous participants, who belonged to these groups, may have been more generally social than the non-polyamorous participants.

The data are beginning to consistently point to an association between relationship orientation and testosterone in men, but the association between testosterone

and partnering in women appears to be either more complex or less immediately apparent. In women, findings support both a state interpretation (i.e. that relationship status is associated with testosterone), and a trait interpretation (i.e. that testosterone predicts partnering). Still, lower testosterone is at least consistently found in women who are in relationships with one person, though this is not always the exclusive case and there appear to be inconsistent moderators of this association (e.g. sexual orientation). Only further data will clarify the underlying pattern in women, and will be valuable in our understanding of how androgens and partnering are associated.

6 CONCLUSIONS ON PARTNERING AND HORMONES

Note: This section is based on the following article, with permission: van Anders, S. M. & Watson, N. V. (2006b). Social neuroendocrinology: Effects of social contexts and behaviors on sex steroids in humans. *Human Nature, 17,* 212-237.

6.1 Summary of Main Findings and Synthesis

In Sections 3, 4, and 5, I described studies that examined associations between testosterone and partnering in men and women. Findings from this research show that testosterone is lower in men who are monoamorously partnered than men who are unpartnered or polyamorous (van Anders and Watson, 2006a; 2007b; van Anders et al., 2007), but possibly only in heterosexual men (van Anders and Watson, 2006a). This fits with past research that has shown that single men have higher testosterone than partnered men (e.g. Booth and Dabbs, 1993; Mazur and Michalek, 1998; Gray et al., 2004a; 2004b), but extends this pattern to include a contrast between partnered and unpartnered (single, dating, nonmonogamously partnered) men based on the testosterone trade-off framework. Additionally, findings show that physical partner presence is not associated with lower testosterone in men, as men in same-city relationships show comparable testosterone levels to men in long-distance relationships (van Anders and Watson, 2007b). Further, results from this dissertation show that men who are currently polyamorous or have polyamorous approaches to relationships have higher testosterone than both monoamorously partnered men and single men (van Anders et al., 2007).

The research with women has shown that partnering and testosterone are associated in women in ways that are complex, and less immediately apparent in comparison to men. For example, sexual orientation appears to at times moderate the partnering-testosterone association. As described in Section 3, research shows that partnered non-heterosexual women have lower testosterone than unpartnered non-heterosexual women (van Anders and Watson, 2006a). In contrast, evidence from other research (van Anders et al., 2007; van Anders and Watson, 2007b) does not suggest that sexual orientation moderates testosterone-partnering associations. Instead, there are effects in women when sexual orientation is statistically controlled or when heterosexual women only are included in analyses. Other findings show that physical partner presence is associated with lower testosterone in women, as same-city partnered women exhibited lower testosterone than single women (van Anders and Watson, 2007b), and that currently having multiple partners is associated with higher testosterone, as polyamorous women had higher testosterone than single women, monoamorously partnered women, and poly lifestyle women (van Anders et al., 2007).

Relevant research with women is in its infancy, and no other labs have examined how partnering and women's testosterone are associated. The findings with women cannot, therefore, be contextualised in a broader literature at this point. Still, findings from the three studies described in this dissertation are suggestive that partnering and testosterone are associated in women in some way, perhaps moderated by partner presence and sexual orientation. Though the relationship between testosterone and partnering in women is far from clear at present, it is noticeable, however, that findings

are consistent in one respect: monoamorously partnered women generally exhibit lower testosterone than other women.

I have generally used 'partnering' throughout this dissertation, but terminology differs among various authors and includes partnering, mating, and pair bonding. Research and results reported in this dissertation can help to refine what it is about partnering or pair bonding that is associated with testosterone. It appears likely that the term 'partnering' in the statement 'partnering is associated with lower testosterone' should be understood to mean partnering that occurs in a 'pair bond' context. It is of a romantic and/or sexual nature; primarily the term appears to connote a committed bond-maintenance relationship, at least in how it can defined based on endocrine findings in human populations. Since multiple partners are associated with higher testosterone, it might be possible to suggest that lower testosterone is associated with pair bonding, instead of partnering, so long as pair bonding is understood to mean a committed and focused relationship of a bond-maintenance nature. However, supplemental analyses on data reported in this dissertation suggest that feelings of commitment are not associated with testosterone (making the term pair bonding perhaps less immediately appropriate).

Currently, research in this field has generally not included social psychological perspectives on personal relationships. For example Diamond (1999) makes a compelling case for the distinction between romantic love and sexual lust, such that there may be different systems for each that are, nevertheless, interconnected. Gonzaga, Turner, Keltner, Campos, and Altemus (2006) report on different correlates for sexual desire (e.g. arousal) and love (e.g. happiness), and that behavioural cues also differ for sexual desire (e.g. sexual cues) and love (e.g. affiliative cues). As noted, endocrine research on

relationships has found that bond-maintenance committed relationships are generally associated with lower testosterone. At the same time, sexual activity is generally associated with higher testosterone (e.g. van Anders et al., in press) but can also facilitate pair bonding (Young et al., 2005) and feelings of intimacy (van Anders et al., in press). In light of these seemingly conflicting patterns (i.e. higher testosterone *and* increased bonding or feelings of intimacy after sexual activity), attending to Diamond's perspectives is likely to be helpful to delineating the aspects of partnering that are associated with higher or lower testosterone.

What brain areas are associated with androgen-partnering links? Neural substrates have not been well mapped out in relation to this question, but research with oxytocin, vasopressin, and the HPA axis in animals (e.g. voles) and humans provides an excellent starting point. Areas like the striatum, ventral pallidum, and nucleus accumbens show higher densities of oxytocin, vasopressin, and corticotrophin releasing factor receptors (respectively) in monogamous pair bonding prairie voles compared to polygamous montane voles (Young et al., 2005). Whether these areas differentially express androgen receptor density has not been established. Young et al. (2005) describe possible neural circuitry associated with pair bonding in voles, with three subcircuits respectively associated with oxytocin, dopamine, or vasopressin. These authors suggest that these three circuits may be differentially associated with social memory, sexual activity, and the reward system, but act together in ways that affect pair bonding. Whether testosterone influences this circuitry, or is associated with additional circuitry that interacts is unclear at present.

Research with humans has shown that individuals in love exhibit neural responses to pictures of their 'beloved' that differs from neural responses to images of acquaintances (Bartels and Zeki, 2000). These areas include the insula, putamen, and anterior cingulate, which are putatively associated with emotions, positive emotions and dopamine, and emotions and social interactions (Bartels and Zeki, 2000). Basal or trait hormone levels (like testosterone) have not been examined with respect to neural activity in these areas known to be related to pair bonding or partnering.

Circulating testosterone (or oxytocin, or vasopressin, or cortisol) informs researchers of only part of the story, since hormones act in concert with other hormones. No human partnering studies (excepting early stage love) have included oxytocin, vasopressin, and cortisol with testosterone, and the inclusion of these hormones known to be related to pair bonding will likely provide additional dimensions to our understanding. We do not currently know whether partnered people exhibit levels of oxytocin or vasopressin that differ from unpartnered people, or whether these peptide hormones might predict partnering in the way that testosterone appears to. The inclusion of steroids (like testosterone and cortisol) and peptides (like oxytocin or vasopressin) is likely to provide a much more comprehensive picture of partnering-hormone associations.

At present, debates continue about directionality in men and women, with some interpreting the evidence as supporting a relationship orientation interpretation (i.e. that lower testosterone predicts partnering) and others supporting a relationship status interpretation (i.e. that partnering decreases testosterone). This next section details how findings from this dissertation contribute to directional interpretations and understandings.

6.2 Partnering and Testosterone: Directional Interpretations

Previous evidence from Booth and Dabbs (1993) and Mazur and Michalek (1997) could be seen as supporting state interpretations (i.e. that partnering behaviours decrease testosterone; see van Anders and Watson, 2006b). As detailed below however, findings in men at this point generally point towards a trait effect (i.e. that testosterone predicts partnering).

Though behaviours related to partnering may have transient state effects on testosterone, there is no simply no evidence at present that entering or being in a relationship decreases testosterone. For example, Gray et al. (2004a) examined whether men's testosterone differed on days spent with wives and offspring versus days spent at work, but found no difference between testosterone levels according to how a day was spent despite expectations. Longitudinal findings from a study with women and men showed no evidence that entering a relationship decreased testosterone (van Anders and Watson, 2006a). In a much larger longitudinal study, Mazur and Michalek (1998) found that individuals who changed marital status or remained single had similarly higher testosterone than individuals who remained married. They did find that divorce was associated with increased testosterone, but this was a time-linked transient increase in testosterone such that after the period of divorce, divorced men's testosterone had decreased to pre-divorce levels. Similarly, early stage love was found to be possibly associated with alterations in androgen levels, but this change appeared to be transient only (Marazziti and Canale, 2004). In a study on potential cues to relationship status, results showed that men who were long-distance partnered and same-city partnered had similarly lower testosterone than single men (van Anders and Watson, 2007b). This

suggests that men who are partnered exhibit lower testosterone than men who are not, even when cues to being partnered and partner-related behaviours differ in frequency and kind as they must between long-distance and same-city partnered men.

Though there is no evidence that entering or being in relationships decreases testosterone, there is evidence that low testosterone predicts entering committed relationships and high testosterone predicts exiting them. For example, in the longitudinal study described above, unpartnered individuals with lower testosterone were more likely to enter relationships than unpartnered individuals with higher testosterone (van Anders and Watson, 2006a). The finding that partnered men (regardless of partner presence) have lower testosterone than single men has been interpreted as evidence for an association between testosterone and relationship orientation because men who are long-distance partnered and thus unable to engage in the day-to-day partner-related behaviours exhibit lower testosterone than single men and similar testosterone to same-city partnered men (van Anders and Watson, 2007b). In addition, McIntyre et al. (2006) have found that being in a relationship is not associated with lower testosterone if partnered individuals are interested in and expect to engage in extra-pair sexual encounters. And, being multipartnered is associated with higher testosterone (Gray, 2003; van Anders et al., 2007). Thus, for men, one's *orientation* towards relationships (e.g. attitudes, likelihood of future behaviour, etc.) appears to be more strongly related to testosterone than one's current relationship *status*. This is the case based on current empirical research.

Relatedly, Gray et al. (2004b) have shown that single men with prior experience in a relationship exhibit higher testosterone than single men without prior relationship experience. This finding is very closely related to Roney et al.'s (2003) finding of greater

testosterone increases in men who have had previous sexual experience. It is possible that prior sexual experience sensitises the HPG axis, but arguably more parsimonious to interpret the finding that men with higher testosterone are more likely to have sexual encounters than that the experiences changed trait levels of testosterone (though this remains possible). Again, this supports a testosterone-relationship orientation interpretation. Of course, only further evidence will clarify whether testosterone is related to relationship orientation or status – or both.

Interestingly, there appear to be both gender similarities and gender differences in the pattern of associations between testosterone and partnering. The most obvious and major gender similarity is, of course, that testosterone and partnering are associated in both men and women. However, that the data are suggestive of associations between relationship orientation and testosterone in men, but may be pointing more towards associations between relationship status and testosterone in women, is indicative of gender differences in the overall pattern. If women's testosterone-partnering associations were secondary to evolutionary selective pressures that had acted upon men, then it could be expected that the pattern of associations in women should be similar to the pattern in men. The findings from this dissertation may thus be suggestive of direct selection pressures on women's androgen-partnering associations. The link between partnering and testosterone in men may, therefore, be dependent on very different mechanisms than in women.

Hormone levels are extremely responsive to environmental stimuli, and, as such, are measures of contextualised physiology or, in other words, a person's physiology as they interact with the world. If relationship orientation is associated with testosterone, i.e.

if a lower characteristic level of testosterone is associated with a characteristic approach to relationships, the focus may move to developmental trajectories for this lower trait testosterone. As traits can be 'inborn' or developed, it may well be that personality traits and associated ways of thinking about and engaging in the social world lead to higher or lower testosterone. Engaging with the social world might then influence directly the likelihood of partnering, which might be further influenced by trait testosterone. This is supported by the majority of evidence linking afternoon and evening, but not morning, testosterone to partnering. We know that partner-related behaviours do not lead to lower testosterone over the day (Gray et al., 2004a). But, we do not know that an ongoing trait way of existing in the social world that is also associated with being partnered does not lead to overall trait levels of testosterone.

Further complicating the issue of relationship status/orientation or state/trait interpretations in neuroendocrine research, however, is the lack of a clear dividing line between trait and state effects. Specific behaviours reducing testosterone are certainly state effects, and levels of testosterone predicting partnering are certainly trait effects. But, if people significantly change their pattern of behaviour and thought when they enter a relationship, and this change is consistent and maintained for the entire duration of their relationship for up to 10 or even 50 years, whether associated lower levels of testosterone would represent a state or trait effect is unclear.

Existing research and findings presented in this dissertation on the associations between partnering and testosterone in women and men thus introduce important neuroscientific (e.g. neural substrates), behavioural neuroendocrine (e.g. androgens; other hormones), psychological (e.g. state/trait; directionality), and evolutionary (e.g.

testosterone trade-offs) questions. Clearly, the fundamental nature of partnering and pairbonding in human affairs and behaviour calls for continued research that attempts to answer these questions.

7 APPENDICES

7.1 Appendix One: Study 1 Questionnaire

Please answer the following questions to the best of your ability. Your responses are strictly confidential and will be used for research purposes only. Your responses will be identified only by a confidential participant number.

1. Age: _____

2. Sex: _____

3. In the last hour, have you: (please circle your answers)

a) Had anything to eat?	YES	NO
b) Had a beverage other than water?	YES	NO
c) Had a cigarette or other nicotine?	YES	NO
d) Brushed your teeth?	YES	NO

4. What is your occupation? _____

5. Are you currently taking any prescription or non-prescription medications, oral contraceptives, or other hormone supplements? (please circle one)

NO; I am not currently taking any medications.

YES; (please list the medications you are taking): _____

_____

6. What is the highest level of education you completed? (please circle one)

Grade 6 or less

Grade 7 – 9

Some high school

High school graduate

At least one year of college, university, or other specialized training

College or university graduate

Some graduate school or professional degree (e.g. MD, PhD, etc)

Master's degree, PhD, MD, or other professional degree

7. Relationship Status (please check all that apply):

-Single

-Dating but not in a long-term relationship

-In a monogamous (just you + your partner) relationship but not living together

-Cohabiting (living and having with a relationship with a same- or opposite sex individual for less than 12 months)

-Common-law (living and having a relationship with a same- or opposite-sex individual for 12 months or more)

-Married

-Divorced/widowed/separated

-In a nonmonogamous relationship, and living with at least one of your partners

-In a nonmonogamous relationship, but not living with any of your partners

8. Do you live with anyone other than a spouse/partner?

NO

YES (please identify, e.g. roommate, mother, child etc): _____

9. Are you sexually active at present (either solitarily or with a partner)?

YES NO

10a. Are you using hormonal contraceptives (e.g. birth control pills, Norplant) at present, either for contraceptive or other reasons? YES NO

10b. If you are not using hormonal contraceptives at present, but you did in the past, how long ago did you discontinue them? _____

11. What is your weight (please indicate kg or lbs): _____

12. What is your height (please indicate m, cm, inches, feet): _____

13. At present, do you have any type of infection (e.g. flu) or physical condition that might alter your hormones (e.g. PCOS)?

YES NO

14. Which of the following best describes your actual sexual experiences (including romantic kissing, petting, intercourse, etc) from puberty until now? Heterosexual refers to interaction with the opposite sex, homosexual refers to the same sex as yourself. Please check one.

_____ Exclusively heterosexual with no homosexual contact

_____ Predominantly heterosexual with only a few homosexual contacts

_____ Predominantly heterosexual with more than a few homosexual contacts

_____ Equally heterosexual and homosexual in contact

_____ Predominantly homosexual with more than a few heterosexual contacts

_____ Predominantly homosexual with only a few heterosexual contacts

_____ Exclusively homosexual with no heterosexual contact

15. Which of the following best describes your sexual fantasies from puberty until now? Please check one.

_____ Exclusively heterosexual with no homosexual fantasies

_____ Predominantly heterosexual with only a few homosexual fantasies

_____ Predominantly heterosexual with more than a few homosexual fantasies

_____ Equally heterosexual and homosexual in fantasies

_____ Predominantly homosexual with more than a few heterosexual fantasies

_____ Predominantly homosexual with only a few heterosexual fantasies

_____ Exclusively homosexual with no heterosexual fantasies

16a. Do you have children? YES NO

16b. If yes, did you give birth to them? YES NO

16c. If you have children, how many children do you have, and what are their ages?

_____

Sleep/Wake Cycle:

1. What time do you normally wake up on weekdays? (please indicate am/pm)

2. What time do you normally wake up on weekends? (please indicate am/pm)

3. What time did you go to sleep last night? (please indicate am/pm)

4. What time did you get up this morning? (please indicate am/pm)

5.If you didn't have to wake up because of external circumstances like school or work, when would you most prefer to wake up? (please check one)

_____ Before 6:30am

_____ 6:35am-7:30am

_____ 7:35am-9:00am

_____ 9:05am-10:30am

_____ 10:35am-12:00pm

_____ 12:05pm-1:30pm

_____ after 1:35 pm

Relationship Only:

1. How long have you been in this relationship?
    a) Less than 1 month
    b) 1 month to 6 months
    c) 6 months to 1 year
    d) 1-2 years
    e) 2-5 years
    f) 5-10 years
    g) More than 10 years

2. How committed are you to this relationship?
    a) Extremely committed
    b) Very committed
    c) Moderately committed
    d) Somewhat committed
    e) A bit committed
    f) Not really committed
    g) Not at all committed

3. How likely do you think it is that you will stay in a relationship with this person "forever"?
    a) Extremely likely
    b) Moderately likely
    c) Somewhat likely
    d) Neither likely nor unlikely
    e) Somewhat unlikely
    f) Moderately unlikely
    g) Extremely unlikely

4. How sexually attracted have you been to this person over the last month?

a) Extremely sexually attracted

b) Very sexually attracted

c) Moderately sexually attracted

d) Somewhat sexually attracted

e) A bit sexually attracted

f) Not really sexually attracted

g) Not at all sexually attracted

5. How frequently have you engaged in sexual activity of any kind with this person over the past month?

a) less than once per month

b) 1-3 times per month

c) once per week

c) 2-4 times per week

d) 5-6 times per week

e) once per day

f) more than once per day

6. What sex is your partner? _____

Women Only:

1. What is the normal length of your menstrual cycle, from the first day of one menstrual period to the first day of the next menstrual period? (please circle one)

a) 23 days or less

b) 24-26 days

c) 27-30 days

d) 31-34 days

e) 35 days or more

2. How regular are your menstrual cycles in their time of onset? (Please circle one)

a) perfectly regular

b) varies by 1-2 days

c) varies by 3-4 days

d) varies by 5-6 days

e) varies by 7 days or more

f) completely unpredictable

3. Are you pregnant or breast-feeding an infant at present? YES
NO

4. Do you ever go through long periods of time without having menstrual periods (for reasons other than pregnancy)? YES

NO

If yes, has this happened in the last 12 months? YES

NO

5. Are you currently menstruating? YES

NO

If yes, what date did your current period begin? _____

If no, what date did your last period begin? _____

7.2 Appendix Two: Study 2 Questionnaire

Please answer the following questions to the best of your ability. Your responses are strictly confidential and will be used for research purposes only. Your responses will be identified only by a confidential participant number. Please fill in responses or circle the appropriate answer. If a question does not fit you well, feel free to write in an answer.

1. Age: _____
2. Sex/Gender: _____
3. In the last hour, have you:
    a. Had anything to eat? YES NO
    b. Had a beverage other than water? YES NO
    c. Had a cigarette or other nicotine? YES NO
    d. Brushed your teeth? YES NO
4. If you are employed, what is your occupation? _____
5. Are you a student? YES NO
    a. If YES, at what level (e.g. undergrad, MA, PhD)?: _____
6. Are you currently taking any prescription or non-prescription medications, hormonal contraceptives (e.g. the Pill), or other hormone supplements?
    a. NO; I am not currently taking any medications
    b. YES; (please list the medications you are taking): _____

    _____
7. What is the highest level of education you have completed?
    a. Grade 6 or less
    b. Grade 7 – 9
    c. Some high school
    d. High school graduate
    e. At least one year of college, university, or other specialized training
    f. College or university graduate
    g. Some graduate school or professional degree (e.g. M.Sc., Ph.D., M.D.)
    h. Master's degree, Ph.D., M.D., or other professional degree

8. Relationship status (please circle all that apply):

-Single

-Dating one person and not in a long-term relationship

-Dating more than one person and not in a long-term relationship

-In a long-term relationship with one person for **less** than 12 months

-Having a long-term relationship with one person for **more** than 12 months

-Married/Common-law

-Divorced/Separated

-Widowed

-In a long-term relationship with **one** person and having other casual partners

-In a long-term relationship with more than **one** person and **no** casual partners

-In a long-term relationship with **more** than one person and having other casual partners

9. Do you live with anyone other than a partner?
    a. NO: I live alone.
    b. NO: I live with my partner.
    c. YES: (please identify with gender, e.g. mother, male roommate)

    _____

10. Are you sexually active solitarily (i.e. masturbation)?
    a. NO: I am not solitarily sexually active.
    b. YES: i) once/month ii) 2-3 times/month iii)once/week
       iv) 2-4 times/week v) once/day vi) more than once/day

11. Are you using hormonal contraceptives at present (e.g. birth control, the Pill, Norplant), either for contraceptive or other reasons? YES NO
    a. If YES, what kind? _____
    b. If NO, have you used them in the past? YES NO
        i. If YES, how long ago did you discontinue using them? _____

12. What is your weight? (please indicate kg or lbs) _____

13. What is your height (please indicate metres, or feet/inches): _____

14. What is your sexual orientation? _____

15. At present, do you have any type of infection or physical condition that you know might alter your hormones (e.g. PCOS)? YES NO

16. Which of the following best describes your actual sexual experiences (including romantic kissing, petting, intercourse, etc.) from puberty until now? Heterosexual refers to interaction with the opposite sex, homosexual refers to the same sex as yourself. Please check one.

-No sexual contact

-Exclusively heterosexual with no homosexual contact

-Predominantly heterosexual with only a few homosexual contacts

-Predominantly heterosexual with more than a few homosexual contacts

-Equally heterosexual and homosexual in contact

-Predominantly homosexual with more than a few heterosexual contacts

-Predominantly homosexual with only a few heterosexual contacts

-Exclusively homosexual with no heterosexual contact

17. Which of the following best describes your sexual fantasies from puberty until now? Please check one.

-No sexual fantasies

-Exclusively heterosexual with no homosexual fantasies

-Predominantly heterosexual with only a few homosexual fantasies

-Predominantly heterosexual with more than a few homosexual fantasies

-Equally heterosexual and homosexual in fantasies

-Predominantly homosexual with more than a few heterosexual fantasies

-Predominantly homosexual with only a few heterosexual fantasies

-Exclusively homosexual with no heterosexual fantasies

18. How many sexual/romantic partners have you had in your lifetime?

    a. None

    b. One or more (please indicate how many): _____

19. Do you have children? YES NO

    If YES, are they biologically related (you gave birth or sperm)? YES NO

    If YES, how many do you have, and what are their genders and ages?

    _____

20. What time do you normally wake up on weekdays? (please indicate am/pm)
21. What time do you normally wake up on weekends? (am/pm) _____
22. What time do you normally go to sleep on weekdays? (am/pm) _____
23. What time do you normally go to sleep on weekends? (am/pm) _____
24. What time did you go to sleep last night? _____
25. What time did you get up this morning? _____
26. If you didn't have to wake up because of external circumstances like school or work, when would you most prefer to wake up? _____
27. What is your ethnicity? _____
28. How long have you lived in Canada?
    a. All my life b. For this long: _____
29. What is your income range?_____
30. With how many different partners have you had sexual activity in the past yr?
31. How many different partners do you foresee yourself having sex with during the next five years? (Please give a *specific, realistic* estimate). _____
32. With how many different partners have you had sex on *one and only one* occasion? _____
33. How often do you fantasize about having sex (other than with your current dating partner[s])? (Circle one).
    a. Never
    b. Once every two or three months
    c. Once a month
    d. Once every two weeks
    e. Once a week
    f. A few times each week
    g. Nearly every day
    h. At least once a day
34. Sex without love is OK.

1	2	3	4	5	6	7	8	9
I strongly disagree								I strongly agree

35. I can imagine myself being comfortable and enjoying "casual" sex with different partners.

1	2	3	4	5	6	7	8	9
I strongly disagree								I strongly agree

36. I would have to be closely attached to someone (both emotionally and psychologically) before I could feel comfortable and fully enjoy having sex with him or her.

1 2 3 4 5 6 7 8 9

I strongly disagree I strongly agree

37. If you have a partner (with whom you are having a romantic/sexual relationship),
    a. Do you consider your partner your partner for the long-term? YES/NO
    b. How long have you and your partner been together? _____
    c. Have you had sexual or romantic contact with someone other than your partner during the relationship?
        i. NO: I only have romantic/sexual contact with my partner
        ii. YES: i) Once ii) Rarely ii) Sometimes iv) Often v) Regularly
    d. Are you sexually active with your partner?
        i. NO: we do not have sexual contact
        ii. YES: i) once/month ii)2-3 times/month iii) once per week iv) 2-4 times/week v) once/day vi) more than once/day
    e. How committed are you to this relationship?

        (Extremely) 1 2 3 4 5 6 7 (Not at all)
    f. How likely is it that you and your partner will be together 'forever'?

        (Extremely) 1 2 3 4 5 6 7 (Not at all)
    g. How sexually attracted have you been to this person over the last month?

        (Extremely) 1 2 3 4 5 6 7 (Not at all)
    h. What sex is your partner? _____
    i. Does your partner live in the same city as you? YES NO
    j. Do you live with your partner? YES NO
        i. If YES, how long have you lived together? _____
    k. If you do not live with your partner,
        i. How often do you see each other on average? _____

ii. How long each year would you estimate you see your partner in person? (e.g. three weeks in total, every day, etc.) _____

Questions Relevant to Women

1) At what age did you get your first period? _____
2) If you menstruate, what is the normal length of your menstrual cycle, from the first day of one menstrual period to the first day of the next menstrual period?
   a) 23 days or less b) 24-26 days c) 27-30 days
   d) 31-34 days e) 35 days or more f) N/A
3) If you menstruate, how regular are your menstrual cycles in their time of onset?
   a) perfectly regular b) varies by 1-2 days c) varies by 3-4 days
   d) varies by 5-6 days e) varies by 7 days or more
   f) completely unpredictable g) N/A
4) Are you pregnant or breast-feeding an infant at present? YES NO
5) If you menstruate, do you ever go through long periods of time without having menstrual periods (for reasons other than pregnancy)? YES NO
   a) If yes, has this happened in the last 12 months? YES NO
6) Are you having your period today? YES NO
   a) If yes, what date did your current period begin? _____
   b) **If no**, what date did your last period begin? _____
7) If you do not menstruate, why?
   a) I am a post-menopausal woman
   b) I have a clinical condition such that I do not menstruate
   c) I am taking hormonal contraceptives that prevent menstruation
   d) Another reason: _____

7.3 Appendix Three: Study 3 Questionnaire

Please answer the following questions to the best of your ability. Your responses are strictly confidential and will be used for research purposes only. Your responses will be identified only by a confidential participant number. **Please feel free to add in your own comments throughout the questionnaire or on the back of the pages.**

1) Age: _____

2) Sex: _____

3) In the last hour, have you: (please circle your answers)

a)	Had anything to eat?	YES	NO
b)	Had a beverage other than water?	YES	NO
c)	Had a cigarette or other nicotine?	YES	NO
d)	Brushed your teeth?	YES	NO

4) If you are employed, what is your occupation? _____

5) Are you currently taking any prescription or non-prescription medications, oral contraceptives, or other hormone supplements? (please circle one)

   a) NO; I am not currently taking any medications.

   b) YES; (please list the medications you are taking): _____

   _____

6) What is the highest level of education you completed? (please circle one)

   a) Grade 6 or less

   b) Grade 7 – 9

   c) Some high school

   d) High school graduate

   e) At least one year of college, university, or other specialized training

   f) College or university graduate

   g) Some graduate school or professional degree (e.g. MD, PhD, etc)

   h) Master's degree, PhD, MD, or other professional degree

7) What is your guardian(s)'/primary caregiver(s)' occupation? Please identify the individual (e.g. mother, father, grandmother, etc.).
   a) Individual 1: _____
   b) Individual 2: _____

8) What is your guardian(s)'/primary caregiver(s)' highest level of education? Please identify the individual (e.g. mother, father, grandmother, etc.).
   a) Individual 1: _____
   b) Individual 2: _____

9) Until the age of 18, what was your socioeconomic status (e.g. lower, middle, upper, etc.)? _____

10) Currently, what is your socioeconomic status? _____

11) How would you characterize your relationship status? (e.g. single, partnered, dating)

_____

12) What are your living arrangements?
   a) I live alone
   b) I live with others (please identify, e.g. roommate, partner, child, etc.):

_____

13) Over the past month including the present, have you been sexually active with someone?

a. no b. just once c. 2-3 times d. once/week e. 2-4 times/week f. once/day g. more than once per day

14) Over the past month including the present, have you been sexually active *solitarily* (e.g. masturbation)?

a. no b. just once c. 2-3 times d. once/week e. 2-4 times/week f. once/day g. more than once per day

15) Have you engaged in sexual activity with someone in the past year? YES NO

16) Have you ever engaged in sexual activity with someone else? YES NO

17) Are you using hormonal contraceptives (e.g. birth control pills, Norplant) at present, either for contraceptive or other reasons? YES NO

18) If you are not using hormonal contraceptives at present, but you did in the past, how long ago did you discontinue them? _____

19) What is your weight? (please indicate kg or lbs) _____

20) What is your height? (please indicate m, cm, inches, feet) _____

21) At present, do you have any type of infection (e.g. flu) or physical condition that might alter your hormones (e.g. PCOS)? YES NO

22) What is your ethnicity? _____

23) How long have you lived in Canada?

a) All my life

b) For this long: _____

24) What is your sexual orientation? _____

25) Has your sexual orientation changed over time?

a) No

b) Yes (please explain): _____

_____

26) Which of the following best describes your actual sexual experiences (including romantic kissing, petting, intercourse, etc) from puberty until now? Heterosexual refers to interaction with the opposite sex, homosexual refers to the same sex as yourself. Please circle one.

a) Exclusively heterosexual with no homosexual contact
b) Predominantly heterosexual with only a few homosexual contacts
c) Predominantly heterosexual with more than a few homosexual contacts
d) Equally heterosexual and homosexual in contact
e) Predominantly homosexual with more than a few heterosexual contacts
f) Predominantly homosexual with only a few heterosexual contacts
g) Exclusively homosexual with no heterosexual contact

27) Which of the following best describes your sexual fantasies from puberty until now? Please check one.

a) Exclusively heterosexual with no homosexual fantasies
b) Predominantly heterosexual with only a few homosexual fantasies
c) Predominantly heterosexual with more than a few homosexual fantasies
d) Equally heterosexual and homosexual in fantasies
e) Predominantly homosexual with more than a few heterosexual fantasies
f) Predominantly homosexual with only a few heterosexual fantasies
g) Exclusively homosexual with no heterosexual fantasies

28) Do you have children? YES NO

29) If yes, did you give birth to them? YES NO

30) If you have children, how many children do you have, and what are their ages?

_____

31) What time do you normally wake up on weekdays?_____ am/pm

32) What time do you normally wake up on weekends?_____ am/pm

33) What time did you go to sleep last night?_____ am/pm

34) What time did you get up this morning? _____ am/pm

35) If you didn't have to wake up because of external circumstances like school or work, when would you most prefer to wake up? (please circle one)

a) Before 6:30am
b) 6:35am-7:30am
c) 7:35am-9:00am
d) 9:05am-10:30am
e) 10:35am-12:00pm
f) 12:05pm-1:30pm
g) after 1:35 pm

Questions Relevant to **Women**:

8) If you menstruate, what is the normal length of your menstrual cycle, from the first day of one menstrual period to the first day of the next menstrual period?

a) 23 days or less b) 24-26 days c) 27-30 days

d) 31-34 days e) 35 days or more f) N/A

9) If you menstruate, how regular are your menstrual cycles in their time of onset?

a) perfectly regular b) varies by 1-2 days c) varies by 3-4 days

d) varies by 5-6 days e) varies by 7 days or more f) completely unpredictable

g) N/A

10) Are you pregnant or breast-feeding an infant at present? YES NO

11) If you menstruate, do you ever go through long periods of time without having menstrual periods (for reasons other than pregnancy)? YES NO

a) If yes, has this happened in the last 12 months? YES NO

12) Are you having your period today? YES NO

a) If yes, what date did your current period begin? _____

b) **If no**, what date did your last period begin? _____

13) If you do not menstruate, why?

e) I am a post-menopausal woman

f) I have a clinical condition such that I do not menstruate

g) I am taking hormonal contraceptives that prevent menstruation

h) Another reason: _____

For People with **NO** Current Romantic/Sexual Partners

(If this does not apply to you, please skip forward to the applicable section).

1) Have you had romantic/sexual partners in the past? YES NO (skip to #2)
   a) How many relationships (not one-nighters) have you had? _____
   b) How many casual partners (not committed relationships) have you had? ___
   c) How long ago did your last relationship end? _____
   d) How long was your last relationship? _____
   e) Have you had relationships with someone other than your partner **without** your partner's knowledge or consent while you were in a relationship? YES NO
   f) Have you had casual partners with someone other than your partner **without** your partner's knowledge or consent while you were in a relationship? YES NO
   g) Have you had relationships with someone other than your partner **with** your partner's knowledge or consent? YES NO
   h) Have you had casual partners with someone other than your partner **with** your partner's knowledge or consent? YES NO
   i) Was your last relationship with multiple individuals (i.e. polyamory)? YES NO
   j) Have you ever been in one relationship with multiple individuals? YES NO
   k) What was the sex of your last partner (if you had multiple partners at the same time, what was each of their sexes)? _____
   l) Were most of your relationships with an individual of a specific sex?
      i) NO ii) YES (please note): _____
   m) How long is the longest relationship you have been in? _____
   n) How would you characterize your past contacts with past partners, on average?
      i) Casual ii) Equally casual and committed iii) Committed
2) Are you interested in finding new partners? YES NO
   a) If YES, would you like to find a partner (casual or serious or both) ? YES NO
   b) If YES, would you like to find one or more partners? YES NO

Please feel free to add in your own comments on the back of the pages.

For People with **ONE** Romantic/Sexual Partner

(If you have more than one partner, please skip forward.)

1) How long have you been in a relationship with this person? _____
2) What sex is your partner? _____
3) Do you live with this person? YES NO
4) Do you live in the same city as this person? YES NO
5) How committed are you to this relationship?
   a) Not at all committed
   b) Not really committed
   c) A bit committed
   d) Somewhat committed
   e) Moderately committed
   f) Very committed
   g) Extremely committed
6) How likely do you think it is that you will stay in a relationship with this person "forever"?
   a) Extremely unlikely
   b) Moderately unlikely
   c) Somewhat unlikely
   d) Neither likely nor unlikely
   e) Somewhat likely
   f) Moderately likely
   g) Extremely likely
7) How sexually attracted have you been to this person over the last month?
   a) Not at all sexually attracted
   b) Not really sexually attracted
   c) A bit sexually attracted
   d) Somewhat sexually attracted
   e) Moderately sexually attracted
   f) Very sexually attracted
   g) Extremely sexually attracted

8) How frequently have you engaged in sexual activity of any kind with this person over the past month?
   a) less than once per month
   b) 1-3 times per month
   c) once per week
   d) 2-4 times per week
   e) 5-6 times per week
   f) once per day
   g) more than once per day
9) How close/intimate have your felt with your partner over the past month?
   a) Not at all close/intimate
   b) Not really close/intimate
   c) A bit close/intimate
   d) Somewhat close/intimate
   e) Moderately close/intimate
   f) Very close/intimate
   g) Extremely close/intimate
10) Have you ever had a relationship with someone other than your partner, **without** your partner's knowledge? YES NO
11) Have you ever had a sexual encounter (not a committed relationship) with someone other than your partner, **without** your partner's knowledge? YES NO
12) Have you ever had a relationship with someone other than your partner, **with** your partner's knowledge? YES NO
13) Have you ever had a sexual encounter (not a committed relationship) with someone other than your partner, **with** your partner's knowledge? YES NO
14) Would you ever have a relationship with someone other than your partner without your partner's knowledge? YES NO
15) Would you ever have a sexual encounter with someone other than your partner without your partner's knowledge? YES NO
16) Have you ever been in more than one relationship at the same time, with the knowledge of all your partners? YES NO

17) Have you ever been in a relationship with multiple partners, when all partners were considered part of the same relationship? YES NO

18) Have you had children with your current partner? YES NO

Please feel free to add in your own comments on the back of the pages.

For People with **MORE THAN ONE** Romantic/Sexual Partner

1) How many romantic/sexual partners do you currently have? _____

2) Do you have one or more relationships that you consider 'primary'? Primary might mean the most important, the most meaningful, the longest, the most committed, but may mean something else to you.

   a) No.

   b) Yes: please explain: _____

   _____

3) Are all of your partners aware that you have multiple partners? YES NO

4) We would like you to describe your relationships with each of your partners. Please indicate how each of the following variables applies to each partner. If you have more than 4 current partners, please take an extra sheet that the researchers are handing out.

	Partner a	Partner b	Partner c	Partner d
5. Length of relationship				
6. Sex of partner				
7. My contacts with this person are mainly: 1 = *not sexual at all* 2 = *not really sexual* 3 = *a bit sexual* 4 = *somewhat sexual* 5 = *moderately sexual* 6 = *very sexual* 7 = *basically only sexual*				
8. My contacts with this person are based on: 1 = *not at all* love 2 = *not really love* 3 = *a bit love* 4 = *somewhat love* 5 = *moderately love* 6 = *very much love* 7 = *all love*				
9. Are any of your partners together? *E.g. Partner A* has a relationship with *Partner B.* If so, indicate which partner(s): *E.g.* under *Partner A* column, put '*Partner B*'; under *Partner B* column, put *'Partner A'*.				
10. Do any of your partners have relationships with people who are not your partners? *E.g. Partner A* has 3 partners not on this list. If so, indicate how many: *E.g.* Under *Partner A,* put '*3*'.				
11. Do any of your relationships involve interconnections that also include yourself? *E.g. you, Partner A,* and *Partner B* are together. If so, indicate which partners: *E.g.* Under *Partner A* column, put '*Partner B*'; Under *Partner B* column, put *Partner A.*				

12. Please indicate the level of commitment you feel to each partner using the following scale: 1 = *not at all committed* 2 = *not really committed* 3 = *a bit committed* 4 = *somewhat committed* 5 = *moderately committed* 6 = *very committed* 7 = *extremely committed*				
13. Please indicate the likelihood of staying in each relationship 'forever' using this scale: 1 = *not at all likely* 2 = *not really likely* 3 = *a bit likely* 4 = *somewhat likely* 5 = *moderately likely* 6 = *very likely* 7 = *extremely likely*				
14. Please indicate your level of attraction to each partner over the past month using this scale: 1 = *not at all attracted* 2 = *not really attracted* 3 = *a bit attracted* 4 = *somewhat attracted* 5 = *moderately attracted* 6 = *very attracted* 7 = *extremely attracted*				
15. Please indicate how intimate or close you feel with each partner using the following scale: 1 = *not at all close* 2 = *not really close* 3 = *a bit close* 4 = *somewhat close* 5 = *moderately close* 6 = *very close* 7 = *extremely close*				
16. Please indicate the frequency of sexual activity of any kind over the past month with each partner: 1 = *less than once per month* 2 = *1-3 times/month* 3 = *once per week* 4 = *2-4 times per week* 5 = *5-6 times per week* 6 = *once per day* 7 = *more than once per day*				
17. Have you had biological children (gave birth or insemination) with any of these partners? If so, please indicate the number of children.				
18. Have you had non-biological children (adopted, step-parent, parental role) with any of these partners? If so, please indicate the number of children.				
Please add in any other comments you would like to make about your relationships with these partners here, in the boxes below, or on the back.				

Please feel free to add in your own comments on the back of the pages.

REFERENCE LIST

Adkins-Regan, E. (1999). Testosterone increases singing and aggression but not male-typical sexual partner preference in early estrogen treated female zebra finches. *Hormones and Behavior, 35,* 63-70.

Aizawa, K., Nakahori, C., Akimoto, T., Kimura, F., Hayashi, K., Kono, I., & Mesaki, N. (2006). Changes of pituitary, adrenal and gonadal hormones during competition among female soccer players. *Journal of Sports Medicine and Physical Fitness, 46(2),* 322-327.

Alatalo, R. V., Höglund, J., Lundberg, A., Rintamäki, P. T., & Silverin, B. (1996). Testosterone and male mating success on the black grouse leks. *Proceedings. Biological Sciences/The Royal Society, 263,* 1697-1702.

Aleman, A., Bronk, E., Kessels, R. P., Koppeschaar, H. P., & van Honk, J. (2004). A single administration of testosterone improves visuospatial ability in young women. *Psychoneuroendocrinology, 29,* 612-617.

Anonymous. (1970). Effects of sexual activity on beard growth in man. *Nature, 226,* 869-870.

Archer, J. (2006). Testosterone and human aggression: an evaluation of the challenge hypothesis. *Neuroscience and Biobehavioral Reviews, 30(3),* 319-345.

Aron, A., Fisher, H. E., Mashek, D. J., Strong, G., Li, H. F., & Brown, L. L. (2005). Reward, motivation and emotion systems associated with early-stage intense romantic love: An fMRI study. *Journal of Neurophysiology, 94,* 327-337.

Axelsson, J., Ingre, M., Skerstedt, T., & Holmback, U. (2005). Effects of acutely displaced sleep on testosterone. *Journal of Clinical Endocrinology and Metabolism, 90,* 4530-4535.

Bachmann, G. A. (2002). The hypoandrogenic woman: Pathophysiologic overview. *Fertility and Sterility, 77(Suppl 4),* S72-S76.

Bagemihl, B. (1999). *Biological exuberance: Animal homosexuality and natural diversity.* St. Martin's Press, New York.

Bancroft, J., Sanders, D., Davidson, D., & Warner, P. (1983). Mood, sexuality, hormones, and the menstrual cycle. III. Sexuality and the role of androgens. *Psychosomatic Medicine, 45,* 509-516.

Bancroft, J., Sherwin, B. B., Alexander, G. M., Davidson, D. W., & Walker, A. (1991). Oral contraceptives, androgens, and the sexuality of young women: II. The role of androgens. *Archives of Sexual Behavior, 20,* 121-135.

Bartels, A. & Zeki, S. (2000). The neural basis of romantic love. *Neuroreport, 11,* 3829-3834.

Bartels, A. & Zeki, S. (2004). The neural correlates of maternal and romantic love. *NeuroImage, 21,* 1155-1166.

Baucom, D. H., Besch, P. K., & Callahan, S. (1985). Relation between testosterone concentration, sex role identity, and personality among females. *Journal of Personality and Social Psychology, 48,* 1218-1226.

Baxendale, P. M., Jacobs, H. S., & James, V. H. (1982). Salivary testosterone: Relationship to unbound plasma testosterone in normal and hyperandrogenic women. *Clinical Endocrinology, 16,* 595-603.

Becker, J. B., Breedlove, S. M., Crews, D., & McCarthy, M. M., Eds. (2002). *Behavioral Endocrinology, 2nd Ed.* Cambridge, MA: MIT Press.

Beletsky, L. D., Orians, G. H., & Wingfield, J. C. (1992). Year-to-year patterns of circulating levels of testosterone and corticosterone in relation to breeding density, experience, and reproductive success of the polygynous red-winged blackbird. *Hormones and Behavior, 26,* 420-432.

Bernhardt, P. C., Dabbs Jr., J. M., Fielden, J. A., & Lutter, C. D. (1998). Testosterone changes during vicarious experiences of winning and losing among fans at sporting events. *Physiology and Behavior, 65,* 59-62.

Bernstein, I. S., Rose, R. M., & Gordon, T. P. (1974). Behavioral and environmental events influencing primate testosterone levels. *Journal of Human Evolution, 3,* 517-525.

Bernstein, I. S., Rose, R. M., & Gordon, T. P. (1977). Behavioural and hormonal responses of male rhesus monkeys introduced to females in the breeding and non-breeding seasons. *Animal Behaviour, 25,* 609-614.

Beyer, C., Morali, G., & Vargas, R. (1971). Effects of diverse estrogens on estrous behavior and genital tract development in ovariectomized rats. *Hormones and Behavior, 2,* 273-277.

Bogaert, A. F. & Fisher, W. A. (1995). Predictors of university men's number of sexual partners. *Journal of Sex Research, 32,* 119-130.

Booth, A. & Dabbs, J. M. Jr. (1993). Testosterone and men's marriages. *Social Forces, 72,* 463-477.

Boyar, R. M., Rosenfeld, R. S., Kapen, S., Finkelstein, J. W, Roffwarg, H. P., Weitzman, E. D., & Hellman, L. (1974). Human puberty. Simultaneous augmented secretion of luteinizing hormone and testosterone during sleep. *Journal of Clinical Investigations, 54,* 609-618.

Burger, H. G., Dudley, E. C., Cui, J., Dennerstein, L., Hopper, J. L. (2000). A prospective longitudinal study of serum testosterone, dehydroepiandrosterone sulfate, and sex hormone-binding globulin levels through the menopause transition. *Journal of Clinical Endocrinology and Metabolism, 85,* 2832-2838.

Burnham, T.C., Flynn Chapman, J., Gray, P.B., McIntyre, M.H., Lipson, S.F., & Ellison, P.T. (2003). Men in committed romantic relationships have lower testosterone. *Hormones and Behavior, 44,* 119-122.

Carani, C., Bancroft, J., Del Rio, G., Granata, A.R.M., Facchinetti, F., & Marrama, P. (1990). The endocrine effects of visual erotic stimuli in normal men. *Psychoneuroendocrinology, 15,* 207-216.

Carre, J., Muir, C., Belanger, J., & Putnam, S.K. (2006). Pre-competition hormonal and psychological levels of elite hockey players: Relationship to the "home advantage". *Physiology and Behavior, 89(3),* 392-398.

Carter, C. S., DeVries, A. C., Taymans, S. E., Roberts, R. L., Williams, J. R., & Chrousos, J. R. (1995). Adrenocorticoid hormones and the development and expression of mammalian monogamy. *Annals of the New York Academy of Sciences, 771,* 82-91.

Cashdan, E. (1995). Hormones, sex, and status in women. *Hormones and Behavior, 29,* 354-366.

Cavigelli, S. A. & Pereira, M. E. (2000). Mating season aggression and fecal testosterone levels in male ring-tailed lemurs (Lemur catta). *Hormones and Behavior, 37,* 246-255.

Cho, M. M., DeVries, A. C., Williams, J. R., & Carter, C. S. (1999). The effects of oxytocin and vasopressin on partner preferences in male and female prairie voles (Microtus ochrogaster). *Behavioral Neuroscience, 113,* 1071–1079.

Christiansen, K. & Knussmann, R. (1987). Androgen levels and components of aggressive behavior in men. *Hormones and Behavior, 21,* 170-180.

Clancy, A.N., Singer, A.G., Macrides, F., Bronson, F.H., & Agosta, W.C. (1988). Experiential and endocrine dependence of gonadotropin responses in male mice to conspecific urine. *Biology of Reproduction, 38,* 183–192.

Clarke, F. M. & Faulkes, C. G. (1998). Hormonal and behavioural correlates of male dominance and reproductive status in captive colonies of the naked mole-rat, Heterocephalus glaber. *Proceedings. Biological Sciences/The Royal Society, 265(1404),* 1391-1399.

Clotfelter, E. D., O'Neal, D. M., Caudioso, J. M., Casto, J. M., Parker-Renga, I. A., Snajdr, E. A., Duffy, D. L., Nolan, V. Jr., & Ketterson, E. D. (2004). Consequences of elevating plasma testosterone in females of a socially monogamous songbird: Evidence of constraints on male evolution? *Hormones and Behavior, 46,* 171-179.

Cochran, C. & Perachio, A. (1977). Dihydrotestosterone propionate effects on dominance and sexual behaviors in gonadectomised male and female rhesus monkeys. *Hormones and Behavior, 8,* 175-187.

Cohan, C. L., Booth, A., & Granger, D. A. (2003). Gender moderates the relationship between testosterone and marital interaction. *Journal of Family Psychology, 17,* 29-40.

Conway, C. A., Jones, B. C., DeBruine, L. M., Welling, L. L., Law Smith, M. J., Perrett , D. I., Sharp, M. A., & Al-Dujaili, E. A. (2007). Salience of emotional displays of danger and contagion in faces is enhanced when progesterone levels are raised. *Hormones and Behavior, 51,* 202-206.

Coquelin, A. & Bronson, F. H. (1979). Release of luteinizing hormone in male mice during exposure to females: Habituation of the response. *Science, 206(4422),* 1099-1101.

Creel, S. R., Wildt, D. E. & Monfort, S. L. (1993). Androgens, aggression and reproduction in wild dwarf mongooses: a test of the challenge hypothesis. *American Naturalist, 141,* 816-825.

Dabbs, J. M. Jr. (1990a). Age and seasonal variation in serum testosterone concentration among men. *Chronobiology International, 7,* 245-249.

Dabbs, J. M. Jr. (1990b). Salivary testosterone measurements: Reliability across hours, days, and weeks. *Physiology and Behavior, 48,* 83-86.

Dabbs, J.M., Jr. (1997). Testosterone, smiling, and facial appearance. *Journal of Nonverbal Behavior, 21,* 45-55.

Dabbs, J.M., Jr., & de La Rue, D. (1991). Salivary testosterone measurements among women: Relative magnitude of circadian and menstrual cycles. *Hormone Research, 35,* 182-184.

Dabbs, J.M., Jr., de La Rue, D., & Williams, P.M. (1990). Testosterone and occupational choice: Actors, ministers, and other men. *Journal of Personality and Social Psychology, 59(6),* 1261-1265.

Dabbs Jr., J.M. & Mohammed, S. (1992). Male and female salivary testosterone concentrations before and after sexual activity. *Physiology and Behavior, 52,* 195-197.

Davis, S. (1999). Androgen replacement in women: A commentary. *Journal of Clinical Endocrinology and Metabolism, 84,* 1886-1891.

Delahunty, K. M., McKay, D. W., Noseworthy, D. E., & Storey, A. E. (2007). Prolactin responses to infant cues in men and women: Effects of parental experience and recent infant contact. *Hormones and Behavior, 51,* 213-220.

De Ridder, E., Pinxten, R., & Eens, M. (2000). Experimental evidence of a testosterone-induced shift from paternal to mating behavior in a facultatively polygynous songbird. *Behavioral Ecology and Sociobiology, 49,* 24-30.

DeVries, A. C., DeVries, M. B., Taymans, S. E., & Carter, C. S. (1996). The effects of stress on social preferences are sexually dimorphic in prairie voles. *Proceedings of the National Academy of Sciences, U.S.A., 93,* 11980-11984.

DeVries, A. C., Guptaa, T., Cardillo, S., Cho, M., & Carter, C. S. (2002). Corticotropin-releasing factor induces social preferences in male prairie voles. *Psychoneuroendocrinology, 27,* 705-714.

Diamond, L.M. (2003). What does sexual orientation orient? A biobehavioral model distinguishing romantic love and sexual desire. *Psychological Reviews, 110,* 173-192.

Dickerson, S. S. & Kemeny, M. E. (2004). Acute stressors and cortisol responses: A theoretical integration and synthesis of laboratory research. *Psychological Bulletin, 130(3),* 355-391.

Domjan, M., Akins, C., & Vandergriff, D. H. (1992). Increased responding to female stimuli as a result of sexual experience: Tests of mechanisms of learning. *The Quarterly Journal of Experimental Psychology, 45,* 139–157.

DonCarlos, L. L., Sarkey, S., Lorenz, B., Azcoita, I., Garcia-Ovejero, D., Huppenbauer, C., & Garcia-Segura, L. M. (2006). Novel cellular phenotypes and subcellular sites for androgen action in the forebrain. *Neuroscience, 138,* 801-807.

Edwards, D. A. Wetzel, K. & Wyner, D. R. (2006). Intercollegiate soccer: saliva cortisol and testosterone are elevated during competition, and testosterone is related to status and social connectedness with teammates. *Physiology and Behavior, 87,* 135-143.

Ellison, P. T., Bribiescas, R. G., Bentley, G. R., Campbell, B. C., Lipson, S. F., Panter-Brick, C., & Hill, K. (2002). Population variation in age-related decline in male salivary testosterone. *Human Reproduction, 17,* 3251-3253.

Exton, M. S., Bindert, A., Kruger, T., Scheller, F., Harmann, U., & Schedlowski, M. (1999). Cardiovascular and endocrine alterations after masturbation-induced orgasm in women. *Psychosomatic Medicine, 61,* 280-289.

Faurie, C., Pontier, D., & Raymond, M. (2004). Student athletes claim to have more sexual partners than other students. *Evolution and Human Behavior, 25(1),* 1-8.

Ferrini, R. L. & Barrett-Connor, E. (1998). Sex hormones and age: A cross-sectional study of testosterone and estradiol and their bioavailable fractions in community-dwelling men. *American Journal of Epidemiology, 147,* 750-754.

Fisher, H., Aron, A., & Brown, L. L. (2005). Romantic love: An fMRI study of a neural mechanism for mate choice. *Journal of Comparative Neurology, 493,* 58-62.

Fisher, H. E., Aron, A., & Brown, L. L. (2006). Romantic love: A mammalian brain system for mate choice. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 361,* 2173-2186.

Fleming, A. S., Corter, C., Stallings, J., & Steiner, M. (2002). Testosterone and prolactin are associated with emotional responses to infant cries in new fathers. *Hormones and Behavior, 42,* 399-413.

Fox, C. A.,. Ismail, A. A. A, Love, D. N., Kirkham, K. E., & Loraine, J. A. (1972). Studies on the relationship between plasma testosterone levels and human sexual activity. *Journal of Endocrinology, 52,* 51-58.

Gangestad, S. W., Simpson, J. A., Cousins, A. J., Garver-Apgar, C. E., & Christensen, P. N. (2004). Women's preferences for male behavioral displays change across the menstrual cycle. *Psychological Science, 15,* 203-207.

Garamszegi, L. Z., Eens, M., Hurtrez-Boussès, & Møller, A. P. (2005). Testosterone, testes size, and mating success in birds: A comparative study. *Hormones and Behavior, 47,* 389-409.

Garde, A. H., Hansen, A. M., Skovgaard, L. T., & Christensen, J. M. (2000). Seasonal and biological variation of blood concentrations of total cholesterol, dehydroepiandrosterone sulfate, hemoglobin A(1c), IgA, prolactin, and free testosterone in healthy women. *Clinical Chemistry, 46,* 551-559.

Gatewood, J. D., Wills, A., Shetty, S., Xu, J., Arnold, A. P., Burgoyne, P. S., & Rissman, E. F. (2006). Sex chromosome complement and gonadal sex influence aggressive and parental behaviors in mice. *Journal of Neuroscience, 26(8),* 2335-2342.

Gladue, B. A. (1991). Aggressive behavioral characteristics, hormones, and sexual orientation in men and women. *Aggressive Behavior, 17,* 313-326.

Gladue, B. A., Coechler, M., & McCaul, K. D. (1989). Hormonal response to competition in human males. *Aggressive Behavior, 15,* 409-422.

Goncharov, N., Katsya, G., Dobracheva, A., Nizhnik, A., Kolesnikova, G., Herbst, V., & Westermann, J. (2006). Diagnostic significance of free salivary testosterone measurement using a direct luminescence immunoassay in healthy men and in patients with disorders of androgenic status. *Aging Male, 9,* 111-122.

Gonzaga, G. C., Turner, R. A., Keltner, D., Campos, B., & Altemus, M. (2006). Romantic love and sexual desire in close relationships. *Emotion, 6,* 163-179.

Gordon, T. P., Bernstein, I. S., & Rose, R. M. (1978). Social and seasonal influences on testosterone secretion in the male rhesus monkey. *Physiology and Behavior, 21(4),* 623-627.

Goymann, W., East, M. L., & Hofer, H. (2003). Defence of females, but not social status, predicts plasma androgen levels in male spotted hyenas. *Physiological and Biochemical Zoology, 76,* 586-593.

Graham, C. A., Bancroft, J., Doll, H. A., Greco, T., & Tanner, A. (2007). Does oral contraceptive-induced reduction in free testosterone adversely affect the sexuality or mood of women? *Psychoneuroendocrinology, 32,* 246-255.

Granger, D. A., Schwartz, E. B., Booth, A., & Arentz, M. (1999). Salivary testosterone determination in studies of child health and development. *Hormones and Behavior, 35,* 18-27.

Granger, D. A., Shirtcliff, E. A., Booth, A., Kivlighan, K. T., & Schwartz, E.B. (2004). The "trouble" with salivary testosterone. *Psychoneuroendocrinology, 29,* 1229-1240.

Gray, A., Berlin, J. A., McKinlay, J. B. & Longcope, C. (1991). An examination of research design effects on the association of testosterone and male aging: results of a meta-analysis. *Journal of Clinical Epidemiology, 44,* 671-684.

Gray, P. B. (2003). Marriage, parenting, and testosterone variation among Kenyan Swahili men. *American Journal of Physical Anthropology, 122,*279-286.

Gray, P. B., Campbell, B. C., Marlowe, F. W., Lipson, S. F., & Ellison, P. T. (2004a). Social variables predict between-subject but not day-to-day variation in the testosterone of US men. *Psychoneuroendocrinology, 29,* 1153-1162.

Gray, P. B., Flynn Chapman, J., Burnham, T. C., McIntyre, M. H., Lipson, S. F., & Ellison, P. T. (2004b). Human male pair bonding and testosterone. *Human Nature, 15,* 19-131.

Gray, P. B., Kahlenberg, S. M., Barrett, E. S., Lipson, S. F., & Ellison, P. T. (2002). Marriage and fatherhood are associated with lower testosterone in males. *Evolution and Human Behavior, 23,* 193-201.

Gray, P. B., Yang, C.- F., J., & Pope, H. G., Jr. (2006). Fathers have lower salivary testosterone levels than unmarried men and married non-fathers in Beijing, China. *Proceedings. Biological Sciences/Royal Society, 273,* 333-339.

Gwinner, H., Van't Hof, T., & Zeman, M. (2002). Hormonal and behavioral responses of starlings during a confrontation with males or females at nest boxes during the reproductive season. *Hormones and Behavior, 42,* 21-31.

Hegner, R. E. & Wingfield, J. C. (1987). Effects of experimental manipulation of testosterone levels on parental investment and breeding success in male house sparrows. *The Auk, 104,* 462-469.

Hellhammer, D. H., Hubert, W., & Schürmeyer, T. (1985). Changes in saliva testosterone after psychological stimulation in men. *Psychoneuroendocrinology, 10,* 77-81.

Hermans, E. J., Putman, P., & van Honk, J. (2006). Testosterone administration reduces empathetic behavior: a facial mimicry study. *Psychoneuroendocrinology, 31,* 859-866.

Higley, J. D., Mehlman, P. T., Poland, R. E., Taub, D. M., Vickers, J., Suomi, S. J. & Linnoila, M. (1996). CSF testosterone and 5-HIAA correlate with different types of aggressive behaviors. *Biological Psychiatry, 40,* 1067-1082.

Hirschenhauser, K., Frigerio, D., Grammer, K., & Magnusson, M. S. (2002). Monthly patterns of testosterone and behavior in prospective fathers. *Hormones and Behavior, 42,* 172-181.

Hirschenhauser, K. & Oliveira, R. F. (2006). Social modulation of androgen levels in Vertebrates: A meta-analysis of the Challenge Hypothesis. *Animal Behaviour, 71,* 265-277.

Hirschenhauser, K., Taborsky, M., Oliveira, T., Canário, A. V. M. & Oliveira, R. F. (2004). A test of the 'challenge hypothesis' in cichlid fish: simulated partner and territory intruder experiments. *Animal Behaviour, 68,* 741-750.

Hirschenhauser, K., Winkler, H., & Oliveira, R. F. (2003). Comparative analysis of male androgen responsiveness to social environment in birds: the effects of mating system and paternal incubation. *Hormones and Behavior, 43,* 508-519.

Hong, Y., Gagnon, J., Rice, T., Pérusse, L., Leon, A. S., Skinner, J. S., Wilmore, J. H., Bouchard, C., & Rao, D. C. (2001). Familial resemblance for free androgens and androgen glucoronides in sedentary black and white individuals: the HERITAGE Family Study. *Journal of Endocrinology, 170,* 485-492.

Hughes, I. A. (2004). Female development - all by default? *New England Journal of Medicine, 351(8),* 792-8.

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 and Behavior, 25,* 206-216.

Insel, T. R. & Shapiro, L. E. (1992). Oxytocin receptor distribution reflects social organization in monogamous and polygamous voles. *Proceedings of the National Academy of Sciences, U.S.A., 13,* 5981–5985.

Introduction to Polyamory, n.d. Retrieved November 15th, 2006, from http://www.polyamorysociety.org/page6.html

Izquierdo, M., Ibanez, J., Gonzales-Badillo J. J., Hakkinen, K., Ratamess, N. A., Kraemer, W. J., French, D. N., Eslava, J., Altadill, A., Asiain, X., & Gorostiaga, E. M. (2006). Differential effects of strength training leading to failure versus not to failure on hormonal responses, strength, and muscle power gains. *Journal of Applied Physiology, 100(5),* 1647-1656.

Jawor, J. M., Young, R., & Ketterson, E. D. (2006). Females competing to reproduce: Dominance matters but testosterone may not. *Hormones and Behavior, 49,* 362-368.

Johnsen, T. S. (1998). Behavioural correlates of testosterone and seasonal changes of steroids in red-winged blackbirds. *Animal Behaviour, 55,* 957-965.

Johnson, S. G., Jopling, G. F., Burrin, J. M. (1987). Direct assay for testosterone in saliva: Relationship with a direct serum free testosterone assay. *Clinica Chimica Acta: International Journal of Chemistry, 163,* 309-318.

Jones, B. C., Little, A. C., Boothroyd, L., Debruine, L. M., Feinberg, D. R., Smith, M. J., Cornwall, R. E., Moore, F. R., & Perrett, D. I. (2005). Commitment to relationships and preferences for femininity and apparent health in faces are strongest on days of the menstrual cycle when progesterone level is high. *Hormones and Behavior, 48,* 283-290.

Joslyn, W. (1973). Androgen induced social dominance in infant female rhesus monkeys. *Journal of Child Psychology and Psychiatry, and Allied Disciplines, 14,* 137-145.

Julian, T. & McKenry, P. C. (1989). Relationship of testosterone to men's family functioning at mid-life: a research note. *Aggressive Behavior, 15,* 281–289.

Kendrick, K. M., Keverne, E. B., & Baldwin, B. A. (1987). Intracerebroventricular oxytocin stimulates maternal behaviour in the sheep. *Neuroendocrinology, 46,* 56-61.

Ketterson, E. D. & Nolan, Jr., V. (1992). Hormones and life histories: An integrative approach. *American Naturalist, 140,* S33-S62.

Ketterson, E. D., Nolan, V. Jr., & Sandell, M. (2005). Testosterone in females: Mediator of adaptive traits, constraint on sexual dimorphism, or both? *American Naturalist, 166,* S85-S98.

Khan-Dawood, F. S., Choe, J. K., & Dawood, M. Y. (1984). Salivary and plasma bound and "free" testosterone in men and women. *American Journal of Obstetrics and Gynaecology, 148,* 441-445.

Kinsey, A. C., Pomeroy, W. B., & Martin, C. E. (1948). *Sexual behavior in the human male.* Bloomington IN: Indiana University Press.

Klein, S. L. & Nelson, R J. (1997). Sex differences in immunocompetence differ between two peromyscus species. *American Journal of Physiology. Regulatory, Integrative, and Comparative Physiology, 273,* 655-660.

Kraemer, H. C., Becker, H. B., Brodie, H. K. H., Doering, C. H., Moos, R. H., & Hamburg, D. A. (1976). Orgasmic frequency and plasma testosterone levels in normal human males. *Archives of Sexual Behavior, 5,* 125-132.

Kriegsfeld, L. J. (2006). Driving reproduction: Rfamide peptides behind the wheel. *Hormones and Behavior, 50,* 655-666.

Krüger, T., Exton, M. S., Pawlak, C., von zur Mühlen, A., Hartmann, U., & Schedlowski, M. (1998). Neuroendocrine and cardiovascular response to sexual arousal and orgasm in men. *Psychoneuroendocrinology, 23,* 401-411.

Kudielka, B. M., Schommer, N. C., Hellhammer, D. H., & Kirschbaum, C. (2004). Acute HPA axis responses, heart rate, and mood changes to psychosocial stress (TSST) in humans at different times of day. *Psychoneuroendocrinology, 29(8),* 983-992.

Langmore, N. E., Cockrem, J. F., and Candy, E. J. (2002). Competition for male reproductive investment elevates testosterone levels in female dunnocks, Prunella modularis. *Proceedings. Biological Sciences/The Royal Society. 269(1508),* 2473-2478.

Lee, P. A., Jaffe, R. B. & Midgley Jr., A. R. (1974). Lack of alteration of serum gonadotropins in men and women following sexual intercourse. *American Journal of Obstetrics and Gynecology, 120,* 985-987.

Lim, M. M., Liu, Y., Ryabinin, A. E., Bai, Y., Wang, Z., & Young, L. J. (in press). CRF receptors in the nucleus accumbens modulate partner preference in prairie voles. *Hormones and Behavior.*

Lim, M. M., Nair, H. P., & Young, L. J. (2005). Species and sex differences in brain distribution of corticotropin-releasing factor receptor subtypes 1 and 2 in monogamous and promiscuous vole species. *Journal of Comparative Neurology, 487,* 75-92.

Lim, M. M., Tsivkovskaia, N. O., Bai, Y., Young, L. J., & Ryabinin, A. E. (2006). Distribution of corticotropin-releasing factor and Urocortin 1 in the vole brain. *Brain, Behavior, and Evolution, 68,* 229-240.

Lim, M. M., Wang, Z., Olazabal, D. E., Ren, X., Terwilliger, E. F. & Young, L.J. (2004). Enhanced partner preference in a promiscuous species by manipulating the expression of a single gene. *Nature, 429,* 754–757.

Lim, M. M. & Young, L. J. (2006). Neuropeptidergic regulation of affiliative behavior and social bonding in animals. *Hormones and Behavior, 50,* 506-517.

Losel, R. M., Falkenstein, E., Feuring, M., Shultz, A., Tillmann, H. C., Rossol-Haseroth, K., & Wehling, M. (2003). Nongenomic steroid action: Controversies, questions, and answers. *Physiological Reviews, 83,* 965-1016.

Luboshitzky, R., Shen-Orr, Z., & Herer, P. (2003). Middle-aged men secrete less testosterone at night than young healthy men. *Journal of Clinical Endocrinology and Metabolism, 88,* 3160-3166.

Luboshitzky, R., Zabari, Z., Shen-Orr, Z., Herer, P. & Lavie, P. (2001). Disruption of the nocturnal testosterone rhythm by sleep fragmentation in normal men. *Journal of Clinical Endocrinology and Metabolism, 86,* 1134-1139.

Maestu, J., Jurimae, J., & Jurimae, T. (2005). Hormonal response to maximal rowing before and after heavy increase in training volume in highly trained male rowers. *Journal of Sports Medicine and Physical Fitness, 45,* 121-126.

Magrini, G., Chiodoni, G., Rey, F., & Felber, J. P. (1986). Further evidence for the usefulness of the salivary testosterone radioimmunoassay in the assessment of androgenicity in man in basal and stimulated conditions. *Hormone Research, 23,* 65-73.

Mank, J. E. (2007). The evolution of sexually selected traits and antagonistic androgen expression in Actinopterygiian fishes. *American Naturalist, 169,* 142-149.

Marazziti, D. & Canale, D. (2004). Hormonal changes when falling in love. *Psychoneuroendocrinology, 29(7),* 931-936.

Martin-Soelch, C., Leenders, K. L., Chevalley, A. F., Missimer, J., Kunig, G, Magyar, S., Mino, A., & Schultz, W. (2001). Reward mechanisms in the brain and their role in dependence: Evidence from neurophysiological and neuroimaging studies. *Brain Research. Brain Research Reviews, 36,* 139-149.

Mazur, A. & Booth, A. (1997). Testosterone and dominance in men. *Behavioral and Brain Sciences, 21,* 353-397.

Mazur, A., Booth, A., & Dabbs Jr., J. M. (1992). Testosterone and chess competition. *Social Psychology Quarterly, 55,* 70-77.

Mazur, A. & Michalek, J. (1998). Marriage, divorce, and male testosterone. *Social Forces, 77,* 315-330.

McCarthy, M. M. (1990). Oxytocin inhibits infanticide in female house mice (*Mus domensticus*). *Hormones and Behavior, 24,* 365-375.

McCaul, K. D., Gladue, B. A., & Joppa, M. (1992). Winning, losing, mood, and testosterone. *Hormones and Behavior, 26,* 486-504.

McIntyre, M. H., Gangestad, S. W., Gray, P. B., Chapman, J. F., Burnham, T. C., O'Rourke, M. T., & Thornhill, R. (2006). Romantic involvement often reduces men's testosterone levels—but not always: The moderating role of extrapair sexual interest. *Journal of Personality and Social Psychology, 91,* 642-651.

McLachlan, R. I., Wreford, N. G., O'Donnell, O., de Krester, D. M., & Robertson, D. M. (1996). The endocrine regulation of spermatogenesis: Independent roles for testosterone and FSH. *Journal of Endocrinology, 148,* 1–9.

Meikle, A. W., Stringham, J. D., Bishop, D. T., & West, D. W. (1988). Quantitating genetic and nongenetic factors influencing androgen production and clearance rates in men. *Journal of Clinical Endocrinology and Metabolism, 67,* 104-109.

Moffat, S. D. & Hampson, E. (2000). Salivary testosterone concentrations in left-handers: An association with cerebral language lateralization? *Neuropsychology, 14(1),* 71-81.

Møller, A. P., Garamszegi, L. Z., Gil, D., Hurtrez-Boussès, S., & Eens, M. (2005). Correlated evolution of male and female testosterone profiles in birds and its consequences. *Behavioral Ecology and Sociobiology, 58*, 534-544.

Moore, I.T. (in press). Advancing the Challenge Hypothesis. *Hormones and Behavior.*

Morley, J. E., Kaiser, F. E., Perry, H. M. 3rd, Patrick, P., Morley, P. M., Stauber, P. M., Vellas, B., Baumgartner, R. N., & Garry, P. J. (1997). Longitudinal changes in testosterone, luteinizing hormone, and follicle-stimulating hormone in healthy older men. *Metabolism, 46,* 410-413.

Morley, J. E., Perry, H. M. 3rd., Patrick, P., Dollbaum, C. M., & Kells, J. M. (2006). Validation of salivary testosterone as a screening test for male hypogonadism. *Aging Male, 9,* 165-169.

Muller, M. N. & Wrangham, R. W. (2004). Dominance, aggression and testosterone in wild chimpanzees: A test of the "challenge hypothesis". *Animal Behaviour, 67,* 113-123.

Muroyama, Y., Shimizu, K., & Sugiura, H. (2007). Seasonal variation in fecal testosterone levels in free-ranging male Japanese Macaques. *American Journal of Primatology, 69,* 603-610.

Nahoul, K. & Roger, M. (1990). Age-related decline of plasma bioavailable testosterone in adult men. *Journal of Steroid Biochemistry, 35,* 293-299.

Najib, A., Lorberbaum, J. P., Kose, S., Bohning, D. E., & George, M. S. (2004). Regional brain activity in women grieving a romantic relationship breakup. *American Journal of Psychiatry, 161,* 2245-2256.

Nelson, R.J. (2000). An introduction to behavioral endocrinology, 2nd Ed. Sunderland Mass: Sinauer Associates, Inc.

Oliveira, R. F. (2004). Social modulation of androgens in vertebrates: Mechanisms and function. *Advances in the Study of Behavior, 34,* 165 – 239.

Oliveira, R. F., Almada, C. V., & Canário, A. V. M. (1996). Social modulation of sex steroid concentrations in the urine of male cichlid fish *Oreochromis mossambicus* (Teleostei: Cichlidae). *Hormones and Behavior, 30,* 2-12.

Oliveira, R. F., Carneiro, L. A., & Canario, A. V. (2005). Behavioural endocrinology: No hormonal response in tied fights. *Nature, 437(7056),* 207-208.

Oliveira, R. F., Hirschenhauser, K. Carneiro, L. A.,& Canario, A. V. (2002). Social modulation of androgen levels in male teloest fish. *Comparative Biochemistry and Physiology, Part B: Biochemistry and Molecular Biology, 132,* 203-215.

Oliveira, R. F., Lopes, M., Carneiro, L. A., & Canario, A. V. (2001). Watching fights raises fish hormone levels. *Nature, 409(6819),* 475.

Oliveira, R. F., Ros, A. F. H., Hirschenhauser, K., and Canario, A. V. M. (2001). Androgens and mating system in fish: Intra- and inter-specific analyses. In: H. J. Th. Goos, R. K. Rastogi, H. Vaudry, & R. Pierantoni, Eds. *Perspectives in Comparative Endocrinology: Unity and Diversity.* Medimond Inc. pp. 985-993.

Olweus, D., Mattsson, A., Schalling, D., & Löw, H. (1988). Circulating testosterone levels and aggression in adolescent males: A causal analysis. *Psychosomatic Medicine, 50,* 261-272.

Pankhurst, N. W., and Barnett, C. W. (1993). Relationship of population density, territorial interaction and plasma levels of gonadal steroids in spawning male demoiselles Chromis dispilus (Pisces: Pomacentridae). *General and Comparative Endocrinology, 90,* 168–176.

Passelergue, P. & Lac, G. (1999). Saliva cortisol, testosterone, and T/C ratio variations during a wrestling competition and during the post-competitive recovery period. *International Journal of Sports Medicine, 20,* 109-113.

Perry, H. M. 3rd, Miller, D. K., Patrick, P., & Morley, J. E. (2000). Testosterone and leptin in older African-American men: Relationship to age, strength, function, and season. *Metabolism, 49,* 1085-1091.

Pfeiffer, C. A. & Johnston, R. E. (1994). Hormonal and behavioral responses of male hamsters to females and female odors: roles of olfaction, the vomeronasal system, and sexual experience. *Physiology and Behavior, 55,* 129–138.

Pfeiffer, C. A. & Johnston, R. E. (1992). Socially stimulated androgen surges in male hamsters: The roles of vaginal secretions, behavioral interactions, and housing conditions. *Hormones and Behavior, 26,*283-293.

Pimental, E. E. (2000). Just how do I love thee? Marital relations in urban China. *Journal of Marriage and the Family, 62,* 32-47.

Pirke, K. M., Kockott, G., & Dittmar, F. (1974). Psychosexual stimulation and plasma testosterone in man. *Archives of Sexual Behavior, 3,* 577-584.

Piro, C., Fraioli, F., Sciarra, F., & Conti, C. (1973). Circadian rhythm of plasma testosterone, cortisol and gonadotropins in normal male subjects. *Journal of Steroid Biochemistry, 4,* 312-329.

Purifoy, F. E. & Koopmans, L. H. (1979). Androstenedione, testosterone, and free testosterone concentration in women of various occupations. *Social Biology, 26,* 179-188.

Purvis, K., Landgren, B.- M., Cekan, Z., & Diczfalusy, E. (1976). Endocrine effects of masturbation in men. *Journal of Endocrinology, 70,* 439-444.

Quissell, D. O. (1993). Steroid hormone analysis in human saliva. *Annals of the New York Academy of Sciences, 694,* 143-145.

Raouf, S. A., Parker, P. G., Ketterson, E. D., Nolan, V. Jr., & Ziegenfus, C. (1997). Testosterone influences reproductive success by increasing extra-pair fertilizations in male dark-eyed juncos, *Junco hyemalis. Proceedings of the Royal Society of London. Series B: Biological Sciences, 264,* 1599-1603.

Reburn, C. J. & Wynne-Edwards, K. E. (1999). Hormonal changes in males of a naturally biparental and a uniparental mammal. *Hormones and Behavior, 35,* 163-176.

Roney, J. R., Mahler, S. V., & Maestripieri, D. (2003). Behavioral and hormonal responses of men to brief interactions with women. *Evolution and Human Behavior, 24,* 365-375.

Ros, A. F., Bruintjes, R., Santos, R. S., Canario, A. V., & Oliveira, R. F. (2004). The role of androgens in the trade-off between territorial and parental behavior in the Azorean rock-pool blenny, Parablennius parvicornis. *Hormones and Behavior, 46,* 491-497.

Rose, R. M., Bernstein, I. S., & Gordon, T. P. (1975). Consequences of social conflict on plasma testosterone levels in rhesus monkeys. *Psychosomatic Medicine, 37,* 50-61.

Rose, R. M., Holaday, J. W., and Bernstein, I. S. (1971). Plasma testosterone, dominance rank, and aggressive behavior in male rhesus monkeys. *Nature, 231,* 366-368.

Rowland, D. L., Heiman, J. R., Gladue, B. A., Hatch, J. P., Doering, C. H., & Weiler, S. J. (1987). Endocrine, psychological and genital response to sexual arousal in men. *Psychoneuroendocrinology, 12,* 149-158.

Sakaguchi, K., Oki, M., Honma, S., & Hasegawa, T. (2006). Influence of relationship status and personality traits on salivary testosterone in Japanese men. *Personality and Individual Differences, 41,* 1077-1087.

Salvador, A., Suay, F., Gonzalez-Bono, E., & Serrano, M. A. (2003). Anticipatory cortisol, testosterone and psychological responses to judo competition in young men. *Psychoneuroendocrinology, 28,* 364-375.

Sapolsky, R. M. (1982). The endocrine stress-response and social status in the wild baboon. *Hormones and Behavior, 16,* 279-292.

Schmitt, D. P. & Buss, D. M. (2001). Human mate poaching: Tactics and temptations for infiltrating existing mateships. *Journal of Personality and Social Psychology, 80,* 894-917.

Schradin, C. & Anzenberger, G. (2004). Development of prolactin levels in marmoset males: From adult son to first-time father. *Hormones and Behavior, 46,* 670-677.

Schultheiss, O. C., Dargel, A., & Rohde, W. (2003). Implicit motives and gonadal steroid hormones: effects of menstrual cycle phase, oral contraceptive use, and relationship status. *Hormones and Behavior, 43,* 293–301.

Schultheiss, O. C. & Rohde, W. (2002). Implicit power motivation predicts men's testosterone changes and implicit learning in a contest situation. *Hormones and Behavior, 41,* 195–202.

Schultheiss, O. C., Wirth, M. M., & Stanton, S. (2004). Effects of affiliation and power motivation arousal on salivary progesterone and testosterone. *Hormones and Behavior, 46*, 592-599.

Schultz, W. (2006). Behavioral theories and the neurophysiology of reward. *Annual Review of Psychology, 57*, 87-115.

Shirtcliff, E. A., Granger, D. A., & Likos, A. (2002). Gender differences in the validity of testosterone measured in saliva by immunoassay. *Hormones and Behavior, 42*, 62-69.

Silverin, B. (1993). Territorial aggressiveness and its relation to the endocrine system in the pied flycatcher. *General and Comparative Endocrinology, 89*, 206-213.

Simpson, J. A. & Gangestad, S. W. (1991). Individual differences in sociosexuality: Evidence for convergent and discriminant validity. *Journal of Personality and Social Psychology, 60*, 870-883.

Soler, H., Vinayak, P., & Quadagno, D. (2000). Biosocial aspects of domestic violence. *Psychoneuroendocrinology, 25*, 721-739.

Spector, I. P., Carey, M. P., & Steinberg, L. (1996). The Sexual Desire Inventory: Development, factor structure, and evidence of reliability. *Journal of Sex and Marital Therapy, 22*, 175-190.

Stearns, E. L., Winter, J. S., & Faiman, C. (1973). Effects of coitus on gonadotropin, prolactin and sex steroids in man. *Journal of Clinical Endocrinology and Metabolism, 37*, 687 – 691.

Stoehr, A. M. & Hill, G. E. (2000). Testosterone and the allocation of reproductive effort in male house finches (Carpodacus mexicanus). *Behavioral Ecology and Sociobiology, 48*, 407-411.

Stoleru, S. G., Ennaji, A., Cournot, A., & Spira, A. (1993). LH pulsatile secretion and testosterone blood levels are influenced by sexual arousal in human males. *Psychoneuroendocrinology, 18*, 205-218.

Storey, A. E., Delahunty, K. M., McKay, D. W., Walsh, C. J., & Wilhelm, S. I. (2006). Social and hormonal bases of individual differences in the parental behaviour of birds and mammals. *Canadian Journal of Experimental Psychology, 60*, 237-245.

Storey, A. E., Walsh, C. J., Quinton, R. L., & Wynne-Edwards, K. E. (2000). Hormonal correlates of paternal responsiveness in new and expectant fathers. *Evolution and Human Behavior, 21*, 79-95.

Strier, K. B., Ziegler, T. E. & Wittwer, D. J. (1999). Seasonal and social correlates of fecal testosterone and cortisol levels in wild male muriquis (Brachyteles arachnoides). *Hormones and Behavior, 35*, 125-134.

Susman, E. J., Inoff-Germain, G., Nottelmann, E. D., Loriaux, D. L., Cutler, G. B. Jr., & Chrousos, G. P. (1987). Hormones, emotional dispositions, and aggressive attributes in young adolescents. *Child Development, 58,* 1114-1134.

Svartberg, J., Jorde, R., Sundsfjord, J., Bonaa, K. H., & Barrett-Connor, E. (2003). Seasonal variation of testosterone and waist-to-hip ratio in men: The Tromso study. *Journal of Clinical Endocrinology and Metabolism, 88,* 3099-3104.

Swinkels, L. M., Meulenberg, P. M., Ross, H. A., & Benraad, T. J. (1988). Salivary and plasma free testosterone and androstenedione levels in women using oral contraceptives containing desogestrel or levonorgestrel. *Annals of Clinical Biochemistry, 25(pt 4),* 354-359.

Taieb, J., Mathian, B., Millot, F., Patricot, M.-C., Mathieu, E., Queyrel, N., Lacroix, I. Somma-Delpero, C., & Boudou, P. (2003). Testosterone measured by 10 immunoassays and by isotope-dilution gas chromatography-mass spectrometry in sera from 116 men, women and children. *Clinical Chemistry, 49,* 1381-1395.

Valero-Politi, J. & Fuentes-Arderiu, X. (1998). Annual rhythmic variations in follitropin, lutropin, testosterone, and sex-hormone-binding globulin in men. *Clinica Chimica Acta: International Journal of Clinical Chemistry, 271,* 57-71.

van Anders, S. M. & Gray, P. B. (under review). Human sexual relationships and hormones. *Annual Review of Sex Research.*

van Anders, S. M. & Hampson, E. (2005). Testing the prenatal androgen hypothesis: Measuring digit ratios, sexual orientation, and spatial abilities in adults. *Hormones and Behavior, 47,* 92-98.

van Anders, S. M. & Watson, N. V. (2006a). Relationship status and testosterone in North American men and women of diverse orientations: Cross-sectional and longitudinal data. *Psychoneuroendocrinology, 31,* 715-723.

van Anders, S. M. & Watson, N. V. (2006b). Social neuroendocrinology: Effects of social contexts and behaviors on sex steroids in humans. *Human Nature, 17,* 212-237.

van Anders, S. M. & Watson, N. V. (2006c). Menstrual cycle irregularities are associated with testosterone in healthy premenopausal women. *American Journal of Human Biology, 18,* 841-844.

van Anders, S. M. & Watson, N. V. (2007a). Effects of ability- and chance-determined competition outcome on testosterone. *Physiology and Behavior, 90,* 634-642.

van Anders, S. M. & Watson, N. V. (2007b). Testosterone levels in women and men who are single, in long-distance relationships, or same-city relationships. *Hormones and Behavior, 51,* 286-291.

van Anders, S. M. (under review). Androgens and diversity in human partnering. In P. B. Gray & P. T. Ellison (Eds.), *Endocrinology of social relationships.* Cambridge, MA: Harvard University Press.

van Anders, S. M., Hamilton, L. D., Schmidt, N., Watson, N. V. (in press). Associations between testosterone secretion and sexual activity in women and men. *Hormones and Behavior.*

van Anders, S. M., Hamilton, L. D., & Watson, N. V. (2007). Multiple partners are associated with higher testosterone in North American men and women. *Hormones and Behavior, 51,* 454-459.

van Anders, S. M., Hampson, E., & Watson, N. V. (2006). Seasonality, month, and testosterone in a North American sample of women and men. *Psychoneuroendocrinology, 31,* 895 – 899.

Vermeulen, A. (1976). The hormonal activity of the postmenopausal ovary. *Journal of Clinical Endocrinology and Metabolism, 42,* 247-253.

Waldinger, R. J., Schultz, M. S., Hauser, S. T., Allan, J. P., & Crowell, J. A. (2004). Reading others emotions: The role of intuitive judgements in predicting marital satisfaction, quality, and stability. *Journal of Family Psychology, 18,* 58-71.

Walker, R. F., Wilson, D. W., Read, G. F., & Riad-Fahmy, D. (1980). Assessment of testicular function by the radioimmunoassay of testosterone in saliva. *International Journal of Andrology, 3,* 105-120.

Wallen K. (2001). Sex and context: Hormones and primate sexual motivation. *Hormones and Behavior, 40,* 339-357.

Wang, C., Plymate, S., Nieschlag, E., & Paulsen, C. A. (1981). Salivary testosterone in men: Further evidence of a direct correlation with free serum testosterone. *Journal of Clinical Endocrinology and Metabolism, 53,* 1021-1024.

Williams, J. R., Carter, C. S., & Insel, T. (1992). Partner preference development in female prairie voles is facilitated by mating or the central infusion of oxytocin. *Annals of the New York Academy of Sciences, 652,* 487–489.

Williams, J. R., Insel, T. R., Harbaugh, C. R., & Carter, C. S. (1994). Oxytocin administered centrally facilitates formation of a partner preference in female prairie voles (Microtus ochrogaster). *Journal of Neuroendocrinology, 6,* 247–250.

Wingfield, J. C. (1984). Androgens and mating systems: Testosterone-induced polygyny in normally monogamous birds. *Auk, 101,* 665-671.

Wingfield, J. C., Hegner, R. E., Dufty, A. M., Jr., & Ball, G. F. (1990). The "challenge hypothesis": Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist, 136,* 829-846.

Wingfield, J. C., Jacobs, J. D., Tramontin, A. D., Perfito, N., Meddle, S., Manney, D. L. & Soma, K. (2000). Toward an ecological basis of hormone-behavior interactions in reproduction of birds. In *Reproduction in Context.* K. Wallen & J. E. Schneider, Eds. Pp85-128. MIT Press: Cambridge, MA.

Winslow, J. T., Hastings, N., Carter, C. S., Harbaugh, C. R., & Insel, T. R. (1993). A role for central vasopressin in pair bonding in monogamous prairie voles. *Nature, 365,* 545–548.

Wisniewski, A. B. & Nelson, R. J. (2000). Seasonal variation in human functional cerebral lateralization and free testosterone concentrations. *Brain and Cognition, 43(1-3),* 429-438.

Wood, R. I. (2004). Reinforcing aspects of androgens. *Physiology and Behavior, 83,* 279-289.

Wynne-Edwards, K. E. (2001).Hormonal changes in mammalian fathers. *Hormones and Behavior, 40,* 139-145.

Young, L. J., Murphy Young, A. Z., & Hammock, E. A. (2005). Anatomy and neurochemistry of the pair bond. *Journal of Comparative Neurology, 493,* 51-57.

Young, L. J. & Wang, Z. (2004). The neurobiology of pair bonding. *Nature Neuroscience, 7,* 1048–1054.

Ziegler, T. E. (2000). Hormones associated with non-maternal infant care: A review of mammalian and avian studies. *Folia Primatologica, 71,* 6-21.