

# Social Neuroendocrinology

## Effects of Social Contexts and Behaviors on Sex Steroids in Humans

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In this paper we provide a critical review of research concerned with social/environmental mechanisms that modulate human neuroendocrine function. We survey research in four behavioral systems that have been shaped through evolution: competition, partnering, sex, and pregnancy/parenting. Generally, behavioral neuroendocrine research examines how hormones affect behavior. Instead, we focus on approaches that emphasize the effects of behavioral states on hormones (i.e., the “reverse relationship”), and their functional significance. We focus on androgens and estrogens because of their relevance to sexually selected traits. We conclude that the body of research employing a reversed or bidirectional perspective has an incomplete foundation: participants are mainly heterosexual men, and the functionality of induced shifts in neuroendocrine factors is generally unknown. This area of research is in its infancy, and opportunities abound for developing and testing intriguing research questions.

KEY WORDS: Androgen; Competition; Estrogen; Gender; Hormones; Mating; Parenting; Pregnancy; Reproduction; Relationships; Sex; Sexuality

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 behavior is largely mediated by sex hormones. In normal 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 masculinize the developing fetus (for an overview, see Nelson 2000), leading to sexual dimorphism in subsequent life. In the absence of an *sry* gene, the

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Received August 16, 2004; revisions requested November 30, 2004; final version accepted February 22, 2005.

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*Human Nature*, Summer 2006, Vol. 17, No. 2, pp. 212–237.

1045-6767/98/\$6.00 = .15

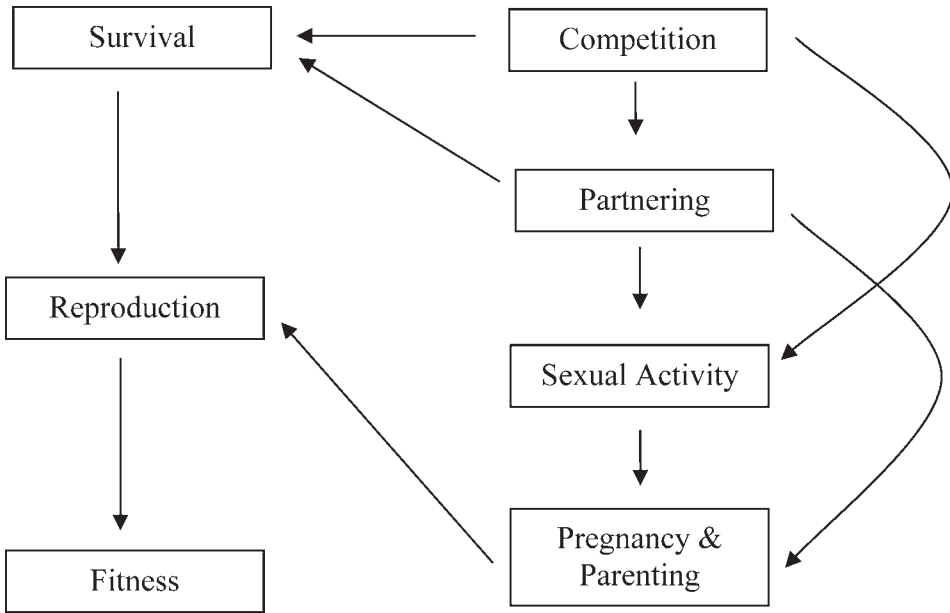
mammalian fetus develops into a phenotypic female (although the dogma of “female as default” is probably an oversimplification; e.g., Hughes 2004). Historically, the bulk of human behavioral endocrinology research has adopted a causal perspective mirroring the unidirectional relationship between hormone secretion and fetal sexual differentiation. Specifically, most studies focus on the effects of hormones on somatic or behavioral measures, and rightly so, because hormones have powerful effects on the nervous system throughout life.

But there is an oft-neglected converse of this perspective. One’s own behavior, the behavior of others, and other environmental influences can all potently alter the functioning of the endocrine system, resulting in pervasive changes in behavior. And in some cases—which we will refer to as bidirectional—a behavior under study and its hormonal correlates are mutually reinforcing: for example, higher testosterone (T) levels may lead to increased competitive encounters, which in turn may lead to increased T, which may support further competitive interactions, and so on and so on. This approach is statistically more complex to examine and interpret, but arguably more interesting and valuable because of the potential to develop a more comprehensive account of the relationship between hormones and behavior. Because bidirectional associations are particularly under-investigated, there are few data to review. However, many of the assumptions underlying research on environmental controls on hormonal functions are bidirectional in nature, if not in form.

Endocrine changes driven by environmental influences are thought to be functional, as the body of this paper will show. That is, the results of such alterations are generally presumed to be behavioral changes that increase fitness. Our goal in this paper is to review and synthesize current knowledge about the influences of a specific set of environmental variables—competition, partnering (a better term than mating for human relationships based on long-term commitment and sexual activity), sexuality, and pregnancy/parenting—on endocrine parameters. We have chosen these four areas because of their primacy to evolution and because they have received enough empirical attention to warrant a review and synthesis. Fitness—the representation of one’s genes in subsequent generations—requires survival and reproduction. As will be discussed in subsequent sections and as illustrated in Figure 1, competition, partnering, sexual activity, and pregnancy/parenting are central to either or both survival and reproduction, and thus ultimately fitness.

The development of salivary steroid immunoassay has greatly simplified the inclusion of endocrine variables in biobehavioral research. Sex steroids are of particular relevance to research into sexually selected behaviors and can be reliably measured in saliva. High concentrations of androgens circulate in men, and they are released from the testes, the adrenal glands, and from precursor hormones in peripheral tissues after conversion. It has been less widely appreciated that androgens also circulate in women, at lower concentrations, and are produced in the ovaries, the adrenal glands, and converted from precursor hormones in peripheral tissues. Estrogens also circulate in both men and women, albeit in higher concentrations in women than in men. Although researchers have typically focused on the higher-

*Figure 1.* Conceptual map of the inter-associations between competition, partnering, sexual activity and pregnancy/parenting, as well as survival and reproduction, and ultimately fitness. Arrows represent direct contributions from one variable to another.



concentration steroids in each sex (i.e., androgens in men and estrogens in women), both steroid classes have significant effects in both sexes. And, in the example of sexual behavior, Sherwin (1998a:422) notes that “the possibility exists that females are more sensitive to the behavioral effects of T” than males are.

Only relatively recently has the sensitivity of salivary assays reached a point where androgens in women can be accurately assessed, and some technical issues concerning its use in women remain to be resolved (e.g., Shirtcliff et al. 2002). However, women seem to be understudied in non-clinical hormone research for a variety of other reasons. Studying hormonal effects in women often requires that women not be using exogenous hormones like oral contraceptives (which large numbers of university-age women are doing) or hormone replacement therapy (which postmenopausal women may be doing), although these factors can be employed as experimental variates. Menopausal status is a further source of variability since women show a dramatic decline in estrogen production at menopause. Finally, varying levels of sex steroids over the menstrual cycle may discourage some from undertaking endocrine research with women, although Dabbs and de La Rue (1990) argue that menstrual phase does not need to be controlled when androgens are being studied, unless menstrual variation is a focus of the study. Although it is inaccurate to view men’s steroid titres as stable—androgen levels exhibit daily and seasonal fluctuations as well as an age-related decline—perhaps it is not surprising that fewer

studies have tackled the somewhat more methodologically complex situation in women. That said, there is much room for research, and even with the methodological constraints, recruiting and testing women while controlling for hormonal variability is not overly difficult.

## COMPETITION

Competition for limited resources drives both natural and sexual selection. In the case of sexual selection, this competition may differ by sex, leading to adaptations that are sex-specific. Most research is predicated upon the idea that men are more competitive than women because males have a steeper reproductive gradient than women, meaning males have more to gain or lose, reproductively speaking. While this may be true, research into primates has shown that though males have a greater variability in reproductive potential, females also have a significant variability, and, as would be predicted, engage in significant competition (Hrdy 1999). For example, many female primates fail to carry pregnancies to term or give birth to viable offspring (Drickamer 1974; Taub 1980). Females' social rank is an important influence on their reproductive fitness; more high-ranking females give birth than low-ranking females, and the offspring of high-ranking females are more likely to survive (Drickamer 1974). Many male primates prefer dominant to subordinate females (Palombit et al. 2001; Zumpe and Michael 1989). And, fertility can be largely influenced by the harassing or stressful behaviors of other females (Bowman et al. 1978; Dunbar 1980; Hrdy 1999; Silk 1980). These points highlight the need for a more inclusive definition of competition (i.e., competition is not only direct fighting). Since both males and females vary in reproductive potential, we would expect both males and females to compete in ways that might include access to mates of high quality, positions in status hierarchies, as well as access to other resources.

When it comes to humans, research shows that women and men are equally competitive in terms of financial success, success at school, family, popularity, status, etc. (Cashdan 1998), though men are more competitive about sports, and women are more competitive about looking attractive. Female competition would be expected in our species because men invest in their offspring with resources and direct care, and do so more than most other male mammals (Storey et al. 2000; Wynne-Edwards 2001). As well, if access to potential long-term partners is limited, as it is for both men and women by law or custom, both men and women should be choosy about and competitive for potential partners. Of course, this delves into the lively debate on the relative likelihood of monogamy and polygamy in our evolutionary history, and present-day laws and customs cannot be held to be representative of past conditions. However, "limited access" to reproductive partners does not merely refer to cultural impositions, but also includes the reproductive "unavailability" of a pregnant woman. Pregnant women in any social group limit the number or fitness of women whom men could potentially inseminate, and limit

themselves—by being pregnant—as to the number and fitness of men who could inseminate them. Regardless of whether access to partners is limited by custom or reproductive reality, if both men and women need and provide resources to support themselves and offspring, both should compete. Though both men and women may compete, the nature of their competition may differ, especially in response to environmental variations. For example, if women do not have equal access to needed financial resources, they may compete for men who can provide these resources (Hrdy 1997). Comparing cultures that differ in economic opportunities for women illustrates this pattern: women with less access to financial resources select partners who hold more wealth, while women with more access to financial resources are less choosy about the wealth held by a prospective partner (Eagly and Wood 2002).

The Challenge Hypothesis (Wingfield et al. 1990) suggests that social interactions affect androgen levels in males, and androgens should be high when challenges for resource (mates, territory, status, etc.), or the likelihood of challenges, are present. The pattern may be the same or differ in females, depending on the species. For example, exposure to a challenge increased progesterone (but not T) and decreased the progesterone/T ratio in female California mice (Davis and Marler 2003), whereas female dunnocks do show an elevation in T (Langmore et al. 2002).

Because overt instances of human competition seem so obviously involved in the selective pressures that drive evolution, there should be associations between competition and sex steroids. Research has generally found more evidence for an effect of competition on hormones, as opposed to the inverse relationship. This body of human research is based on findings by Mazur and Lamb (1980) and Elias (1981), in which winners of a competition showed increases in T compared with precompetition levels and losers (Table 1). This research, though unidirectional, is conceptually bidirectional; an increase in T following a win may increase the likelihood of future competition or make the winner more prepared to engage in future competition. However, no research to date has directly examined the function of the induced T increase in humans.

Research into competition and hormones has largely been conducted in the context of sports events, generally employing small samples of men. As Booth et al. (1989:557) state: “Preliminary research has focused on athletic competition because sporting events are formalized contests for status that are exceedingly convenient for study.” Though this seems valid, research has not always borne out the contention that athletic competitions provide an optimal paradigm for this research. Results have been mixed to say the least, but significant findings, when they are found, are at least in a consistent direction: competitive success results in increased T. Winners of tennis matches show higher T than pre-match levels or losers (Booth et al. 1989; Mazur and Lamb 1980), as do winners of wrestling matches (Elias 1981). But investigations with other sports have found no significant T increase: In judo competitions (Filaire et al. 2001; Salvador et al. 1987; Suay et al. 1999) and basketball games (Gonzalez-Bono et al. 1999), no significant increase in T was

identified among winners. The differences in these findings may be a consequence of using sports to test competition and hormones. The sports that have been studied (e.g., basketball, tennis, wrestling, judo) differ in many ways, including the degree of physical contact, the length of the competition, team versus individual efforts, and so on. In addition, athletes generally play “at home” or “away,” and T can be higher prior to games played at home (Neave and Wolfson 2003). So though athletic competitions are a fascinating way to study physiological sequelae of exertion, team bonding, personal contribution, cognitive attribution, and so on, they probably are not straightforward models for examining the effects of competition on T. Additionally, the mixed findings could also be a result of the decreased power associated with the very small sample sizes utilized (see Table 1), or confounds associated with intense physical and athletic training (e.g., Sallinen et al. 2004). In light of these considerations, it is not especially surprising that the sole study that exam-

*Table 1.* The Effects of Winning a Competition on Testosterone

Competition	Study	Sample	Outcome
ATHLETIC PARTICIPANTS			
Tennis	Mazur and Lamb 1980	4 ♂, grad students	Increase
	Booth et al. 1989	6 ♂, varsity	Increase
Wrestling	Elias 1981	15 ♂, varsity	Increase
Judo	Salvador et al. 1987	14 ♂, regional	No change
	Suay et al. 1999	26 ♂, club players	No change
	Filaire et al. 2001	18 ♂, interregional	No change
Basketball	Gonzalez-Bono et al. 1999	16 ♂, professional	No change
Rugby	Bateup et al. 2002	17 ♀, varsity	No change
ATHLETIC FANS			
Basketball and Soccer	Bernhardt et al. 1998	8 ♂ at an arena; 21 ♂ at a sports bar	Increase
NON-ATHLETIC			
Chess	Mazur et al. 1992	16 ♂, city club	Increase
Coin toss	McCaul et al. 1992	101 ♂, intro psych	Increase
Lottery	Mazur and Lamb 1980	14 ♂, grad students	No change
Video game	Mazur et al. 1997	28 ♂, 32 ♀; mostly undergrads	No change
Reaction time	Gladue et al. 1989	39 ♂, intro psych	Increase

ined the effects of winning or losing at sports in women (Bateup et al. 2002) found no change in T levels, especially since hormonal contraceptive use was apparently not controlled.

Non-athletic paradigms have been more successful at testing the hypothesis that winning increases T. For example, winners of chess matches display increased T relative to losers (Mazur et al. 1992). Additionally, Mazur and colleagues showed that players who are successful over many competitions have increased T relative to baseline levels. Like athletic competitions, the chess paradigm is *ability-oriented*, meaning that each player's ability makes a strong contribution to the competition's outcome. In contrast, other studies have employed a *chance-oriented* paradigm, in which each player's ability is irrelevant to the competition's outcome. For example, participants declared to be winners of a reaction-time competition show increases in T over losers even with experimental control of winning and losing (Gladue et al. 1989). Men who win a series of coin tosses exhibit increases in T even with explicit reminders of the chance nature of the competition (McCaul et al. 1992). Finally, men who win a lottery do not show increases in T (Mazur and Lamb 1980). It may be that the lottery is too brief for participants to internalize it as a competition, and they instead view it as a random event. In contrast, McCaul and colleagues' coin toss series and Gladue and colleagues' reaction-time task may be sufficiently long and structured for participants to view them as a competition, even though they contain the same chance-orientated nature as the lottery in Mazur and Lamb's study. These aspects (investment and length of involvement, chance vs. ability) of competition clearly warrant further experimentation.

Indeed, investment—but not necessarily effort—in a win may be sufficient to induce a T increase. Male fans watching basketball and soccer show vicarious increases in T if their favored team wins (Bernhardt et al. 1998). This parallels a finding in cichlid fish, where T increased in fish who were watching other fish fight (Oliveira et al. 2001). Objective effort evidently is not required in order for a competitive interaction to elicit a T increase.

Only one non-sport study has examined competition and hormone levels in women (Mazur et al. 1997), directly comparing men and women using a video game. Neither men nor women show an increase in T after winning. On the basis of this null finding, along with two unpublished studies on samples of three or four women, Mazur and Booth (1998) conclude that there probably is no link between competition and T in women. In commentary, Kemper (1998) rightly suggests that the data are insufficient to make conclusions about a competition-T link in women. Although Bateup and colleagues (2002) also found no evidence of a competition-T link in women rugby players, the substantial number of null findings in men in certain sport categories (see Table 1) renders such conclusions extremely premature. Indeed, women with higher T (among other androgens) may be more likely to act on competitive feelings than women with lower T (Cashdan 2003). Stated another way, women who acted on competitive feelings were more likely to have higher T.

Table 2. The Association between Partnering and Testosterone (T) Levels

Relationship Parameter	Study	Population	Findings
Falling in love vs. controls	Marazziti and Canale 2004	12 ♂, 12 ♀; med students and residents	♂: in love < controls ♀: in love > controls
Partnered vs. single	Burnham et al. 2003	122 ♂ Harvard business students	Long-term committed < single
	Gray, Chapman et al. 2004	107 ♂ Harvard undergrads	Committed < single
	Mazur and Michalek 1998	1,881 ♂ U.S. Air Force veterans	Married < single
	Gray et al. 2002	58 Boston-area ♂	Married < single
	Gray, Campbell et al. 2004	65 U.S. ♂	Married < single
	Gray 2003	88 Kenyan Swahili ♂	Polygynous > married = single
Likelihood of getting married	Booth and Dabbs 1993	>7,748 ♂ former U.S. servicemen	↑T = ↓ likely



Research into the endocrine effects of competition is situated in an evolutionary context, and authors mainly interpret their findings in evolutionary terms. However, the functions served by the increased T remain to be empirically established. Perhaps they are associated with future competitive engagement or success, as mentioned earlier. Or, they may be associated with favorable alterations in other variables, such as general arousal, which may be affected by T (e.g., Dabbs et al. 2002). Findings from the nonhuman animal literature are also suggestive: for example, T administration reduces fear responses in cattle (Boissy and Bouissou 1994) and reduces anxiety in male house mice (Aikey et al. 2002).

## PARTNERING

Like competition, partnering or relationship status has been examined with regard to endocrine regulation in an evolutionary context (Table 2), and earlier research looked at how T would affect relationship status. Men with higher T are less likely to marry, and married men with higher T titres may have higher degrees of marital instability (Booth and Dabbs 1993). In addition, married men exhibit significantly lower T than single men (Mazur and Michalek 1998), and T appears to increase with divorce and decrease with marriage. These two studies are interpreted by the authors as indicating that men with high T experience marital interaction that is of a lower quality, likely because of associated increases in risk-taking and antisocial behavior that may have paid off in ancestral environments but are not adaptive in current society. Newer research has examined partnering and hormones with a focus on the reverse relationship.

It appears that T is higher in single men than married men with or without children (Gray, Campbell et al. 2004; Gray et al. 2002). It has been suggested that diminished T titres in men in committed relationships represent a potential trade-off between two classes of activities. The first class, to which we refer in this paper as “competitive,” includes behaviors intended (consciously or not) to attract partners or accrue resources. In Gray and colleagues’ (2002) study of men, these behaviors would be male competition and mate attraction. The second class, to which we refer as “bond maintenance,” includes behaviors intended to develop bonding/intimacy with a partner, infant, or other. Some might question our proposing new terminology, since the terms *mating* and *parenting effort* are commonly used. However, mating effort can refer to anything that has to do with mating or sexual energy expenditure, and parenting effort refers to energy expended on offspring. Our terminology is meant to distinguish the difference between, for example, finding a partner and relating with a partner, both of which would be subsumed under mating effort, but which we propose are very different.

It would be expected that both married men and men in a committed relationship (both bond-maintenance states) exhibit lower T than single men (for many, akin to a competitive state), and this is exactly what research has established (Burnham et al. 2003; Gray, Chapman et al. 2004).

Overall, we see the results as suggesting that forming a committed relationship leads to decreased T, although there have been no longitudinal studies to establish the cause-effect relationship. It remains possible that lower-T men are simply more likely to marry, as suggested in Mazur and Michalek (1998) and Booth and Dabbs (1993), instead of marriage or commitment decreasing T. Plus, the two possibilities do not have to be mutually exclusive.

If commitment does decrease T, another possible function (in addition to facilitating decreased competitive or increased bond-maintenance behaviors) might be to facilitate improved immune function. Curiously, T seems to have immunosuppressive qualities (Grossman 1985; Yao et al. 2003). The immunocompetence handicap hypothesis (Folstad and Karter 1992) argues that there is a trade-off between attractive characteristics and immunocompetence. Thus, having higher T to facilitate partner competition and attraction might also be associated with decreased immune function and health factors as is seen in other species (Wingfield et al. 2001). A reduction in T titres while in a relationship might thus be adaptive (Wingfield et al. 2001), as long as being in a relationship indicates ample opportunity to reproduce. Married men are known to have reduced morbidity and mortality compared with single men (Hu and Goldman 1990)—though unstudied, this likely includes men in marriage-like relationships. It follows, then, that decreased T in married (or married-like) men may increase immunocompetence, leading to better health parameters.

The mechanism by which a committed relationship leads to decreased T (if, indeed, that is the causal relationship) remains to be explicated, but it is possible that decreased daily competitions for sexual or romantic attention may be at play. One recent study (Roney et al. 2003) found that T increases in heterosexual men exposed to brief conversations with women. Interestingly, display (or “show off”) behaviors are associated with the degree of T increase. Gray (2003; also Gray, Chapman et al. 2004) shows that evening but not morning samples of T were lower in partnered men than single men, again suggesting that some aspect of daily behaviors or thoughts are associated with the decreased T in men in committed relationships. Together, these findings may be suggestive that daily competitive interactions involving access to women lead to a smaller circadian decrease in evening T in heterosexual men from morning baseline levels. By definition, behaviors aimed at attracting members of the opposite sex should be less frequent among heterosexual men in committed relationships. Gray, Campbell et al. (2004) found that married men’s T levels are no different depending on whether they have a “wife/child-day” (i.e., spend time with their wives and/or children) or a non-wife/child day. Perhaps increases in bond-maintenance activities (which vary according to the presence of one’s spouse and/or child) are less relevant to T than a decrease in competitive activities (which should remain constant) that should accompany committed relationships. Though speculative, it follows that individuals in committed relationships engage in less partner competition than singles do. So, they would

show fewer increases in T levels because of fewer competitive engagements over the day, perhaps leading to lower T measures in the evening.

Gray, Chapman et al. (2004) found that unpartnered men who did not have relationship experience had lower T than unpartnered men with relationship experience. This could be viewed as additional support for our conjecture that men with prior experience may be interested in finding a new partner (competitive state), whereas men with no experience may lack the will, interest, or know-how for finding partners. In addition, Roney and colleagues (2003) found that only (heterosexual) men with recent sexual experience responded to conversations with women with testosterone spikes, and that these spikes were associated with "courtship-like" behaviors. Roney and colleagues note that prior experience with women may have sensitized men's responses to women, much as occurs in the non-human animal literature. We suggest therefore that encounters must be perceived as competitive to be associated with higher T or T spikes; for example, a heterosexual man conversing with a woman might be displaying competitive behavior only if the man sees the situation as an attempt to attract her, but not if he sees it as stressful or merely friendly. Wingfield and colleagues (1990) provide evidence that reproductive state has a direct effect on the encoding of social cues and suggest their conclusions may be equally applicable to all other vertebrates.

Relationship status does not merely include single and partnered; other categories deserve attention. For example, Gray (2003) examined a population of Kenyan Swahili men and found that married men did not have lower T than single men, but that polygynously married men had higher T than all other men. Gray notes that these men differ strongly from the Harvard-based men in earlier studies 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 or had children, whereas the single Harvard men had no children and had never been married. Although not examined by Gray, 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 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 would support the notion that daily competitive interactions for women's attention increases heterosexual men's T levels. Is physical monogamy a factor with which decreased T is associated, perhaps cued by the one partner's vaginal secretions and/or pheromones? This begs the question of whether monogamous men in committed relationships have lower T than men who cheat in "committed" relationships (thus engaging in more competitive activities than their more trustworthy parallels). Indeed, Booth and Dabbs (1993) found in their study that men with higher T were more likely to report having extramarital sex with at least three partners.

Though love may seem too esoteric a topic for an evolutionary discussion of hormones, it underlies our understanding of partnering, and as Carter (1998:780)

notes: "Love and social attachments function to facilitate reproduction. . . ." Oxytocin and vasopressin are most closely linked to love and affiliation (Carter 1998), and these hormones can increase bonding behaviors. As a behavioral and/or cognitive state, falling in love may effect changes in sex steroids. Men and women who had recently fallen in love do show different hormonal parameters than men and women who are either single or in long-term relationships (Marazziti and Canale 2004). Men falling in love show lower T than controls, whereas women falling in love show higher T. After having fallen in love (i.e., 12–28 months into the relationship), the experimental participants no longer differed from controls. The authors did not explore the functionality of the finding (though they note future such studies are underway), but again, it is tempting to point to a possible association with competitive encounters. People falling in love would likely engage in fewer competitive activities than normal, as they focus their energies and time on bonding with the one individual who is focusing, in return, on them; this explanation works for men's decreased T but obviously not women's increased T.

## SEXUAL ACTIVITY

A now-famous study published in *Nature* (Anonymous 1970) details the effects of sexual activity on T. A lone researcher on an isolated island measured his beard growth by the weight of its clippings, and noted that his beard appeared to grow more around the time of trips to the mainland, during which he would engage in sexual activity with his female partner. As beard growth can be a type of bioassay for T levels, he theorized in his paper that the sexual activity increased his T, which in turn increased his beard growth. Apparently, actual sexual activity was not necessary: his beard clippings were heavier even on the days before he left the island, as if in anticipation of the sexual activity to come.

Other early studies (Table 3) also examined nonphysical sexual stimulation in heterosexual men. For example, sexually explicit movies increase men's T compared with sexually neutral films (Pirke et al. 1974; Rowland et al. 1987; Stoleru et al. 1993; cf. Carani et al. 1990) and neutral or aggressive films (Hellhammer et al. 1985). These studies parallel findings in other animals: for example, exposure without access to female mice increases the testosterone levels of male mice (Amstislavskaya and Popova 2004). Luteinizing hormone, which can stimulate T production, also increases in men following exposure to erotic stimuli (LaFerla et al. 1978; Rowland et al. 1987; Stoleru et al. 1993; cf. Carani et al. 1990). The function of these alterations, like those related to competition or partnering, has not been studied directly. However, men exhibit increased optimism scores and decreased exhaustion scores after movies with sexual content but those without sexual content (Hellhammer et al. 1985), and T is correlated with relaxation following sexual arousal (Rowland et al. 1987). Thus, sexually explicit material increases T, which in turn may be associated with increased confidence, optimism, or relaxation, and decreased exhaustion. T does have a positive effect on mood in clinical populations (e.g., Sherwin 1988b).

Table 3. The Effects of Sexual Activity on Testosterone

Activity	Study	Population	Findings
Watching erotic movies	Pirke et al. 1974	16 ♂	Increase
	Hellhammer et al. 1985	20 ♂	Increase
	Rowland et al. 1987	7 ♂ (controls)	Increase
	Stoleru et al. 1993	9 ♂	Increase
	Carani et al. 1990	8 ♂	No change
Penis-vagina intercourse	Fox et al. 1972	1 ♂	No change
	Lee et al. 1974	8 ♂; 5 ♀	No change
	Stearns et al. 1973	6 ♂ from couples	No change
	Kraemer et al. 1976	19 ♂	Increase after 24 hrs
	Dabbs and Mohammed 1992	4 couples; 4 ♂, 4 ♀	Increase
Masturbation	Krüger et al. 1998	10 ♂	No change
	Exton et al. 1999	10 ♀	Increase
	Purvis et al. 1976	34 ♂; national conscripts	Increase
Sexual activity with unfamiliar or multiple partners	Hirschenhauser et al. 2002	13 ♂	Increase next A.M.

An increase in T may lead to increased mood parameters, which may then translate into behavior depending on the individual's personality, predisposition, or environmental circumstance. For example, men in whom a positive mood has been induced show greater physiological and subjective sexual arousal during subsequent erotic stimuli compared with men in a neutral control condition, whereas men in whom a negative mood has been induced show decreases in sexual arousal (Mitchell et al. 1998). The effects of mood on sexual activity are complex, though, and some men may show seemingly paradoxical associations (i.e., negative mood leading to increased sexual activity), and the frequency and type of this association may be differentially associated with gay or heterosexual sexual orientations (Bancroft et al. 2003a, 2003b). There may be more steps involved in the T-mood-sexuality link: Increases in mood may translate into increased confidence or energy depending on the individual and the environmental circumstance, leading to an increased likelihood of seeking out or responding to sexual stimuli or encounters. An alternative and likely complementary explanation is that the increase in positive affect may act as a positive reinforcement. Because both T increases and affective increases are seen quickly—15 minutes following the stimuli—conditioning effects are certainly possible.

Early studies that attempted to link increases in T to actual sexual activity (all in

heterosexual men) provided mixed results. For example, Fox et al. (1972) sampled blood from one man before, during, and 5 minutes after ejaculation. T was higher in samples around coitus than before coitus, but there was no difference between pre-coitus and post-ejaculation T. As well, masturbation did not lead to significant increases in T. Lee et al. (1974) studied eight married men and found no difference in T from pre- to post-coitus. Both studies conclude that sexual activity has no effect on T titres. However, Fox et al. may have sampled T too early following coitus for changes to have occurred, and both studies (as well as Carani et al. [1990], cited earlier regarding nonphysical erotic stimuli) had small samples despite wide individual variation in T levels. As such, studies with appropriate sample sizes and timing would be more likely to uncover significant effects of sexual activity on T. For example, with a larger sample of 24 men, androgens and estrogens are found to be significantly higher following masturbation, but not after "sham masturbation" in which 11 men were only led to believe that they would masturbate (Purvis et al. 1976).

Other studies have also found support for an increase in T following sexual activity (again, all data from heterosexual men). Kraemer et al. (1976) measured T daily, finding higher levels on the days following sexual activity. Interestingly, increases in T were not predictive of sexual activity. It may be that the increase in T does not necessarily function to promote further sexual activity but instead may be related to sperm quality or some other parameter. Since LH and FSH are needed for sperm production, it makes sense that increases in T would follow ejaculation (and thus depletion of sperm stores and possible gonadotropin-releasing hormone increases). For example, in men with poor sperm parameters, a second semen sample collected 2 hours after a first sample is more effective at facilitating pregnancy than the first sample (Barash et al. 1995). Although plausible, this function of the T increase remains to be established.

More recent work has also shown T increases following sexual activity and has also included women, though again only heterosexuals. Dabbs and Mohammed (1992), utilizing salivary assays, examined salivary concentrations before and after sexual activity in both men and women. Compared with pre-activity samples, T is higher after sexual activity. On days with no sexual activity, however, T decreases. As found by Kraemer and colleagues (1976), no anticipatory rise in T is detectable. This well-designed study certainly points to effects of sexual activity on T titres, though the addition of control conditions like physical exertion and close partner contact would be more conclusive. Masturbation-induced orgasm also leads to increased T in heterosexual women (Exton et al. 1999) and men (Purvis et al. 1976; cf. Kruger et al. 1998). Does sexual activity without the presence of orgasm lead to T increases, or is orgasm necessary? Because the majority of studies have examined sexual activity accompanied by orgasm (or have not reported the presence/absence of orgasm), this question remains unaddressed.

As mentioned earlier, sexual activity may increase T secondarily to sperm production, but the induced elevation of T does not appear to be predictive of more

sexual activity. It is possible that sexual encounters are themselves at least quasi-competitive activities and that T may thus increase as it does following successful competition (this begs the question as to whether orgasm, and/or bringing a partner to orgasm, would lead to greater increases than sexual activity without such culmination). This approach would contextualize the findings from another study in which men who reported sexual activity with unfamiliar or multiple partners showed quite dramatic increases in T the morning following the activity (Hirschenhauser et al. 2002). Though not examined by the authors, these activities may be self-perceived as particular successes or triumphs. In a different vein, Carter (1998) notes that mating and/or vaginal cervical stimulation can lead to increases in oxytocin, which may promote feelings of bonding and affiliation. So, sexual activity may promote pair-bond formation and/or retention. Whether sexual activity leads to feelings of success or affiliation, either avenue or both provide tantalizing research questions open to investigation.

## PARENTING AND PREGNANCY

Human parenting and pregnancy should be strongly influenced by evolutionary pressures because of the long-term requirements of gestation and postnatal development. To maintain pregnancy, the mother's hormonal state is altered quite considerably compared with her non-pregnant state. A father would also likely show alterations in hormones during his offspring's gestation, as is observed in various other mammalian fathers (depending on their level of paternal investment). A father's endocrine changes would presumably be somewhat different than those of a mother because fathers do not need to support gestation hormonally. Because the pregnant mother and the gestating fetus may need more resources than the mother alone can provide (Hrdy 1999), it would be adaptive for fathers (or perhaps another designated parental figure) to be hormonally primed to fulfill these functions. Following birth, a few sex-specific, offspring-oriented behaviors, breastfeeding being the most obvious, require sex-specific endocrine states. The effects of hormonal alterations in women caused by breastfeeding and pregnancy are relatively well-known and are detailed by Ellison (2003) in an evolutionary context. Still, both parents can provide other sources of nourishment, as well as baby-oriented nurturance, stimulation, or play. The effects of these other behaviors or activities on parents' hormonal states are much less well known.

If individuals having children are in partnerships, their partners can be considered an environmental variable (Table 4). In a study of partnered men and women who were soon to be parents, Berg and Wynne-Edwards (2002) found no significant correlation between the partners' T, although there was a trend towards significance ( $p = .054$ ). Though Berg and Wynne-Edwards collected 249 saliva samples for hormonal analysis, only nine couples were used. Since T levels vary widely between individuals, it is possible that individual variation may have obscured the underlying relationship for T levels between partners having children.

Table 4. The Effects of Human Pregnancy and Parenting on Estradiol (E2), Testosterone (T), Dihydrotestosterone (DHT), Cortisol (C), Oxytocin (O<sub>t</sub>), and Prolactin (PRL)

Category	Study	Population	Findings
Partners' influence on each other	Berg and Wynne-Edwards 2002	Soon-to-be parents, 9 couples: 9♂, 9♀	Partners' T trend for correlation
Taped baby cries	Fleming et al. 2002	67 fathers; experienced (E) and first-time (FT)	PRL: E ↑, FT ↓; C: E < FT; ↑ T
Baby stimuli: holding, hearing, watching birthing	Storey et al. 2000	31 ♂	↑T in early postnatal
Breast suckling	Chiodera et al. 1991 Amico et al. 1994 Light et al. 2000	13 ♀ 6 ♀ 25 ♀	↑O <sub>t</sub> ; ↓ C ↑O <sub>t</sub> ; ↓ C ↑O <sub>t</sub>
Maternal hormones in pregnant women carrying male versus female fetuses	Meulenberg and Hofman 1991 Nagamani et al. 1979 Fleming et al. 1997 Hines et al. 2002 van de Beek et al. 2004 Rodeck et al. 1985	37 (sex ratio not reported) 50 ♀; 51 ♂ 29 (sex ratio not reported) 331 ♀, 342 ♂ 79 ♀, 77 ♂ 58 (sex ratio not reported)	↑ T weeks 20–40 ↑ DHT < week 20 ↑ T ( <i>trend</i> ) no association no association no association



Though not a sex steroid, prolactin has been implicated in parenting, and it seems especially relevant to this discussion. Fleming et al. (2002) found that experienced fathers display an increase in prolactin titres following exposure to a baby's cry, whereas first-time fathers show a decrease. Both kinds of fathers show increases in cortisol following the cry, but the increase is greater for first-time fathers than for experienced fathers. This suggests that previous paternal experience moderates the perception or interpretation of baby stimuli. The increase in prolactin and smaller increase in cortisol following the cry seen in experienced fathers may reflect their know-how and that they perceive a baby crying as a mildly stressful but paternal situation. The larger increase in cortisol and decrease in prolactin seen in first-time fathers may represent their perception of a baby's cry as a stressful situation for which they are unsure of the correct paternal response—making it stressful, and less paternal. Storey et al. (2000) also found that prolactin decreases after exposure to baby-related stimuli, but in the absence of a suitable control group it remains possible that this was simply due to the passage of time.

Other hormonal associations in soon-to-be fathers have been examined in relation to their partners' stage of pregnancy (e.g., Storey et al. 2000). Holding babies while simultaneously hearing baby cries and watching birthing stimuli is associated with increases in men's T, but only in the early postnatal period. Another study looking at both fathers and non-fathers showed that hearing a baby cry also increases men's T, though only experienced fathers exhibit an increase in prolactin (Fleming et al. 2002). Storey and colleagues suggest that an increase in T might be functional; it might lead men to be prepared to protect their babies. Since the early prenatal period is a time of particular vulnerability for babies, and since baby cries are aversive and stressful stimuli and fathers had no opportunity to address the cries, increased T might be adaptive as an inclination to protect rather than bond.

In contrast, lower overall T was associated with greater paternal responsiveness in both studies, perhaps reflecting a difference between longer-term (nurturance and responsiveness) and shorter-term (protection) parenting behaviors. For example, Storey and colleagues (2000) found that men with more *couvade* (sympathetic pregnancy) symptoms during their partners' pregnancy (i.e., prenatal period) showed a greater decrease in T following exposure to infant cues. They suggest that *couvade* symptoms reflect changes in physiology that are associated with preparation for fatherhood. Men's T also decreases from the late prenatal period to the early postnatal period, suggesting that men are becoming more paternal in the early postnatal period. For example, men with lower T hold test dolls longer than men with higher levels in the prenatal period, and greater responsivity to infant cues is associated with lower T levels. Storey et al. suggest that postnatal decreases in T may enhance paternal responsiveness by decreasing men's likelihood of engaging in non-nurturant behaviors (e.g., aggression). Fleming and colleagues (2002) found that fathers and non-fathers with lower baseline levels of T have higher objective responses (e.g., heart rate) and subjective responses (e.g., negative affect, sympathy) to baby cry stimuli. They also suggest that lower T may be reflective of a more nurturant dispo-

sition. Whether transient increases in T following exposure to infant cues is adaptive in the early postnatal period, and decreases are adaptive at other times, remains to be clarified. Wynne-Edwards (2001) provides an excellent review of hormonal changes in mammalian fathers, suggesting that paternal and maternal behavior are homologous at a neural and endocrine level. She notes that, in species with extensive paternal care, new fathers show decreased T, expectant fathers have lower T than controls, and T is suppressed overall around birth. Wynne-Edwards suggests this might be to reduce the likelihood of aggression towards infants, or of distraction from the mother and infant caused by attention to courtship and mating, or to facilitate parental care or social bonding to the infant—in other words, to increase bond-maintenance behaviors and decrease competitive ones.

There has been a paucity of research looking at the effects of infant cues on maternal sex steroids in humans, with the exception of infant suckling. However, Fleming and colleagues have extensively examined associations between hormones and maternal behaviors, attitudes, and cognitions (for a review, see Corter and Fleming 2002). Storey and colleagues (2000) found that prolactin concentrations decrease in women over a 30-minute period while being exposed to infant cues, though as noted before, there was no control group. Women who report feeling concern about the baby cry show a greater cortisol decrease than other women, which is difficult to interpret.

The effects of suckling/breastfeeding on hormones have been relatively well researched. Infant suckling (or mechanical breast stimulation) compared with sham stimuli increases maternal oxytocin levels and decreases adrenocorticotropic hormone levels and cortisol (Chiodera et al. 1991). Further research has confirmed the decrease in cortisol that follows breastfeeding (Amico et al. 1994). Chiodera and colleagues suggest that an inhibitory relationship exists between oxytocin and cortisol, which would imply that decreased stress (or stress reactivity) is an important consequence of breastfeeding, perhaps leading to increased bonding and ultimately improved maternal function.

Light et al. (2000) found that women who breastfeed, but not women who bottlefeed, show an increase in oxytocin levels and a decrease in blood pressure following a stressful speech after holding their baby. The authors point to the self-selected nature of each group; it may be that women who choose to breastfeed are less easily stressed. This is a plausible explanation, but since evidence points to a breastfeeding-mediated increase in oxytocin, the self-selection likely interacts with the decreased stress response seen in breastfeeding mothers. The influence of breastfeeding on hormonal levels and subsequent responses to stimuli is indicative of a strong bidirectional relationship between hormones and behavior. It remains to be established whether the decreased stress translates into other behavioral parameters.

Since partners or infant cues may affect an individual's sex steroids, the sex of the fetus may also be an environmental influence on maternal hormones. Because male fetuses produce T, it is possible that women carrying male fetuses exhibit higher T. Meulenbergh and Hofman (1991) found that women carrying male fetuses

had higher T than women carrying female fetuses during weeks 20–40 of pregnancy (but not prior to or following this period). Fleming and colleagues (1997) also found that women carrying male fetuses had marginally higher levels of circulating T than women carrying female fetuses, though this did not reach conventional levels of significance ( $p = .08$ ). Finally, one additional study found higher DHT (but not testosterone) in mothers carrying male fetuses prior to 20 weeks of pregnancy (Nagamani et al. 1979). In contrast, three studies have not found differences in maternal hormones based on fetal sex. Hines and colleagues (2002) did not find any difference in maternal T related to fetal sex during sampling from weeks 16 to 20, nor did van de Beek and colleagues (2004) with sampling occurring during weeks 15–18 or Rodeck and colleagues (1985) in weeks 15–23. While the difference in maternal androgens, if it exists, may simply be a nonadaptive artifact of higher fetal T, there may be behavioral implications that are adaptive in some way; further research is needed to verify this phenomenon and examine possible functionality.

## CONCLUSION

A review of how behavioral and environmental influences affect hormone secretion, and the functional consequences of these changes, illustrates that this approach can be productive in two ways: it is a fertile source of testable hypotheses, and it is favorable to experimentalists because of the relative ease with which manipulations can be wrought.

The effect of sexuality on hormones is, of course, a key area for evolutionary researchers because of its relevance to reproduction. It appears that, though ovulation can be detected with detailed methods (Alliende et al. 2005; Weschler 2001), nonindustrialized societies are not aware of fertile periods (Marlowe 2004), and modern men and women often engage in sexual activity that is largely removed from its reproductive function. Thus, sexual activity is more often than not an end in its own right, as opposed to a conscious attempt at reproduction. But it is theoretically possible for a woman's body to "know" whether sexual activity involved penile penetration with ejaculation, because semen contains substances (e.g., prostaglandins) which can bind to receptors in the woman's cervix (Myatt and Lye 2004). Vaginal intercourse without condoms (putatively associated with the presence of semen in the vagina) is associated with lower levels of depression in women than intercourse with condom use (Gallup et al. 2002), though of course the groups (condom use vs. non-condom use) are likely confounded in some way. Still, does sexual activity without barrier methods of birth control (and thus free movement of semen) lead to other, different physiological responses in women?

Relatively little research has examined how infant cues and interaction can alter sex steroid concentrations in humans, but those studies already conducted show that the area is a promising one. Are hormones in male and female children, adolescents, reproductive-age adults, and postmenopausal women affected by infant cues

in similar or different ways? What are the functions of hormonal responses to infants? For example, would decreased T and/or increased cortisol following exposure to babies make an individual more likely to respond to a baby or more likely to hold the baby longer? Do babies, toddlers, young children, older children, or teenagers differ in terms of hormonal effects on parents or others? And what effect do baby stimuli (other than suckling) have on hormones in the mother?

The near-complete focus on heterosexual men also affords current researchers various intriguing lines of inquiry. No studies have been published that look at the effects of relationship status on hormonal functions in women. This is an unfortunate oversight because there are good reasons to suspect such phenomena to be present: after all, women also engage in competition for partners (e.g., attention from the opposite sex; Cashdan 1998). This oversight extends to GLBT (gay, lesbian, bisexual, trans-identified) populations. Do partnered lesbians and gay men show decrements in T titres, compared with singles? If competition underlies lower T, then the same effect would be expected in gay and lesbian individuals (if they have access to receptive individuals during the day). However, if the effect is mediated by exposure to cross-sex pheromones or other like cues, then the decrease in T might be specific to heterosexual men and women. Alternatively, if the effect that has been documented in men is mediated by exposure to cues from women, lesbians but not heterosexual women or gay men may show decreased T when in relationships.

Since sex steroids can now be accurately measured through salivary assays in both sexes, data collection is much easier and more agreeable to many than in the days when blood was the sole assay substrate. Producing saliva samples, while admittedly not a charming addendum to sexual activity, is likely better tolerated than venipuncture and should make the design of studies into sexual activity both freer and more creative. As well, the majority of studies have focused on T, leaving relationships between environmental influences and other hormones unaddressed.

Finally, explorations of the functional significance of induced hormonal fluctuations are conspicuously absent. What purpose do they serve? For example, are men with lower T more attentive to their own babies' distress or more willing to provide care for their offspring? Does the early postnatal increase in T following infant cues predict or contribute to defensive aggression in men? Does prolactin affect paternal behavior? Though it is somewhat less complex to examine these questions in men, who lack the variable fluctuations in hormonal levels that women experience pre-, peri-, and postnatally, these questions—among others—are of at least equal interest in women.

This paradigm—examining how behavioral influences affect hormones and how this plays back onto behavior—lends itself to hypothesis-generation; its derivations are quite testable, its findings are fascinating, and its contributions to evolutionary theory are—and will be—significant.

The authors would like to thank the anonymous reviewers for their comments and suggestions, and N. Schmidt for reviewing a version of this manuscript. S.M.vA. was supported by funding from a Post-

Graduate Scholarship from the Natural Sciences and Engineering Research Council of Canada (NSERC), a UNESCO-NSERC-L'Oreal For Women In Science Supplement, and a C. D. Nelson Scholarship and other awards from Simon Fraser University. This paper was written in partial fulfillment of S.M.v.A.'s doctoral dissertation requirements.

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## REFERENCES

- Aikey, J. L., J. G. Nyby, D. M. Anmuth, and P. J. James  
2002 Testosterone Rapidly Reduces Anxiety in Male House Mice (*Mus musculus*). *Hormones and Behavior* 42:448–460.
- Alliende, M. E., C. Cabezon, H. Figueroa, and C. Kottman  
2005 Cervicovaginal Fluid Changes to Detect Ovulation Accurately. *American Journal of Obstetrics and Gynecology* 193:71–75.
- Amico, J. A., J. M. Johnston, and A. H. Vagucci  
1994 Suckling-Induced Attenuation of Plasma Cortisol Concentrations in Postpartum Lactating Women. *Endocrine Research* 20:79–87.
- Amstislavskaya, T. G., and N. K. Popova  
2004 Female-Induced Sexual Arousal in Male Mice and Rats: Behavioral and Testosterone Response. *Hormones and Behavior* 46:544–550.
- Anonymous  
1970 Effects of Sexual Activity on Beard Growth in Man. *Nature* 226:869–870.
- Bancroft, J., E. Janssen, D. Strong, and Z. Vukadinovic  
2003a The Relation between Mood and Sexuality in Gay Men. *Archives of Sexual Behavior* 32:231–242.
- Bancroft, J., E. Janssen, D. Strong, L. Carnes, Z. Vukadinovic, and J. S. Long  
2003b The Relation between Mood and Sexuality in Heterosexual Men. *Archives of Sexual Behavior* 32:217–230.
- Barash, A., S. Lurie, A. Weissman, and V. Insler  
1995 Comparison of Sperm Parameters, in vitro Fertilization Results, and Subsequent Pregnancy Rates using Sequential Ejaculates Collected Two Hours Apart from Oligoasthenozoospermic Men. *Fertility and Sterility* 64:1008–1011.
- Bateup, H. S., A. Booth, E. A. Shirtcliff, and D. A. Granger  
2002 Testosterone, Cortisol, and Women's Competition. *Evolution and Human Behavior* 23:181–192.
- Berg, S. J., and K. E. Wynne-Edwards  
2002 Salivary Hormone Concentrations in Mothers and Fathers Becoming Parents Are Not Correlated. *Hormones and Behavior* 42:424–436.

- Bernhardt, P. C., J. M. Dabbs Jr., J. A. Fielden, and C. D. Lutter  
1998 Testosterone Changes during Vicarious Experiences of Winning and Losing among Fans at Sporting Events. *Physiology and Behavior* 65:59–62.
- Boissy, A., and M. F. Bouissou  
1994 Effects of Androgen Treatment on Behavioral and Physiological Responses of Heifers to Fear-Eliciting Situations. *Hormones and Behavior* 28:66–83.
- Booth, A., and J. M. Dabbs Jr.  
1993 Testosterone and Men's Marriages. *Social Forces* 72:463–477.
- Booth, A., G. Shelley, A. Mazur, G. Tharp, and R. Kittok  
1989 Testosterone, and Winning and Losing in Human Competition. *Hormones and Behavior* 23:556–571.
- Bowman, L. A., S. R. Dilley, and E. B. Keverne  
1978 Suppression of Oestrogen-Induced LH Surges by Social Subordination in Talapoin Monkeys. *Nature* 275:56–58.
- Burnham, R. C., J. Flynn Chapman, P. B. Gray, M. H. McIntyre, S. F. Lipson, and P. T. Ellison  
2003 Men in Committed, Romantic Relationships Have Lower Testosterone. *Hormones and Behavior* 44:119–122.
- Carani, C., J. Bancroft, G. Del Rio, A. R. M. Granata, F. Facchinetti, and P. Marrama  
1990 The Endocrine Effects of Visual Erotic Stimuli in Normal Men. *Psychoneuroendocrinology* 15:207–216.
- Carter, C. S.  
1998 Neuroendocrine Perspectives on Social Attachment and Love. *Psychoneuroendocrinology* 23:779–818.
- Cashdan, E.  
1998 Are Men More Competitive Than Women? *British Journal of Social Psychology* 37:213–229.  
2003 Hormones and Competitive Aggression in Women. *Aggressive Behavior* 29:107–115.
- Chiodera, P., C. Salvani, A. Bacch-Modena, R. Spallanzani, C. Cigarini, A. Alboni, E. Gardini, and V. Coiro  
1991 Relationship between Plasma Profiles of Oxytocin and Adrenocorticotrophic Hormone during Suckling or Breast Stimulation in Women. *Hormone Research* 35:119–123.
- Corter, C. M., and A. S. Fleming  
2002 Psychobiology of Maternal Behavior in Human Beings. In *Handbook of Parenting 2: Biology and Ecology of Parenting*, second ed., M. H. Bornstein, ed. Pp. 141–182 Mahwah, New Jersey: Lawrence Erlbaum Associates.
- Dabbs, J. M. Jr., and D. de La Rue  
1990 Salivary Testosterone Measurements among Women: Relative Magnitude of Circadian and Menstrual Cycles. *Hormone Research* 35:182–184.
- Dabbs, J. M. Jr., and S. Mohammed  
1992 Male and Female Salivary Testosterone Concentrations before and after Sexual Activity. *Physiology and Behavior* 52:195–197.
- Dabbs, J. M. Jr., A. E. Karpas, N. Dyomina, J. Juechter, and A. Roberts  
2002 Experimental Raising or Lowering of Testosterone Level Affects Mood in Normal Men and Women. *Social Behavior and Personality* 30:795–806.
- Davis, E. S., and C. A. Marler  
2003 The Progesterone Challenge: Steroid Hormone Changes Following a Simulated Territorial Intrusion in Female *Peromyscus californicus*. *Hormones and Behavior* 44:185–198.
- Drickamer, L. C.  
1974 A Ten-Year Summary of Reproductive Data for Free-Ranging *Macaca mulatto*. *Folia Primatologica* 21:61–80.
- Dunbar, R. I. M.  
1980 Determinants and Evolutionary Consequences of Dominance among Female Gelada Baboons. *Behavioral Ecology and Sociobiology* 7:253–265.
- Eagly, A. H., and W. Wood  
2002 A Cross-Cultural Analysis of the Behavior of Women and Men: Implications for the Origins of Sex Differences. *Psychological Bulletin* 128:699–727.

- Elias, M.  
1981 Serum Cortisol, Testosterone, and Testosterone-Binding Globulin Responses to Competitive Fighting in Human Males. *Aggressive Behavior* 7:215–224.
- Ellison, P. T.  
2003 *On Fertile Ground*. Cambridge: Harvard University Press.
- Exton, M. S., A. Bindert, T. Kruger, F. Scheller, U. Harmann, and M. Schedlowski  
1999 Cardiovascular and Endocrine Alterations after Masturbation-Induced Orgasm in Women. *Psychosomatic Medicine* 61:280–289.
- Filaire, E., F. Maso, M. Sagnol, C. Ferrand, and G. Lac  
2001 Anxiety, Hormonal Responses, and Coping during a Judo Competition. *Aggressive Behavior* 27:55–63.
- Fleming, A. S., C. Corter, J. Stallings, and M. Steiner  
2002 Testosterone and Prolactin Are Associated with Emotional Responses to Infant Cries in New Fathers. *Hormones and Behavior* 42:399–413.
- Fleming, A. S., D. Ruble, H. Krieger, and P. Y. Wong  
1997 Hormonal and Experiential Correlates of Maternal Responsiveness during Pregnancy and the Puerperium in Human Mothers. *Hormones and Behavior* 31:145–158.
- Folstad, I., and A. J. Karter  
1992 Parasites, Bright Males, and the Immunocompetence Handicap. *American Naturalist* 139:603–622.
- Fox, C. A., A. A. A. Ismail, D. N. Love, K. E. Kirkham, and J. A. Loraine  
1972 Studies on the Relationship between Plasma Testosterone Levels and Human Sexual Activity. *Journal of Endocrinology* 52:51–58.
- Gallup, G. G. Jr., R. L. Burch, and S. M. Platek  
2002 Does Semen Have Antidepressant Properties? *Archives of Sexual Behavior* 31:289–293.
- Gladue, B. A., M. Boechler, and K. D. McCaul  
1989 Hormonal Response to Competition in Human Males. *Aggressive Behavior* 15:409–422.
- Gonzalez-Bono, E., A. Salvador, M. A. Serrano, and J. Ricarte  
1999 Testosterone, Cortisol, and Mood in a Sports Team Competition. *Hormones and Behavior* 35:55–62.
- Gray, P. B.  
2003 Marriage, Parenting, and Testosterone Variation among Kenyan Swahili Men. *American Journal of Physical Anthropology* 122:279–286.
- Gray, P. B., B. C. Campbell, F. W. Marlowe, S. F. Lipson, and P. T. Ellison  
2004 Social Variables Predict Between-Subject But Not Day-to-Day Variation in the Testosterone of U.S. Men. *Psychoneuroendocrinology* 29:1153–1162.
- Gray, P. B., J. F. Chapman, T. C. Burnham, M. H. McIntyre, S. F. Lipson, and P. T. Ellison  
2004 Human Male Pair Bonding and Testosterone. *Human Nature* 15:119–131.
- Gray, P. B., S. M. Kahlenberg, E. S. Barrett, S. F. Lipson, and P. T. Ellison  
2002 Marriage and Fatherhood Are Associated with Lower Testosterone in Males. *Evolution and Human Behavior* 23:193–201.
- Grossman, C. J.  
1985 Interactions between the Gonoidal Steroids and the Immune System. *Science* 227:257–261.
- Hellhammer, D. H., W. Hubert, and T. Schürmeyer  
1985 Changes in Saliva Testosterone after Psychological Stimulation in Men. *Psychoneuroendocrinology* 10:77–81.
- Hines, M., S. Golombok, J. Rust, K. J. Johnston, J. Golding, and the Avon Longitudinal Study of Parents and Children Study Team  
2002 Testosterone during Pregnancy and Gender Role Behavior of Preschool Children: A Longitudinal, Population Study. *Child Development* 73:1678–1687.
- Hirschenhauser, K., D. Frigerio, K. Grammer, and M. S. Magnusson  
2002 Monthly Patterns of Testosterone and Behavior in Prospective Fathers. *Hormones and Behavior* 42:172–181.
- Hrdy, S. B.  
1997 Raising Darwin's Consciousness: Female Sexuality and the Prehominid Origins of Patriarchy. *Human Nature* 8:1–49.

- 1999 *The Woman That Never Evolved*, revised ed. Cambridge: Harvard University Press.
- Hu, Y. R., and N. Goldman  
1990 Mortality Differentials by Marital Status: An International Comparison. *Demography* 27:233–250.
- Hughes, I. A.  
2004 Female Development—All by Default? *New England Journal of Medicine* 351:792–798.
- Kemper, T. D.  
1998 Fantasy, Females, Sexuality, and Testosterone [Open peer commentary on Mazur and Booth, 1998]. *Behavioral and Brain Sciences* 21:378–379.
- Kraemer, H. C., H. B. Becker, H. K. H. Brodie, C. H. Doering, R. H. Moos, and D. A. Hamburg  
1976 Orgasmic Frequency and Plasma Testosterone Levels in Normal Human Males. *Archives of Sexual Behavior* 5:125–132.
- Krüger, T., M. S. Exton, C. Pawlak, A. von zur Mühlen, U. Hartmann, and M. Schedlowski  
1998 Neuroendocrine and Cardiovascular Response to Sexual Arousal and Orgasm in Men. *Psychoneuroendocrinology* 23:401–411.
- LaFerla, J. J., D. L. Anderson, and D. S. Schalch  
1978 Psychoendocrine Response to Sexual Arousal in Human Males. *Psychosomatic Medicine* 40:166–172.
- Langmore, N. E., J. F. Cockrem, and E. J. Candy  
2002 Competition for Male Reproductive Interest Elevates Testosterone in Female Dunnocks, *Prunella modularis*. *Proceedings of the Royal Society of London, B: Biological Sciences* 269:2473–2478.
- Lee, P. A., R. B. Jaffe, and A. R. Midgley Jr.  
1974 Lack of Alteration of Serum Gonadotropins in Men and Women following Sexual Intercourse. *American Journal of Obstetrics and Gynecology* 120:985–987.
- Light, K. C., T. E. Smith, J. M. Johns, A. Brownley, and J. A. Hofheimer  
2000 Oxytocin Responsivity in Mothers of Infants: A Preliminary Study of Relationships with Blood Pressure during Laboratory Stress and Normal Ambulatory Activity. *Health Psychology* 19:560–567.
- Marazziti, D., and D. Canale  
2004 Hormonal Changes When Falling in Love. *Psychoneuroendocrinology* 29:931–936.
- Marlowe, F. W.  
2004 Is Human Ovulation Concealed? Evidence from Conception Beliefs in a Hunter-Gatherer Society. *Archives of Sexual Behavior* 33:427–432.
- Mazur, A., and A. Booth  
1998 Testosterone and Dominance in Men. *Behavioral and Brain Sciences* 21:353–397.
- Mazur, A., and T. A. Lamb  
1980 Testosterone, Status, and Mood in Human Males. *Hormones and Behavior* 14:236–246.
- Mazur, A., and J. Michalek  
1998 Marriage, Divorce, and Male Testosterone. *Social Forces* 77:315–330.
- Mazur, A., A. Booth, and J. M. Dabbs Jr.  
1992 Testosterone and Chess Competition. *Social Psychology Quarterly* 55:70–77.
- Mazur, A., E. J. Susman, and S. Edelbrock  
1997 Sex Difference in Testosterone Response to a Video Game Contest. *Evolution and Human Behavior* 18:317–327.
- McCaul, K. D., B. A. Gladue, and M. Joppa  
1992 Winning, Losing, Mood, and Testosterone. *Hormones and Behavior* 26:486–504.
- Meulenberg, P. M. M., and J. A. Hofman  
1991 Maternal Testosterone and Fetal Sex. *Journal of Steroid Biochemistry and Molecular Biology* 39:51–54.
- Mitchell, W. B., P. M. DiBartolo, T. A. Brown, and D. H. Barlow  
1998 Effects of Positive and Negative Mood on Sexual Arousal in Sexually Functional Males. *Archives of Sexual Behavior* 27:197–207.
- Myatt, L., and S. J. Lye  
2004 Expression, Localization, and Function of Prostaglandin Receptors in Myometrium. *Prostaglandins, Leukotrienes and Essential Fatty Acids* 70:137–148.



- Nagamani, M., P. G. McDonough, J. O. Ellegood, and V. B. Mahesh  
1979 Maternal and Amniotic Fluid Steroids throughout Human Pregnancy. *American Journal of Obstetrics and Gynecology* 134:647–680.
- Neave, N., and S. Wolfson  
2003 Testosterone, Territoriality, and the “Home Advantage.” *Physiology and Behavior* 78:269–275.
- Nelson, R. J.  
2000 *An Introduction to Behavioral Endocrinology*, second ed. Cambridge, Massachusetts: Sinauer Associates.
- Oliveira, R. F., M. Lopes, L. A. Carneiro, and A. V. Canario  
2001 Watching Fights Raises Fish Hormone Levels. *Nature* 409(6819):475.
- Palombit, R. A., D. L. Cheney, and R. M. Seyfarth  
2001 Female-Female Competition for Male “Friends” in Wild Chacma Baboons, *Papio cynocephalus ursinus*. *Animal Behaviour* 61:1159–1171.
- Pirke, K. M., G. Kockott and F. Dittmar  
1974 Psychosexual Stimulation and Plasma Testosterone in Man. *Archives of Sexual Behavior* 3:577–584.
- Purvis, K., B.-M. Landgren, Z. Cekan, and E. Diczfalusy  
1976 Endocrine Effects of Masturbation in Men. *Journal of Endocrinology* 70:439–444.
- Rodeck, C. H., D. Gill, D. A. Rosenberg, and W. P. Collins  
1985 Testosterone Levels in Midtrimester Maternal and Fetal Plasma and Amniotic Fluid. *Prenatal Diagnosis* 5(3):175–181.
- Roney, J. R., S. V. Mahler, and D. Maestripieri  
2003 Behavioral and Hormonal Responses of Men to Brief Interactions with Women. *Evolution and Human Behavior* 24:365–375.
- Rowland, D. L., J. R. Heiman, B. A. Gladue, J. P. Hatch, C. H. Doering, and S. J. Weiler  
1987 Endocrine, Psychological and Genital Response to Sexual Arousal in Men. *Psychoneuroendocrinology* 12:149–158.
- Sallinen, J., A. Pakarinen, J. Ahtiainen, W. J. Kraemer, J. S. Volek, and K. Hakkinen  
2004 Relationship between Diet and Serum Anabolic Hormone Response to Heavy-Resistance Training in Men. *International Journal of Sports Medicine* 25:627–633.
- Salvador, A., V. Simón, F. Suay, and L. Llorens  
1987 Testosterone and Cortisol Responses to Competitive Fighting in Human Males: A Pilot Study. *Aggressive Behavior* 13:9–13.
- Sherwin, B. B.  
1988a A Comparative Analysis of the Role of Androgen in Human Male and Female Sexual Behavior: Behavioral Specificity, Critical Thresholds, and Sensitivity. *Psychobiology* 16:416–425.  
1988b Affective Changes with Estrogen and Androgen Replacement Therapy in Surgically Menopausal Women. *Journal of Affective Disorders* 14:177–187.
- Shirtcliff, E. A., D. A. Granger, and A. Likos  
2002 Gender Differences in the Validity of Testosterone Measured in Saliva by Immunoassay. *Hormones and Behavior* 42:62–69.
- Silk, J. B.  
1980 Kidnapping and Female Competition among Captive Bonnet Macaques. *Primates* 21:100–110.
- Stearns, E. L., J. S. D. Winter, and C. Faiman  
1973 Effects of Coitus on Gonadotropin, Prolactin and Sex Steroid Levels in Man. *Journal of Clinical Endocrinology and Metabolism* 37:687–690.
- Suay, F., A. Salvador, E. González-Bono, C. Sanchís, M. Martínez, S. Martínez-Sanchís, V. M. Simón, and J. B. Montoro  
1999 Effects of Competition and Its Outcome on Serum Testosterone, Cortisol and Prolactin. *Psychoneuroendocrinology* 24:551–566.
- Stoleru, S. G., A. Ennaji, A. Cournot, and A. Spira  
1993 LH Pulsatile Secretion and Testosterone Blood Levels Are Influenced by Sexual Arousal in Human Males. *Psychoneuroendocrinology* 18:205–218.

- Storey, A. E., C. J. Walsh, R. L. Quinton, and K. E. Wynne-Edwards  
2000 Hormonal Correlates of Paternal Responsiveness in New and Expectant Fathers. *Evolution and Human Behavior* 21:79–95.
- Taub, D. M.  
1980 Age at First Pregnancy and Reproductive Outcome among Colony-Born Squirrel Monkeys (*Saimiri sciureus*, Brazilian). *Folia Primatologica* 33:262–272.
- van de Beek, C., J. H. H. Thijssen, P. T. Cohen-Kettenis, S. H. M. van Goozen, and J. K. Buitelaar  
2004 Relationship between Sex Hormones Assessed in Amniotic Fluid, and Maternal and Umbilical Cord Serum: What Is the Best Source of Information to Investigate the Effects of Fetal Hormonal Exposure? *Hormones and Behavior* 46:663–669.
- Weschler, T.  
2001 *Taking Charge of Your Fertility*, revised ed. New York: HarperCollins.
- Wingfield, J. C., R. E. Hegner, A. M. Dufty Jr., and G. F. Ball  
1990 The “Challenge Hypothesis”: Theoretical Implications for Patterns of Testosterone Secretion, Mating Systems, and Breeding Strategies. *American Naturalist* 136:829–846.
- Wingfield, J. C., S. E. Lynn, and K. K. Soma  
2001 Avoiding the “Costs” of Testosterone: Ecological Bases of Hormone-Behavior Interactions. *Brain, Behavior, and Evolution* 57:239–251.
- Wynne-Edwards, K. E.  
2001 Hormonal Changes in Mammalian Fathers. *Hormones and Behavior* 40:139–145.
- Yao, G., J. Liang, X. Han, and Y. Hou  
2003 In vivo Modulation of the Circulating Lymphocyte Subsets and Monocytes by Androgen. *International Immunopharmacology* 3:1853–1860.
- Zumpe, D., and R. P. Michael  
1989 Female Dominance Rank and Behavior During Artificial Menstrual Cycles in Social Groups of Rhesus Monkeys (*Macaca mulatto*). *American Journal of Primatology* 17:287–304.

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