ELSEVIER

Review

Testosterone and human aggression: an evaluation of the challenge hypothesis

John Archer

Department of Psychology, University of Central Lancashire, Preston, Lancashire PR12HE, UK

Abstract

Research on testosterone-behavior relationships in humans is assessed in relation to a version of the challenge hypothesis, originally proposed to account for testosterone-aggression associations in monogamous birds. Predictions were that that testosterone would rise at puberty to moderate levels, which supported reproductive physiology and behavior. Sexual arousal and challenges involving young males would raise testosterone levels further. In turn, this would facilitate direct competitive behavior, including aggression. When males are required to care for offspring, testosterone levels will decrease. Testosterone levels will also be associated with different behavioral profiles among men, associated with life history strategies involving emphasis on either mating or parental effort. Most of these predictions were supported by the review of current research, although most studies were not designed to specifically test the challenge hypothesis.
© 2005 Elsevier Ltd. All rights reserved.

Keywords: Androgens; Testosterone; Challenge hypothesis; Sexual arousal; Competition; Aggression; Dominance; Paternal care; Life history strategies

Contents

E-mail address: jarcher@uclan.ac.uk.

1. Introduction

There are a large number of studies investigating the possible association between testosterone and aggression in humans. Two sets of well-known findings provide the background for such studies. The first is the clear association between physical aggression and the age and sex of the perpetrator. As in many other vertebrate species, young adult males show higher levels of physical aggression, violence, and homicides to members of the same sex (Archer, 2004; Daly and Wilson, 1988), than do other age and sex categories. These findings fit the view that human male aggression is, like that of many other mammals, heightened when reproductive competition is most intense.

Among birds and mammals, one widespread mechanism that increases the readiness of males to fight during phases of the life-history when reproductive opportunities are greatest is the action of testosterone on areas of the brain controlling aggressive behavior (Archer, 1988). The co-option of testosterone in the control of inter-male aggression ensures that this is enhanced at times in the life-cycle when males need to compete for receptive females or the resources necessary to attract such females, i.e. in the breeding season or after sexual maturity. The involvement of testosterone in the control of aggression has been shown in many species, from fish to mammals, but with substantial interspecies variation (Archer, 1988). Experimental studies from the first half of the last century, on animals such as the domestic fowl and the house mouse (Allee et al., 1939; Beeman, 1947a,b) have shown a causal link between the hormone and aggressive behavior.

This background provided the basis for a number of studies, beginning in 1971 (Persky et al., 1971), investigating a possible link between circulating testosterone levels and aggression in humans. The view that testosterone secreted by males at puberty and throughout adult life facilitates human male aggression, despite its superficial appeal and its incorporation into media accounts of young men's behavior, is at best an oversimplification. The consensus is that there is a weak and inconsistent association between testosterone levels and aggression in adults (Albert et al., 1993; Archer, 1991, 1994; Archer et al., 1998, 2005; Book et al., 2001), and that the administration of testosterone to volunteers typically does not increase their aggression (O'Connor et al., 2001a, 2004).

In this article, I first outline an alternative theory of the role of testosterone in the control of male aggression to the simple view based on studies of laboratory mammals such as the house mouse. This alternative is 'the challenge hypothesis'. Predictions derived from it are contrasted with those from the view that there is a simple causal relationship between circulating testosterone and aggression ('the mouse model'). The evidence concerning testosterone and human behavior is then reviewed in relation to predictions from the challenge hypothesis. Because the challenge hypothesis concerns attributes other than aggression, it will be necessary to review a more extensive body of research than that concerned with testosterone and aggression. Since it also concerns bi-directional causal links, studies of testosterone levels as a consequence of changes in behavioral or environmental contingencies are evaluated. Since it also concerns the trade-off with other forms of adaptive behavior, such as paternal care, studies linking this with testosterone are also covered. Finally, the link between testosterone and overall life-history strategies is considered as an extension of the challenge hypotheses to apply to adaptive individual differences.

2. The challenge hypothesis

The challenge hypothesis was originally proposed to account for testosterone-aggression associations in birds with a monogamous mating system (Wingfield et al., 1990). It holds that there are specific context-dependent increases in testosterone levels that are associated with aggression. Testosterone levels rise to moderate levels at the start of the breeding season and these levels support reproductive physiology and behavior. During challenges to males in contexts that are relevant to reproduction, testosterone levels rise further. In turn, this facilitates aggression in the context of territory formation, dominance disputes, and mate-guarding (Wingfield et al., 2000). When males are required to care for offspring, their testosterone levels decrease. The challenge hypothesis applies to a variety of monogamous bird species (Wingfield et al., 1990, 2000, 2001; Wingfield, 1985; Vleck and Brown, 1999), or rather to those that show paternal care (Wingfield et al., 2000), but not to all that have been studied (Moore et al., 2004; van Duyse et al., 2000). In polygynous birds, without paternal care, males show high levels of testosterone throughout the breeding season, and it is suggested that their lack of response to challenge occurs because testosterone levels are close to maximum (Wingfield et al., 1990, 2000).

Administering high levels of exogenous testosterone to several species (the song sparrow, the house sparrow, and the European starling) increased their mating and aggressive behavior, and suppressed their paternal behavior (Wingfield, 1984; de Ridder et al., 2000; Hegner and Wingfield, 1987; Peters, 2002). For example, implants to the male white-crowned sparrows altered their mating system from monogamous to polygynous (Wingfield, 1984).

Male superb fairy wrens are unusual in that they show long periods of both courtship behavior, together with high levels of parental care. They live as stable monogamous pairs with a small number of helper males, although most offspring are not sired by any of the males in these groups. Males visit and try to mate with neighboring females during the time of parental care. Administering testosterone to male fairy-wrens with dependent nestlings caused them to direct much more courtship behavior to their females (but not to seek more extra-pair copulations) and to drastically decrease the time they spent on parental behavior (Peters, 2002).

Most of what has been written on the challenge hypothesis concerns males. In different species of birds, there is marked variation in the testosterone levels of females, and it is clear from studies of mammals that androgens can play an important part in female aggression in some species (Albert et al., 1989; Frank et al., 1991; Gray et al., 1978). In an analysis of different species of socially monogamous birds, Wingfield et al. (2000) found that the testosterone levels of females relative to those of males were higher when sexual dimorphism was less pronounced. They suggest that in these cases, testosterone may play a part in female competition for male parental investment.

For psychologists and physiologists concerned with humans, birds represent a rather distant taxonomic group. However, there are a number of studies indicating that the challenge hypothesis applies more widely to other groups of vertebrates, including mammals, supporting the view that the challenge hypothesis 'may have wide implications for vertebrates in general' (Wingfield et al., 1990, p. 830). Studies have found hormonal and behavioral changes consistent with the hypothesis in several species of fish (Pankhurst and Barnett, 1993; Hirschenhauser et al., 2004), two species of lizard (Greenberg and Crews, 1990; Moore, 1986), and among primates, such as the ring-tailed lemur (Cavigelli and Pereira, 2000), rhesus monkey (Rose et al., 1972, 1974), and chimpanzee (Muller and Wrangham, 2004).

The study by Muller and Wrangham (2004), on wild Chimpanzees, is particularly relevant to the human case. Unlike the bird species on which the hypothesis was based, Chimpanzees are neither seasonal breeders nor monogamous. Reasoning that the hypothesis may apply in different ways to mammals, the researchers predicted that since access to receptive and fertile females was relatively uncommon for male chimpanzees, there should be maximal aggression at such times. Indeed, it is known that males are more aggressive in the presence of parous estrous females. Muller and Wrangham also predicted that testosterone levels would be greater for dominant than for low-status males, since dominant males were more aggressive at all times.

Their study, involving multiple testosterone assays from the urine samples of 11 wild male chimpanzees, supported the modified version of the challenge hypothesis in the following ways. When parous females were in estrus, there was a significant increase in testosterone and also an increase in aggressive competition. This did not occur in the presence of nulliparous females, whom males generally find less attractive but with whom they still copulate. Also consistent with predictions, dominant males were more aggressive than low-ranking ones, and produced higher levels of testosterone.

Based on these findings, Muller and Wrangham proposed a modified version of the challenge hypothesis, which they indicated might also apply to humans. First, even though the Chimpanzee has a polygynous mating system, males still respond to challenges with increased testosterone. Males maintain testosterone levels sufficient for reproductive activity throughout the year. A challenge occurs when cycling parous females are present, and testosterone levels are associated with dominant status, which in turn is maintained by high levels of aggression.

3. The challenge hypothesis applied to humans

The extension of the challenge hypothesis to humans involves some modification of both the original, and of Muller and Wrangham's version, since this is based on a polygynous species in which parental care is absent. Human mating systems are variable, and have been described in evolutionary terms as involving mild polygyny, together with paternal care (Geary, 2000). The range of possible mating systems, which can be linked to ecological conditions (Alexander et al., 1979; Smith, 1998) in a way similar to that found in birds such as the Dunnock (Davies and Lundberg, 1984), prompts the suggestion that there could be a role of testosterone in these alternative mating systems in humans.

Humans show neither breeding seasons nor estrus. They show paternal care, but the extent to which individual males are committed to paternal care is variable, both according to ecological conditions as outlined above, and according to individual variation. There may be considerable variation between men in this and other attributes resulting from sexual selection, for example in mate choice preferences and physical aggression (Archer and Mehdikhani, 2003). The basic principles of the challenge hypothesis can be extended to incorporate such individual differences.

The first prediction from the challenge hypothesis applied to humans is that adult levels of circulating testosterone, beginning at puberty, do not produce an increase in aggression, as they do in laboratory species such as the house mouse (Edwards, 1969) and the rat (Albert et al., 1990). This would be consistent with findings that the increase in testosterone at the start of the breeding season does not lead to an increase in aggression in seasonally breeding birds that show paternal care. Much of the research seeking to link human aggression and testosterone has implicitly used the mouse model. This predicts that testosterone levels facilitate aggression from young

adulthood onwards, and that correlations between aggression and the hormone in adults will be due to the action of the hormone on brain areas involved in controlling aggression.

A second prediction from the challenge hypothesis is that adult males should show sensitivity to challenges in a range of situations involving sexual arousal or competition with other males. Thus, the presence of a sexually attractive and apparently available woman should lead to increased testosterone, as should competitive situations between young men. We can extend this prediction to apply to situations in which a young man experiences a challenge that is seen as being directed towards his honor or reputation. In all these situations, a testosterone surge is to be expected. A third prediction is that we would also expect an increase in aggression under such circumstances, if the provocation is deemed to be relevant to reproductive competition. This can either be direct, involving a dispute over a woman or her reputation, or indirect involving a dispute over resources or status.

A fourth prediction is that since humans do show paternal care, men who are involved in, or who are preparing for, paternal care, should show decreased testosterone levels, as has been found for monogamous birds.

A fifth prediction concerns individual differences. In Chimpanzees, dominant males showed higher testosterone levels than did low-status males (Muller and Wrangham, 2004). They also showed consistently high levels of aggression. There is evidence from other primates that the association between rank and aggression is mediated through aggressiveness (Higley et al., 1996; Rose et al., 1971, 1975; Sapolsky, 1991; Zumpe and Michael, 1996). Muller and Wrangham (2004) therefore argued that testosterone levels supported the high levels of aggression in dominant Chimpanzees. We should therefore expect, in humans, an overall correlation between aggression and testosterone in adult males, but not necessarily a correlation between high status and testosterone, unless this high status was achieved and maintained by physical aggression.

The fourth and fifth predictions can be extended. The general principle underlying the challenge hypothesis is that there are adaptive costs, as well as benefits, of high testosterone levels (Wingfield et al., 2001; Vleck and Brown, 1999; Klein et al., 1997). There is, therefore, a trade-off between mating effort (supported by high levels of testosterone), which involves the cost of maintaining high testosterone levels, but may lead to enhanced fitness benefits, and parental effort (supported by lower testosterone levels), which involves a lower cost and a lower maximum fitness benefit. Testosterone levels vary among human males, and this variation may reflect a relatively enduring preference for one of two life-history strategies. The first (high parental investment) involves an emphasis on long-term commitment to one mate and paternal care, accompanied by low mating effort, whereas the second (low parental investment) involves low commitment to one mate

and no paternal care, accompanied by high mating effort. It is unlikely that these will be absolute differences in humans, as they are in the males of some other species (Gross, 1985, 1996; Thompson and Moore, 1992; Van Rhijn, 1974). Rather, there will be relative differences in the degree to which males devote time and energy to mating and parental effort. These individual differences will be associated with differences in testosterone levels, and they represent long-term differences in life history strategies.

As indicated in Section 2, Wingfield et al. (2000) suggested that testosterone may play a part in female competition in species of birds with higher levels of paternal investment. Other studies indicate that variation in the levels of testosterone and other androgens can be important for female aggression in some species of mammals. Since a number of studies of testosterone and behavior in humans have involved women's testosterone levels, we examined the extent to which the challenge hypothesis also applied to women, on the basis that heightened female competition would also be adaptive both for preferred mates (Campbell, 1995) and for paternal investment.

4. Hypothesis 1: There is no increase in aggression at puberty

The challenge hypothesis makes a clear prediction that there are two types of testosterone-behavior relationships, the first is to support courtship and mating, and the second is to facilitate competitive behavior in relevant circumstances. The first occurs in birds throughout the breeding season in seasonal breeders, and from sexual maturation onwards in non-seasonal breeders. The second involves increases in testosterone that are facilitated by reproductive competition. We would therefore expect no testosterone-induced increase in aggression at puberty in human males, in contrast to the facilitation of sexual interest by testosterone at this time. This prediction contrasts with the pattern expected from the mouse model, that aggression is increased considerably in males as a consequence of pubertal testosterone.

Halpern et al. (1994a) reported a 3-year longitudinal study of 100 adolescent boys, whose initial mean age was 13.3 years. Measures included plasma hormone levels and a self-report rating of physical and verbal aggression, the OMAI, which showed high correlations with testosterone among 15–17 year old boys (Olweus et al., 1980). Although, as expected, testosterone levels greatly increased when the boys went through puberty, no change in direct aggression was found, and there was no correlation between testosterone and aggression. In the same sample, there was a clear increase in sexual activity as the boys went through puberty, although this was moderated by religious attendance (Halpern et al., 1994b). Subsequent studies showed that the influence of testosterone on sexual behavior at adolescence is partly mediated by the social consequences

of physical maturation and partly by a direct influence of testosterone (Halpern et al., 1998).

These findings are supported by those of van Bokhoven et al. (unpublished manuscript), who measured testosterone levels among a sample of boys at 13 and 16 years of age, along with several behavioral measures including reactive and proactive aggression. Although testosterone levels increased slightly from 13 to 16 years of age, both types of aggression declined through the years from 12 to 15 (measured at two intermediate points). Again, this is not what would be predicted by the mouse model.

Three other studies that followed up boys through puberty, but did not involve testosterone measures, also found no increase in direct aggression at puberty. Cairns et al. (1989) followed a sample of boys and girls from the ages of 10–15 years, and found no change in physical aggression among the boys, either according to self or teachers' reports. According to the teachers' ratings, adolescents of both sexes showed less aggression than they did in middle childhood. Finkelstein et al. (1994) also assessed whether aggression increased at puberty among a sample of boys and girls from around age 10 years, following them up 2 and 4 years later. They too found no sign of increased aggression at puberty in the boys. Physical aggression fell from 12 to 14 years in the boys, and there was no association between aggression and pubertal stage. The third study involved a larger sample of 909 boys studied from kindergarten to 17 years of age (Lacourse et al., 2002). Physical aggression was measured from self-reports for ages 11–17, and the results are presented in terms of developmental trajectories. In none of these was there any sign of an increase in aggression coinciding with the rise in testosterone at puberty.

In a series of meta-analyses of sex differences in aggression (Archer, 2004), the magnitude of sex differences in direct aggression did not show a pronounced increase at puberty. For example, for self-reports of overall direct aggression, effect sizes (mean weighted) were $d = 0.56$ for ages 6–11 years, and $d = 0.46$ for ages 11–17 years. For peer reports, effect sizes were substantial for physical aggression during childhood (under 11 years: $d = 0.69$), early adolescence (12–13 years: $d = 0.82$), and in the teenage years (14–17 years: $d = 0.97$).

Ablation-replacement is the classic way of investigating whether a hormone facilitates a particular form of behavior in animals. It involves removing the source of the hormone, and subsequently replacing it. The nearest to this procedure that is possible in humans is to inject boys whose puberty is delayed with testosterone. Finkelstein et al. (1997) studied both boys and girls whose puberty was delayed and injected them with testosterone and estrogen, respectively, in a randomized, double-blind, cross-over, design. They used low, medium, and high doses of testosterone during the testing period, to approximate levels at early, middle and late puberty. Using the self-report measure the OMAI (see above), they found in both sexes that hormone

administration led to increased aggressive impulses, and to increased physical aggression towards adults and to peers. These effects were generally more pronounced for the middle dose. The effect sizes for the difference between placebo and treatment show that the changes were relatively small (aggressive impulses: $d = 0.31$–0.37; physical aggression to adults: $d = 0.13$–0.40; physical aggression to peers: $d = 0.12$–0.39). Nevertheless, this study provides the only evidence that pubertal testosterone facilitates aggression. However, very similar levels of increase were found for the smaller sample of girls injected with estrogen. Although overall the evidence supports the prediction from the challenge hypothesis that there is no testosterone-induced increase in aggression at puberty, this study indicates that the issue is still to some extent open, although the increased aggression in estrogen-treated girls would not have been predicted by the alternative 'mouse model'.

5. Hypothesis 2A: Men respond to sexual arousal with increased testosterone

In this section, I consider one aspect of the prediction that testosterone is increased in situations involving mating effort, that the testosterone levels of young men increase in response to sexual stimuli. Several studies have examined changes in testosterone in relation to sexual activity, or the influence of exposure to erotic stimuli on men's testosterone levels. The first of these studies (Fox et al., 1971) measured testosterone levels of a single male volunteer during and immediately after intercourse, and found these to be considerably increased. No comparable effects were found for masturbation among seven participants. Three further studies also find that that sexual intercourse leads to increased testosterone. A 2-month study of the association between testosterone and orgasmic frequency (Kraemer et al., 1976) found that, within participants, levels of testosterone were higher during periods of sexual activity than inactivity. Testosterone levels were higher following a period in which orgasms occurred than one in which they did not ($d = 0.39$, $n = 19$). Knussmann et al. (1986) followed 33 young men over a 2-week period during which they supplied six blood samples, and kept daily records of sexual activity. There were small but significant positive correlations between testosterone levels, and both the extent of preceding sexual stimulation from any source (rho = 0.17) and sexual activity that resulted in orgasm (rho = 0.20). Dabbs and Mohammed (1992) measured salivary testosterone levels in four heterosexual couples during 11 evenings when they had intercourse and 11 when they did not. On the days when they did not have sex, the testosterone levels declined from early to late evening for both men and women, whereas there was an increase from early to late evening when they had intercourse. Although these were reported as significant, it is not clear how between-

and within-participants variation were separated, and thus the reported p values may have been inflated.

Two other studies involve the influence of watching erotic films or videos. Hellhammer et al. (1985) examined salivary testosterone levels among 20 young men before, during, and after exposure to erotic, sexual, aggressive, stressful, and neutral films. Testosterone levels showed an increase 15 min after the beginning of the erotic and sexual films (with means of 35 and 20%, respectively). Effect sizes for the increases were calculated as $d = 1.07$ for erotic and $d = 0.72$ for sexual films (from the one-tailed p values), with no significant increases for the other three types of film. Stoléru et al. (1999) used PET scans to investigate the brain areas involved when watching an erotic film. They also measured testosterone levels and found that these were higher among the eight male participants after watching a sexual than a neutral film ($d = 0.65$). Compared to a humorous film, the difference was slightly smaller ($d = 0.47$).

Only one study has involved measuring men's testosterone levels as a consequence of brief interactions with a potential mate. Roney et al. (2003) exposed young men to a brief friendly conversation with young women or (as a control) young men. Although they found a significant increase in testosterone levels after interacting with the woman ($d = 0.99$), there was also a non-significant increase among the participants who interacted with the young man ($d = 0.44$), rendering the difference between the two conditions non-significant for this small sample ($d = 0.17$; $n = 39$). However, from the challenge hypothesis we might predict an increase in testosterone levels when meeting a young man for the first time, as he might represent a competitor. A third condition, not involving a social interaction, or involving an interaction with an older person, would have served as a control for this. The study did therefore provide clear evidence that interacting with a potential mate raised young men's testosterone levels. Further, it was found that this increase was largely restricted to those men who said that they had had a recent sexual experience. There was also a strong correlation ($r = 0.52$) between testosterone levels and the woman confederate's ratings of the male participant's display behavior towards her. Although based on a small sample, these results do provide encouragement for future research based on evolutionary considerations. Overall, the studies considered in this section do indicate that sexual stimulation leads to increased testosterone secretion.

6. Hypothesis 2B: Men respond to competition with increased testosterone

Most of the research relevant to this question has not been designed from an evolutionary viewpoint, and therefore it does not acknowledge the centrality of competition associated directly or indirectly with mating opportunities.

Studies of competition have tended to center around competitive sports and laboratory tasks that are convenient to use with undergraduates. In this section, I consider first some research involving reputation and insults, which are particularly important in disputes between young men, especially where there are few legal or moral restraints. I then consider studies of physical and non-physical competition between young men, to assess whether winning and losing such competitions produces surges in testosterone consistent with the challenge hypothesis. I also consider the available evidence for women, to assess the extent to which women's competition raises testosterone levels in a similar way.

6.1. Inter-male competition, reputation and insults

Perhaps the strongest prediction from the challenge hypothesis is that testosterone should rise in young men who are in direct competition for the attention of an attractive woman. The study by Roney et al. (Dabbs and Mohammed, 2003)—described in Section 5—is the nearest to this, although it would have to be extended to introduce competition to conform to this situation.

Research on young male violence has identified the importance of responding violently to a challenge or insult in many cultures. This is associated with the concept of masculine honor, which involves the principle that a man must demonstrate by his own physical actions that he can demand compliance and respect from other men (Nisbett and Cohen, 1996). Insults are especially important in such social contexts: if ignored, they mark the man out as someone who can be defeated physically, and cannot defend his possessions, his woman, and family from other men. Nisbett and Cohen (1996) argued that the culture of honor arises in herding societies, where a man's livelihood could be taken from him if he were seen to be defenseless. Where there is no effective rule of law, developing a reputation for credible retaliation emerges as the only effective way of maintaining the integrity of women, family and resources (Daly and Wilson, 1988; Courtwright, 1996; Ruff, 2001).

Cohen et al. (1996) reported an experimental study of students from the North and the South of the United States, in which they were insulted or not insulted, and their subsequent behavior and physiology studied. There were greater increases in testosterone from before to after the insult among insulted southerners than in the other three conditions (insulted northerners and both non-insulted conditions), and also much higher cortisol levels. These physiological changes paralleled several psychological changes. These included greater immediate expression of anger, being more likely to complete a questionnaire involving sexual jealousy with violence, greater willingness to challenge a larger individual, and being more domineering to a smaller person. This study indicates that young men who are from a culture where honor is important do respond to an insult—a challenge to honor—with an increase in

testosterone levels, and also with more aggressive, domineering, behavior. Whether the testosterone surge plays any causal role cannot be inferred from the study.

6.2. Reactions to competition

Most other studies relevant to the issue of whether there is a testosterone surge to a challenge either concern competitive sports or laboratory situations designed to involve competition. Sports competitions between men, particularly those involving bodily contact are equivalent to a challenge situation. We would expect there to be a rise in testosterone in anticipation of the competitive event, and/or a rise throughout the competition, and a subsequent further rise in the winner of the competition. Studies involving non-physical competitive situations seem to produce comparable results to sports competitions, and therefore they are considered together with the evidence on sports competitions. Most of these studies enable effect sizes to be calculated for one or more of the comparisons where rises in testosterone are expected. Studies where this was not possible are described first, before considering the remaining evidence using meta-analytic statistics.

Mazur and Lamb (1980) reported three studies of the effects of intermale competition on testosterone levels. The first involved tennis doubles matches for a $100 prize. Testosterone assays were from blood samples taken in the hour before the match and within an hour of its completion, followed by three more samples at hourly intervals. Most of the winners showed a rise in testosterone levels at 1 h after the match, despite this being the time of day when testosterone levels normally decline. All the losers showed a decline in testosterone during this time. The second study involved a lottery for the same value prize. Again, blood samples were taken from participants before, and at hourly intervals after, the lottery: in this study, the winners and losers did not show a different pattern of testosterone. The third study measured plasma testosterone in five students before and after a successful graduation ceremony for MD degrees, finding some indication of an increase following graduation that was variable, and tended to follow the time of maximum mood elevation. Although these studies provided evidence that situations involving winning a competitive sport or an important academic achievement led to increased testosterone, there were no precise figures presented for the differences.

A subsequent study (Booth et al., 1989) followed a university men's tennis team through a season, measuring testosterone levels before and after six matches. Testosterone was higher on match days than on those before or after the match. There was a pre-match rise that tended to decline during the match, but victory reversed this trend. In singles matches, the testosterone of winners increased across the match while that of losers declined. Testosterone increases from before to during the match were correlated with improvement in mood. However, this study has

a methodological problem: although there were only six participants, their performance in six matches were treated as independent data points, thus inflating the power of the test to reject the null hypothesis, and inflating any effect sizes derived from their statistics.

It was similarly difficult to obtain effect size estimates from a subsequent study (Mazur et al., 1992) that involved small samples of young men participating in two chess competitions. In a regional contest, testosterone levels were considerably higher in the winners than the losers on the day after the tournament. In a city contest lasting across eight weeks, winners began to show higher testosterone levels after the sixth game (by the third week).

These studies, involving a variety of competitive situations, do suggest a rise in testosterone throughout the competition, and greater increases for winners than losers. There are now a number of other studies generally confirming these findings, with the exception that Mazur and Lamb's (1980) null findings for the lottery competition have not been replicated for other chance-based tests (Gladue et al., 1989; McCaul et al., 1992). Most other studies provide statistics suitable for computing effect sizes. I therefore analyzed these quantitatively, using meta-analytic software (Johnson, 1989). Table 1 shows, where possible, the effect sizes (Hedges' g, the standardized mean difference, uncorrected for small samples) for the following: anticipatory change (resting baseline to immediately pre-competition); change during the competition (before to after); and the difference between the levels of winners and losers. Only one of the samples shown in Table 1 involved women (Bateup et al., 2002) and there was no indication of any difference from studies involving men.

For the pre-competition anticipatory change, across nine samples, there was a mean weighted d value of 0.13 (CI −0.06/0.32) which was not significantly different from zero ($p = 0.18$). Removing the two largest outliers (Mazur et al., 1997 study 2; Schultheiss and Rhode, 2002) increased this value to $d = 0.27$ (CI 0.02/0.52; $p = 0.04$). These two studies, along with the first study by Mazur et al. (1997), involved contrived laboratory tasks, as opposed to real sports competitions. Removing these three studies produced a value of $d = 0.30$ (CI 0.01/0.58; $p = 0.045$) for the remaining six studies using sports competitions. There was therefore, evidence for a small anticipatory effect for studies involving sports competitions. One further study (Neave and Wolfson, 2003) showed that pre-match testosterone levels were higher before home than away games in British soccer players, and were highest when the game was against a team who were extreme rivals.

For the change in testosterone during the competition, irrespective of whether the sample involved winners or losers or both, the mean weighted d was 0.16 (CI 0.02/0.29) over 23 samples, indicating an overall significant ($p = 0.022$) increase in testosterone during the competition, irrespective of whether it involved a contrived laboratory task or a sport competition. Comparing the rather small

Table 1
Studies of the effect of competition, and of winning vs losing on testosterone levels

Study	N	Anticipation	During	Study coding	Winner vs loser	N
Elias (1981)	15	–	0.93	1,2,1,1,1,1,1	0.85	7/6
Salvador et al. (1987)[a]	14	–	−0.23	2,1,2,2,2,1,1	−0.02	6/6
Gladue et al. (1989)	40	–	Increase	7,1,5,1,4,8,1	0.90	20/20
McCaul et al. (1992): 1a[b]	14	–	0.25	6,1,3, 2,1,2,1	0.74	14/14
McCaul et al. (1992): 1b[b]	14	–	−0.22	6,1,3, 2,1,3,1		
McCaul et al. (1992): 2a[b]	35	–	0.22	6,1,3, 2,1,2,1	0.75	35/35
McCaul et al. (1992): 2b[b]	35	–	−0.12	6,1,3, 2,1,3,1		
Gerra et al. (1997): 1	15	–	0.34	5,2,12,5,2,6,1		
Gerra et al. (1997): 2	15	–	0.55	5,2,12,5,2,7,1		
Mazur et al. (1997): 1	28	0.19	−0.04	7,1,8,1,5,1,1	0.00[c]	14/14
Mazur et al. (1997): 2	32	−0.20	−0.30	7,1,8,1,5,1,1	0.00[c]	16/16
González-Bono et al. (1999): 1	7	–	0.26	4,1,4,2,2,2,1	0.49	7/8
González-Bono et al. (1999): 2	8	–	−0.48	4,1,4,2,2,3,1		
Passelergue and Lac (1999)[d]	15	0.31	0.83	1,1,9,3,2,1,1		
Schultheiss et al. (1999)	42	–	0.31	7,1,1,1,2,1,1	0.28	21/21
(same sample)	(21)	–	0.43	7,1,1,1,2,2,1		
(same sample)	(21)	–	0.18	7,1,1,1,2,2,1		
Suay et al. (1999)	26	0.28	0.17	2,2,1,2,2,1,1	0.13	14/13
(same sample)	(14)	–	0.27	2,2,1,2,2,2,1		
(same sample)	(13)	–	0.14	2,2,1,2,2,3,1		
Filaire et al. (2001): 1	9	0.28	0.065	2,1,7,3,2,2,1	−0.96	9/9
Filaire et al. (2001): 2	9	0.54	1.44	2,1,7,3,2,3,1		
González-Bono et al. (2000): 1	9	–	0.59	4,1,4,2,2,4,1		
González-Bono et al. (2000): 2	8	–	0.00	4,1,4,2,2,5,1		
Bateup et al. (2002)[e]	17	0.36	0.69	3,1,6,1,3,1,2		
Schultheiss and Rohde (2002)	66	0.03	0.00	7,1,10,4,2,1,1	0.00[c]	33/33
Salvador et al. (2003)	17	0.24	–	2,1,11,2,2,1,1		

Effect sizes (g values) are shown, where possible, for the anticipation period, from before to during or shortly after the competition, and comparisons between winners and losers. The numbers and letters after the studies denote sub-samples, either where two studies are reported in one paper, or where the sample was subdivided, for example into winners and losers (see study coding 6). Study characteristics: 1=sport or activity (1=wrestling; 2=judo; 3=rugby; 4=basketball; 5=competitive point-subtraction task for monetary reward); 6=multiple coin-tossing for a monetary reward; 7=competitive laboratory tasks with contrived winners and losers, e.g. reaction time task, videogame, numbers task). 2=Testosterone measure (1=saliva; 2=plasma). 3=Time period (1= 10 min before, 10 min after; 2=10 min before, 45 min after; 3=immediately before, 10 and 20 min into the 20-minute task, and 10 and 20 min after; 4=45 or 50 min before and 15 min after a match; 5=10 min before and every 10 min throughout 25 min competition and every 10 min afterwards; 6=24 h before, 15 min before, and immediately after games; 7=3 weeks before competition, 5 min before and 5 min after last fight; 8=five samples before during and at the end of the competition; 9=3 weeks before competition, immediately before, immediately afterwards, and 2 h later; 10=six times throughout the experimental session, from baseline to being primed about the task, to completing the task and afterwards, at 130 min after the start; 11=1 h and 30 min before the contest; comparisons are with resting days at the same time; 12=just before the contest and 20 and 30 min during it). 4=Country (1=US; 2=Spain; 3=France; 4= Germany; 5=Italy). 5=Derivation of g value (1=raw data; 2=means, and standard deviations or standard errors; 3=t-tests; 4=w^2). 6=Values for the within-participants comparison derived from (1=the whole sample; 2=winners; 3=losers; 4=easy winners; 5=winners of close competitions; 6=sample selected for high aggression; 7=sample selected for low aggression; 8=not applicable). 7=Sex (1=men; 2=women). All studies are from refereed journal articles.

[a] Similar measures were taken from the same participants before and after physical exercise as a control. In contrast to the findings for the judo bouts, there was an increase from before to after exercise (d=0.42). In addition, although there were no differences between winners and losers, men with a previous history of success in bouts showed a greater increase from before to after the current bout (r=0.52), indicating a greater rise in testosterone levels for men more used to winning.

[b] Eventual winners and losers did not differ in salivary testosterone levels at baseline (Study 1: g=0.01; Study 2: g=0.03). The values for the changes are from pre-test to the time when levels were maximal for the winners. This was different in the two samples, 20 min after the end of the test in the first, and 10 min after the end in the second, with no differences 10 min afterwards in the first sample, and 20 or 30 min in the second sample.

[c] The comparisons between winners and losers are an approximation from the finding of no significant differences.

[d] Pre-competition change was from resting levels 3 weeks before to immediately before the competition, at the same time of day in each case. The increase due to competition was taken from the mean over the three values taken on competition day compared with the mean of the three values from the rest day: these values were the same for each of the 2 days of the competition.

[e] The game was the unit of analysis (17 women completing an average of three games each). Therefore t-values, and effect sizes derived from these, would have been greatly inflated. To correct for this, g values, obtained from t values, were divided by 3.

samples of winners ($k=8$) and losers ($k=6$) showed higher increases among the winners ($d=0.25$; CI $-0.00/0.51$) than the losers ($d=0.05$; CI $-0.23/0.33$), although the difference was non-significant (QB$=1.13$). Values for samples where winners and losers were not distinguished were in between ($d=0.15$; CI $-0.04/0.34$).

When the studies were grouped into those that involved a sport (wrestling, judo, basketball or rugby) and those that involved contrived competitive exercises that were not sport, and did not involve activity, there were clear differences in the size of the testosterone increase. Over 12 samples involving sport, the mean weighted d was 0.37 (CI 0.13/0.61), whereas over 11 involving contrived tasks it was $d=0.06$ (CI $-0.10/0.22$). These values were significantly different (QB$=4.3$; $p=0.04$). In other words, the increase in testosterone was greater for sport competitions than for contrived competitive situations involving a monetary reward.

A direct comparison of the extent of change in testosterone through the competition for winners and losers was possible in 12 samples (Table 1). These data produced an overall mean weighted d value of 0.31 (CI 0.10/0.51; $p=0.003$), indicating a higher change in the positive direction for winners than for losers. Removing the largest outlier (Filaire et al., 2001), which involved a large difference in the reverse direction, produced a mean weighted d of 0.36 (CI 0.15/0.57; $p=0.0006$).

A comparison of the five samples where a sport was involved with those seven where a contrived competition was used showed a weighted mean of $d=0.05$ (CI $-0.38/0.49$) for sports and $d=0.38$ (CI 0.15/0.60) for contrived competitions (QB$=1.65$; $p=0.20$). It would seem that although sport produces larger increases in testosterone than a contrived competition does (see above), overall winners and losers differ more during contrived than sport competitions.

We can therefore conclude from the evidence on competitions that there is a small anticipatory rise in testosterone before sport competitions and that overall there is evidence of a small increase from before to after a competitive situation. Further analysis revealed that this was more pronounced for sport competitions than contrived ones, and was greater in winners than in losers. The extent of the increase was greater for winners than for losers, and this applied particularly to contrived situations.

Bernhardt and Dabbs (1997, 1998) reported two small-scale studies showing that the vicarious experience of winning, i.e. being a fan whose team wins, can also lead to increased testosterone levels. The first study involved college basketball games, finding that testosterone levels increased from pre- to post-match in fans whose team won ($d=0.39$) whereas they decreased in fans whose team lost ($d=-0.36$). Larger changes were found among a very small sample ($n=4$) of soccer fans. These findings are in line with those analyzed above, indicating differences between actual winners and losers.

6.3. Mediators and moderators of the effects of competition

Several studies have sought to investigate individual variables that might mediate or moderate (Baron and Kenny, 1986) the effects of competition, and in particular winning, on testosterone levels. Using a chance-based task, McCaul et al. (1992) investigated whether mood changes mediated the association between winning and increased testosterone levels. They found increases in testosterone that were transitory, and whose timing differed in two samples. Self-rated positive moods, such as feeling jovial or surprised, increased for the winners and decreased slightly for the losers. Negative moods, such as guilt and sadness, showed a reverse trend. However, mood showed a lower association with testosterone levels ($r=0.22$) than did winning or losing ($r=0.36$), and partialing out the mood scores led to only a small overall decline in the association between outcome and testosterone levels ($r=0.29$ and -0.30 for positive and negative moods), indicating that mood changes did not mediate the association between winning and testosterone levels.

González-Bono et al. (1999) investigated psychological variables that might moderate the effect of winning on testosterone levels, in this case among basketball players. They found that a measure of how much the individual participated in the outcome was positively correlated with the change scores ($r=0.56$; $n=15$) and negatively correlated with pre-match levels ($r=-0.66$) of testosterone. Among the winners ($n=7$), post-match testosterone levels were negatively correlated with attributing the outcome to luck ($r=-0.82$) and to making attributions to the referees' decisions ($r=-0.82$), both being forms of external attributions. Thus, if a winner considered the outcome to be due to an external source, his testosterone levels would be lower after the match, relative to others in a winning team. Among the losers, testosterone levels were positively related to referees' decisions ($r=0.84$; $n=8$) and negatively related to appraisal of the player's own performance ($r=-0.92$), an internal attribution. Thus, if a loser considered the outcome to be due to an external source, his testosterone levels would be higher after the match, and if he attributed it to his own performance, they would be lower, relative to others in a losing team.

González-Bono et al. (2000) studied psychological variables that might moderate the pre- to post competition rise in testosterone levels, and thereby account for some of the inconsistent findings regarding the effect of winning. Two basketball teams were studied before (50 min) and after (15 min) winning a match. The first team won easily and the second won more narrowly in a more even contest. The first team showed the expected pre- to post-match overall rise in testosterone levels whereas the second team did not (Table 1). Over both teams, the pre- to post-match rise in testosterone was significantly predicted ($R^2=23\%$) by an internal attribution for the outcome (winning), involving attributes such as personal effort and technical

skill, rather than external influences, such as luck, opponents' mistakes, and referees' decisions.

These two studies go some way in identifying the psychological processes moderating the effect of winning or losing on the extent of the rise in testosterone. Winning a competition and attributing this to one's own efforts and skills accentuates the rise in testosterone. However, losing a competition and attributing this to external influences to some extent buffers the person against the impact of losing on changes in testosterone levels.

Suay et al. (1999) found a positive correlation ($r = 0.42$) between motivation to win and the rise in testosterone levels from before to after a judo competition. Schultheiss et al. (1999) investigated an individual's implicit motivation for power as a possible moderator of the testosterone increase found after winning a competitive encounter. To assess implicit power, they analyzed the fantasies produced in response to picture cues that are related to power or dominance. Two sorts of implicit power motives were distinguished, the first being personalized power (p Power) which involves asserting oneself over others, and the second being socialized power (s Power), involving trying to influence others through prosocial acts: s Power is regarded as attenuating the effects of p Power. The researchers used a contrived competitive task involving number sequencing to establish equal numbers of winners and losers among their 42 male participants. Testosterone levels were assessed from saliva samples taken upon entering the laboratory, immediately before, and after, the 10-minute task. There was a strong correlation between immediately preceding testosterone levels and p Power for those individuals who had low levels of s Power ($r = 0.77$), which did not occur in those with high levels of s Power. Overall, there was a higher increase in testosterone among winners than among losers (Table 1). The testosterone levels of winners, immediately after the task, showed a large positive correlation with p Power in the absence of s Power ($r = 0.88$), but the correlation was negative ($r = -0.62$) in the presence of s Power. The losers showed comparable, but weaker, associations ($r = 0.54$ in the absence of s Power, and $r = -0.41$ in its presence). These findings are important in that they identify a strong moderating influence on both the pre-task levels of testosterone and the levels in winners and to a lesser extent in losers after a competitive task. This moderating influence involves a personal need to dominate others, and it is counteracted by the need to influence others by prosocial actions. This attribute would fit the challenge hypothesis in that it coincides with the type of individual assertiveness that would be adaptive in competitive encounters with other young males.

Schultheiss and Rohde (2002) investigated whether the combination of a high power motive combined with low levels of activity inhibition would also be associated with increased testosterone levels after winning a competitive contest. The reasoning behind this was that uninhibited people with a strong motive for power would seek to exert their power in a personalized, assertive, way, whereas inhibited people with a strong power motive would seek more socialized and controlled ways of exerting their power. Thus, uninhibited people with a high power motive would be equivalent to those high in p Power in the previous study, whereas inhibited people with a high power motive are equivalent to those with a high s Power motive. There were no changes in testosterone levels over the whole sample in this study (Table 1), and no differences between winners and losers. However, among uninhibited participants, the power motive was strongly correlated with increases in testosterone levels after winning the task ($r = 0.71$) but not after losing it ($r = -0.08$). This association was not found among inhibited participants. A follow-up study (Schultheiss et al., 2005) found only a small association between the power motive and increased testosterone levels after winning the task ($r = 0.21$) but a larger association with decreased levels after losing ($r = -0.38$). In contrast, women showed a substantial association between the power motive and increased testosterone levels after losing ($r = 0.53$) but not after winning ($r = 0.08$) (Schultheiss et al., 2005). There are clearly associations in these three samples, but their inconsistencies preclude any conclusions at present.

Schultheiss and Rohde's (2002) study also measured implicit learning by embedding a repetitive visuomotor pattern in the competitive task (pen movements in a particular direction), and assessing the extent to which this was learned afterwards. Among uninhibited power-motivated winners, implicit learning was enhanced by winning ($r = 0.68$) and impeded by losing ($r = -0.58$), a finding that has subsequently been replicated (Schultheiss et al., 2005). Although testosterone change showed no association with implicit learning overall, it did show a moderate association in the uninhibited participants ($r = 0.38$). The power motive no longer had a significant effect on implicit learning when testosterone change was controlled, suggesting that the testosterone increase may have acted as a mediator between the power motive and increased implicit learning in the winners. This finding was connected to the known reinforcing effects of testosterone found in animal studies (Arnedo et al., 2000). A follow-up study (Schultheiss et al., 2005) found evidence for a mediating effect of testosterone on the association between power motivation and implicit learning in men, but only in losers and not in winners. This effect was not found for women (Schultheiss et al., 2005).

6.4. Conclusions on the effects of competition on testosterone levels

The research reviewed in Section 6 broadly supports the hypothesis that men respond to competitive situations with increased testosterone levels. In the single study where the challenge took the form of an insult to someone from a culture of honor testosterone levels were increased. They were also increased when sport and contrived

competitive non-sporting situations were considered together, although it was clear that competing in sport competition led to greater increases in testosterone levels. These were also greater for winners than losers when both sorts of competitions were considered together. However, further analysis did show that the difference between winners and losers was greater for contrived situations for a monetary reward than for sport participation. Studies of the psychological moderators of the rise in testosterone levels among winners identified making a personal attribution for the win, rather than attributing it to an external influence such as luck or the referee's decisions. Three studies using a contrived laboratory task showed a strong association between the extent of the rise in testosterone levels after winning and a having a particular way of seeking to exercise power over others. This involved an uninhibited, assertive, style—seeking to dominate others in face-to-face interactions—as opposed to a more inhibited style associated with seeking to exercise power in a more controlled way by interpersonal influence. As mentioned above, this is the sort of individual assertiveness that would be adaptive in competitive encounters with other young males under most situations, and certainly in pre-state societies.

7. Hypothesis 3: The testosterone response to challenge increases aggression

The other side to the challenge hypothesis—and indeed its whole point in adaptive terms—is that the testosterone surge should increase aggressiveness in competitive situations. The evidence for this is hard to find in studies of humans, which have tended to examine the association between levels of testosterone and aggressiveness among samples of adults (see Section 9), or have involved the impact of competition on testosterone levels.

In an extension of an earlier study on judo competitors (Salvador et al., 1987), coaches rated participants' behavior during the bouts (Salvador et al., 1991; Suay et al., 1996), and these were correlated with changes in hormonal levels before and after the fight. Larger increases in testosterone were highly correlated with looking angry while fighting ($r=0.78$), responding to a challenge ($r=0.52$), and being a violent competitor ($r=0.52$). Absolute levels of testosterone were significantly correlated with one measure, 'offensive play'. These findings provide some evidence that the higher the increase in testosterone production during the bout, the greater is the angry and competitive mood. If such a mood outlasted the particular conditions that produced the testosterone surge, this would provide evidence that the testosterone response to challenge increases aggressiveness in the short-term. However, there remains the possibility that this study was picking up the behavioral manifestations of the sorts of individual differences investigated by the studies on power motivation:

that people with an uninhibited personalized power motive would become more angry and violent in a competitive situation involving bodily contact.

A follow-up study of 28 judo fighters from sports clubs in Valencia (Salvador et al., 1999) involved video-recordings of their competitive sessions, and coding of the behavior by two judo specialists. Categories included attack, threat fighting and domination. Plasma testosterone levels measured 10 min before, and 10 min after, the competition were highly correlated ($r=0.93$). Nevertheless, levels taken before the contest showed higher correlations with behavioral measures than those taken afterwards. Highest correlations were with attack ($r=0.54$), fighting ($r=0.45$) and threat ($r=0.40$). The findings indicate that pre-contest levels of testosterone predicted offensive fighting. As indicated in Table 1, pre-contest levels are likely to represent an anticipatory rise in testosterone. This rise could produce a short-term influence on subsequent aggressive behavior (as predicted by the challenge hypothesis), or alternatively both the pre-contest levels and offensive behavior may be influenced by longer-term testosterone levels (again an interpretation based on the impact of individual differences in testosterone levels).

A study using a laboratory competitive situation, designed to assess aggressiveness, also found that higher levels of testosterone predicted higher aggression levels. Berman et al. (1993) measured plasma testosterone among a sample of young men and then tested them in a laboratory aggression paradigm to assess aggressiveness, involving a competitive reaction time task in which participants administered shocks to a supposed confederate. Not only was there a substantial positive correlation ($r=0.42$) between initial levels of testosterone and subsequent aggression (measured by higher shock settings), but there was also evidence that high testosterone participants were more motivated in the task than were low testosterone participants. Yet again, these findings can alternatively be interpreted in terms of consistent individual differences.

In some field experiments with animals, it has been possible to mimic the impact of the increase in testosterone in response to challenge by injecting testosterone into males. The result is that the animal shows more mating effort—including competitive aggression—and less parental behavior (Wingfield, 1984; de Ridder et al., 2000; Hegner and Wingfield, 1987). There have been a few studies involving injecting testosterone or related synthetic androgens into healthy human male volunteers, either to investigate the impact of the supraphysiological doses of testosterone involve in anabolic androgenic steroid users, or to study the impact of lower doses that are effective as a male contraceptive. Although the dosage is different in the two types of study, it is useful to consider their findings together, to assess whether there is any sign of the sorts of changes in behavior reported in the animal studies. Of course, the measures used in these human studies are very

different, as they are concerned with investigating the possible harmful consequences of taking the hormones. Measures involve psychiatric symptoms, mood and aggression.

Table 2 summarizes studies involving the injection of testosterone. Effect sizes were calculated for the difference in measures of anger, aggression or hostility, between testosterone-treated and untreated participants, and between testosterone and placebo-controlled participants. Ideally, for a clear effect of testosterone to be established, both values should be positive and substantial. This was only found in two studies. O'Connor et al. (2001a) reported that ratings of physical aggression by the participants' partners, and a scenario measure of physical aggression both showed

Table 2
Studies involving controlled trials of testosterone on measures of mood and aggression in men, showing sample size (N), effect sizes (g) for testosterone-untreated comparisons (TvU), and testosterone-placebo comparisons (TvP), and study characteristics

	N	TvU	TvP	Study coding
Anderson et al. (1992): 1[a]	16	−0.59	_[b]	2,3,3,4,5,5,1,2,1,2
[same sample]	[16]	−0.59	_[b]	2,3,3,4,5,13,1,2,1,2
Anderson et al. (1992): 2[a]	15	0.05	0.11	2,3,3,4,5,5,1,2,1,2
[same sample]	[15]	0.04	−0.16	2,3,3,4,5,13,1,2,1,2
Su et al. (1993)	20		0.02	2,2,1,3,3,5,1,1,1,1
[same sample]	[20]		0.23	2,2,1,3,4,5,1,1,1,1
[same sample]	[20]		0.78	2,2,1,3,3,6,1,1,1,1
[same sample]	[20]		0.72	2,2,1,3,4,6,1,1,1,1
van Goozen et al. (1994a)	22		0.26	5,6,6,2,9,3,1,3,2,1
[same sample]	22		0.55	5,6,6,2,9,14,1,3,2,1
Tricker et al. (1996)[c]	40	0.44	0.12	3,3,3,5,7,10,1,1,1,2
[same sample][c]	[40]	−0.28	_[b]	3,3,3,5,7,11,1,1,1,2
[same sample][c]	[40]	0.32	_[b]	3,3,3,5,7,12,1,1,1,2
Yates et al. (1999)	31	0.08	0.00	2,1,2,2,2,3,1,1,1,1
[same sample]	[31]	0.47	0.17	2,1,2,2,2,4,1,1,1,1
Pope et al. (2000)	51	0.06	−0.04	1,1,1,1,1,1,1,1,1,1
[same sample]	[27]	0.57	0.51	1,1,1,1,1,2,1,1,1,1
O'Connor et al. (2001)[d]	29	0.13	0.39	2,3,3,4,5,7,1,2,1,2
[same sample][d]	[29]	0.48	0.39	2,3,3,4,5,9,1,2,1,2
[same sample][d]	[29]	0.34	0.73	2,3,3,4,5,8,1,2,1,2
Dabbs et al. (2002): 1	15		1.0	4,5,4,6,3,6,2,1,1,1
Dabbs et al. (2002): 2	17		1.30	4,5,4,6,8,6,2,1,2,1
O'Connor et al. (2004)[e]	24	−0.08	0.11	2,4,1,4,6,7,1,2,1,2
[same sample][e]	[24]	0.14	0.15	2,4,1,4,6,8,1,2,1,2
[same sample][e]	[18]	−0.04	0.00	2,4,1,4,6,9,1,2,1,2

Study characteristics: 1=Sample (1=men recruited from local gym; 2=community sample; 3=ex-weightlifters; 4=convenience sample; 5=female-to-male transexuals). 2=Testosterone preparation (1=testosterone cypionate; 2=methyltestosterone; 3=testosterone enanthate; 4=testosterone undecanoate; 5=micronized testosterone in an absorbant gel; 6=Tesoviron depot, testosterone esters). 3=Design (1=double blind placebo-controlled cross-over; 2=double-blind controlled, testosterone followed by placebo; 3=randomized testosterone or placebo-controlled design; 4=double-blind controlled, counterbalanced order; 5=within-participants comparison of before and after androgen administration). 4=Duration of testosterone administration (1=6 weeks; 2=12 weeks or 3 months; 3=3 days of each of two doses; 4=8 weeks; 5=10 weeks; 6=5 days of testosterone and of placebo). 5=Dosage (1=increasing dose from 150 to 500 mg per week; 2=100 or 250 or 500 mg—data are for all three combined; 3=40 mg per day; 4=240 mg per day; 5=200 mg per week; 6=single injection of 1000 mg; 7=600 mg per week; 8=10 mg per day; 9=250 mg every 3 weeks). 6=Aggression or mood measure (1=Aggression Questionnaire (AQ, Buss and Perry, 1992) total scores; 2=Point Subtraction Aggression Paradigm (PSAP, Cherek et al., 1996); 3=Buss Durkee Hostility Inventory (BDHI, Buss and Durkee, 1957) assault scale; 4=BDHI assault scale, completed by informant; 5=mood ratings of violent feelings or 'ready to fight'; 6=hostility ratings on a symptom checklist; 7=AQ physical aggression scale; 8=Aggression Provocation Questionnaire (APQ, O'Connor et al., 2001b) physical aggression; 9=AQ physical aggression scale, partner report; 10=Anger arousal from the Multidimensional Anger Inventory (MAI, Seigel, 1986); 11=Mood Inventory (MI, Tricker et al., 1996), angry behavior; 12=Observer Mood Inventory (OMI, Tricker et al., 1996), angry behavior; 13=daily diary ratings of anger; 14=ASQ (van Goozen et al., 1994b) anger proness. 7=Source of g values (1=Means and standard deviations or standard errors; 2=proportions). 8=Country (1=US; 2=UK; 3=the Netherlands). 9=Sex (1=male; 2=female). 10=Mean age (1=20–29; 2=30–39). All studies are from refereed journal articles.

[a] Findings were presented separately for the group receiving testosterone only for two 4-week periods (n=16) and the group receiving placebo for the first 4 weeks followed by testosterone (n=15). All comparisons are within-participants. The two groups were not combined because their baseline values were not comparable.

[b] These values are not included since the baseline levels of the testosterone and placebo groups were substantially different.

[c] Values for testosterone vs untreated are the means of the effect sizes for weeks 6 and 10 of testosterone condition (N=21).

[d] Values are for within-participants comparisons from baseline to week 4, and for between-participants comparisons at week 4.

[e] Although this study found no indication that testosterone treatment had any effects on three types of aggression measure, there was an increase in self-rated anger-hostility on the Profile of Mood States from weeks 1 to 2 in the treatment arm (d=0.43), producing a significant difference between treatment and control arms at 2 weeks after injection (d=0.66). These differences were not reflected in measures of anger and hostility from self or partner reports on the Aggression Questionnaire.

positive effect sizes in the predicted direction, although these were non-significant. Pope et al. (2000) found effects in the predicted direction for a laboratory competitive task among men taking high doses of testosterone cypionate. The particular task (Cherek et al., 1996) involves subtracting points that eventually lead to a monetary reward rather than any direct or indirect physical aggression to a competitor. Although performance on the task is associated with measures of aggression, it is in some ways similar to the competitive tasks that have been used in studies of the effects of competition on testosterone. Looked at in this light, the finding may indicate the following. In the sort of task that increases testosterone levels, especially in winners, an artificially-induced higher level of testosterone produces more competitive behavior. This would be in line with the challenge hypothesis.

Having said this, there are few positive findings in the studies summarized in Table 2. Their variability precludes any meaningful meta-analysis. They vary in a number of ways, the type of testosterone preparation involved, the dosage used, the duration of treatment, and whether the study involved a within-participants comparison (usually a double-blind, placebo-controlled, cross-over) or a between-participants comparison (usually comparison of placebo and control conditions).

Perhaps more importantly, a range of different aggression measures has been used. One issue that has been raised in relation to these findings is that self-report measures such as the Aggression Questionnaire (Buss and Perry, 1992) and the Buss-Durkee Hostility Inventory (Buss and Durkee, 1957) may not be suitable for measuring changes over time within participants since they were designed as trait measures. Some studies using these scales have modified them as state rather than trait measures (O'Connor et al., 2001a, 2004). However, even the original form of the AQ has been shown to be sensitive to changes over time in the same group of participants. Ritter (2003) found higher levels of physical aggression at menses than during the mid-luteal phase of the menstrual cycle using the AQ.

Looking at the positive findings in Table 2, it is difficult to see any pattern in terms of the measures involved. There are positive findings for one of the two comparisons for hostility and anger proneness, for the laboratory task, and for a scenario measure. But there is little consistency across the studies or the measures involved. At present, we must conclude that there is no consistent evidence for increases in measures associated with aggression following the artificial raises of testosterone levels. Future studies may be more profitable if they are based on predictions from the challenge hypothesis, for example that testosterone may increase competitiveness between males, especially where some status-related outcome is at stake. Men whose disposition makes them prone to be directly competitive with other men may react more strongly when their testosterone levels are artificially raised. One clue from a study that involved a short-acting effect of testosterone is

that it may lower sensitivity to punishment and increased sensitivity to reward in the short-term (van Honk et al., 2004), at least in women performing the particular gambling task used in the study.

8. Hypothesis 4: Testosterone levels are lower among paternal men

There is evidence for a consistent pattern of hormonal changes in paternal birds and mammals (at around the time of birth, which does not occur in males of non-paternal species (Wingfield et al., 1990, 2000; Wynne Edwards, 2001). To assess whether a similar pattern occurred in humans, Storey et al. (2000) obtained salivary samples from 34 couples at one of four times before and after birth, and measured cortisol, prolactin and testosterone levels. The men showed differences paralleling those found in the women. Testosterone levels were 33% lower in samples taken in the early postnatal than in the late prenatal phase. Additionally, men who were more responsive to auditory, visual and olfactory cues from newborn infants had lower testosterone levels, or larger decreases from before. Although the sample size was small, the effect size for the difference between men in the late prenatal and early postnatal phases was substantial ($d = 0.56$). Comparable findings were found in a longitudinal study of 23 first-time fathers (Berg and Wynne-Edwards, 2001), who were studied through a 3-month period after the birth of their children. Samples from the first week after birth were lowest and those from between 30 days and 3 months after the birth were the highest ($d = 0.44$ for the difference).

Berg and Wynne-Edwards (2001) also found that testosterone levels were lower in the fathers than in 14 age-matched controls ($d = 0.99$). In a study of men's responses to babies' cries (Fleming et al., 2002), fathers also showed lower testosterone levels than men who were not. Levels among fathers were also negatively correlated with experience of holding and changing infants ($r = -0.78$), sympathetic responses to infant cries ($r = -0.42$ to -0.61), and feeling the need to respond to hunger cries from infants ($r = -0.59$ and -0.73). Gray et al. (2002) also found that testosterone levels were significantly lower among fathers than among unmarried men ($d = 1.10$), and among married men without children ($d = 0.47$). Similarly, Burnham et al. (2003) found, that married men who were fathers had lower testosterone levels than paired or married men without children ($d = 0.35$), and unpaired men ($d = 0.69$).

Although the evidence is based on few studies involving small samples, it seems clear that fatherhood is associated with lowered testosterone levels. There is also evidence of lowered testosterone levels, and other hormonal changes, similar to those found in other paternal species, at the time of birth and infant care. This is also the pattern predicted from the challenge hypothesis. Wynne Edwards (2001) has

argued that the hormonal changes associated with paternity involve homologous neuroendocrine circuits to those involved in changes associated with maternity.

9. Hypothesis 5: Aggressive dominance is correlated with testosterone levels

According to challenge hypothesis applied to primates (Muller and Wrangham, 2004) the result of the cumulative effects of successful challenges should be that aggressive dominance will be positively correlated with testosterone levels. Among non-human animals, dominance is based, at least initially, on physically-based contests. This is probably also the case in most pre-state human societies, and in the modern world where there is no effective rule of law. We should therefore predict from the challenge hypothesis that aggression-based dominance is associated with higher testosterone levels. Other forms of dominance, such as those achieved through social networks or occupational skills, will not necessarily relate to testosterone levels in this way.

A considerable number of studies have assessed the association between measures of aggression and testosterone, mostly in adult men, but also in women and in children. An earlier quantitative review (Archer, 1991) found higher associations between testosterone and peer or staff ratings ($r = 0.38$; $n = 125$) than with trait-based questionnaire measures ($r = 0.15$; $n = 180$), such as the Buss-Durkee Hostility Inventory (Buss and Durkee, 1957). Studies involving prisoners generally reported higher testosterone levels among those classed as aggressive or violent than in non-violent prisoners ($r = 0.24$–0.62). Subsequent studies have tended to support these earlier findings of an overall association between testosterone and aggression, which varies considerably from study to study. A limited meta-analysis of 18 studies (Archer et al., 1998) found a value of $r = 0.20$

Book et al. (2001) reported an overall $r = 0.14$, from a meta-analysis of 45 studies of testosterone and aggression. There were, however, conceptual and methodological difficulties with their analysis, principally a lack of consistency in taking measures of direct aggression, rather than related attributes, and the inclusion of studies investigating the impact of competition on testosterone levels. When their data were reanalyzed to correct these and other problems (Archer et al., 2005), a lower overall association ($r = 0.08$; $N = 42$) was found. Values were highest ($r = 0.18$; $N = 22$) for the age group 22–35 years, and higher in those studies where testosterone samples were taken in the morning ($r = 0.10$; $N = 34$) than in the afternoon or at night ($r = 0.03$; $N = 9$). As in a previous analysis (Archer, 1991), correlations were higher for behavioral ($r = 0.13$; $N = 18$) than for self-report measures ($r = 0.08$; $N = 27$). Our re-analysis found higher associations in offender ($r = 0.16$; $N = 14$) than in non-offender

populations ($r = 0.06$; $N = 30$). Associations were also higher among female ($r = 0.13$; $N = 8$) than male samples ($r = 0.08$; $N = 36$).

Taken together, the evidence shows that there is an overall association between measures of aggression and testosterone, that it is not found in some samples (Archer et al., 1998; Campbell et al., 1997), and is pronounced in others (Gerra et al., 1996). Our most recent meta-analysis (Archer et al., 2005) found that it was higher in offender samples, in people in their twenties and early thirties, and for behavioral rather than self-report measures, all of which may be confounded. The association was not confined to men—in fact, it tended to be higher among women. Subsequent studies have found even higher associations for women (Cashdan, 2003; van Honk et al., 1999; von der Pahlen et al., 2002). This finding fits the suggestion (Wingfield et al., 2000) that in species where sexual dimorphism is less pronounced, and there is more paternal care, testosterone plays an important part in female competition for resources, and for males and their parental investment.

Mazur and Booth (1998) have argued that the main link with testosterone is with dominance rather than with aggression. As noted in Muller and Wrangham's (2004) discussion of the challenge hypothesis, the link with dominance in non-human primates seems to be confined to situations in which aggression underlies dominance. As indicated in commentaries on Mazur and Booth's article (Archer, 1998; Hines, 1998), there were major problems with the evidence base used to support their thesis. Many of the studies concerned the effects of winning a competition on subsequent testosterone levels, which is very different from an effect of testosterone levels on dominance. The narrative method used in their review prevented a systematic assessment of the evidence. Table 3 shows studies that enable an association between testosterone levels and measures of dominance—used in the sense of an individual attribute—to be calculated. Although few in number, there is a consistent association between testosterone levels and attributes described as leadership, toughness, personalized power, and aggressive dominance, which is found in a variety of samples.

For all 13 samples shown in Table 3, the mean weighted r value $= 0.124$ ($d = 0.25$; CI 0.19/0.31). However, there are two notable exceptions to the overall pattern, the reversal found for one measure of dominance by Cashdan (1995) and the small positive association found by Gray et al. (1991). There is significant heterogeneity among the 13 samples ($Q_w = 58.13$; $p < 0.001$), with these two studies being outliers. When they were removed, the other 11 studies were homogeneous ($Q_w = 10.0$; $p = 0.44$), and the mean weighted r value 0.27 ($d = 0.56$; CI 0.44/0.67). Thus, for the majority of studies there is a consistent association between testosterone levels and various measures of dominance.

Although Cashdan (1995) found a negative association between testosterone and ratings of status by peers among

Table 3
Studies measuring the association between testosterone levels and measures associated with dominance

	N	r	Study coding
Ehrenkranz et al. (1974)	12/12	0.54	3,2,4,1,2,1,1,4
Scaramella and Brown (1976)	14	0.20	1,1,1,1,1,2,1,4
Daitzman and Zuckerman (1980)	40	0.31	2,2,6,1,1,1,1,3
Christiansen and Knussmann (1987)	110	0.22	2,1,6,4,1,1,1,4
Udry and Talbert (1988)	102	0.33	4,2,6,1,1,2,1,2
Gray et al. (1991)	1709	0.08[a]	5,1,6,1,1,1,1,7
Cashdan (1995)	32	−0.35	2,2,8,2,1,1,2,4
[same sample]	[32]	0.37	2,2,9,2,1,1,2,4
Schaal et al. (1996)	79/92	0.19	4,1,5,3,3,4,1,2
Dabbs and Hargrove (1997)	87	0.34	3,1,7,1,5,1,2,5
Schultheiss et al. (1999)	42	0.29	2,1,2,1,1,2,1,3
Grant and France (2001)	52	0.24	2,2,3,2,1,3,2,3
Schultheiss et al. (2003): 1	18	0.44	2,1,2,4,1,2,1,4
Schultheiss et al. (2003): 2	36	0.10	2,1,2,4,1,2,2,4

Study characteristics: 1=sample (1=university hockey players; 2=student volunteers; 3=prisoners; 4=population sample of boys; 5=adult community sample). 2=Testosterone measure (1=saliva; 2=plasma). 3=measure (1=ratings of leadership by team coach; 2=Measure of personalized power from Picture Story Exercise [PSE: Smith (1992)]; 3=Adjective test (Grant, 1992); 4=ratings from other prisoners and from staff; 5=ratings of toughness by unfamiliar peers; 6=Personality Questionnaire measures; 7=ratings of aggressive dominance by staff on 3-point scale; 8=ratings by peers of their overall status in groups of co-residential women; 9=tendency to over-rank self relative to peers). 4=Country (1=US; 2=New Zealand; 3=Canada; 4=Germany). 5=Source of r value (1=correlations from the source; 2=means and standard deviations for dominant and control groups; 3=F values). 6=Time of day sample was collected (1=morning [6.00 a.m. to 1.00 p.m.]; 2=afternoon [1–6 p.m.]; 3=not specified; 4=throughout the day). 7=Sex (1=male; 2=female). 8=Mean age (1=under 13 years; 2=13–18 years; 3=18–21 years; 4=22–30 years; 5=31–40 years; 6=41–50 years; 7=51–60 years). All studies are from refereed journal articles.

[a] This was the correlation with free testosterone; the correlation with testosterone was lower (r=0.03).

groups of co-residential women, the tendency to over-rank oneself relative to peers was positively associated with testosterone (Table 3). Perhaps we are here dealing with a situation where an assertive interpersonal style does not succeed as well as forming alliances and more subtle manipulative ways of achieving status. Using the measure of over-ranking, the mean weighted r value across the 13 studies was 0.13 (d=0.27; CI 0.21/0.33), with only the study of Gray et al. (1991) being an outlier. The association between testosterone and over-ranking is more consistent with the findings in the other three studies involving female samples: together they produced a mean weighted r value of 0.28 (d=0.36; CI 0.39/0.77), which is significantly higher

than that for the nine male samples (QB=11.04; p<0.001) (r=0.12; d=0.24; CI 0.18/0.30).

The other outlier was a study of various androgen measures, anger and dominance, among a large sample of older men, whose mean age was 54.5 years (Gray et al., 1991). This study found low correlations between individual measures of dominance and anger, and testosterone (Table 3). However, the researchers also computed a canonical correlation, a form of Principle Components Analysis that identifies groupings of variables that are associated together. Their variables formed two canonical groups, first, aggressive dominance, consisting of dominance and anger measures, and second, availability of androgens, consisting of associated hormonal measures, testosterone and other androgens in combination with lack of luteinizing hormone, and lack of sex-hormonal binding globulin. The canonical correlation between these two groups was 0.18, indicating that by combining measures of aggression and dominance a higher relationship was found than for dominance alone, even in this older population. It also indicated that measuring only testosterone levels may be limited, and that there may be closer associations with a range of variables indicating the availability of the testosterone and other hormones in plasma.

Schaal et al. (1996) distinguished between having a history of fights, toughness, and leadership (assessed by others) in a longitudinal sample of boys aged 6–12. Those with a history of many fights had lower testosterone levels than those with fewer fights. At age 13, it was the boys who were rated as tough by unfamiliar peers who had high testosterone levels. A combination of high ratings on toughness and on leadership predicted the highest levels of testosterone in this sample. However, a follow-up study of the same sample (van Bokhoven et al., unpublished manuscript) found no association between testosterone and leadership at 16 and 21 years of age: at 16 years there was a positive association between testosterone and aggression, which was not found at 21 years of age, and an association between testosterone and delinquency, which was not found at earlier ages.

van Honk et al. (1999) found that testosterone levels measured 6 h previously were more closely associated with attending to angry faces on a Stroop task than were levels taken 4 h before or concurrently. They suggested that this is another manifestation of the association between physically-based dominance and testosterone levels, since aggressively dominant people are likely to perceive an angry face as a challenge and stare at it rather than looking away. These associations were found in both sexes and were stronger for women than for men (r=0.61 and r=0.44, n=16 for each sex). A follow-up study (van Honk et al., 2001) involving administering testosterone to 14 young women in a double-blind placebo-controlled design, found that this increased their defense reflex to angry, but not happy or neutral faces. The effect size for the difference between placebo and testosterone arms was d=0.70. Again, this was

attributed to facilitation of dominance behavior by testosterone.

Another finding that has been attributed to the association between testosterone and status striving is that of Josephs (Josephs et al., 2003). In two studies, they designed situations to challenge people's self-worth through priming them with cues that alerting them to a stereotype that would threaten belief in their abilities. In particular, they examined participants who had indicated that math or math ability was especially important to them, and created situations where they performed math tests under conditions that did and did not challenge a stereotypic view about math performance. First, they activated the stereotype that women's math ability is weak. For higher ability women who regarded their math ability as important, high testosterone participants showed poorer performance when the negative stereotype was made salient than when it was not ($d=0.81$), whereas this effect was not found for low-testosterone women, or for men. In a second study, high testosterone men who were told prior to a math test that it was a test of exceptional ability, outperformed low testosterone men ($d=0.81$), and also high testosterone men who were told that the task was to identify weak ability ($d=0.92$). The researchers explained their findings in terms of high testosterone people being more sensitive to stereotype-threat, because this represents a challenge to their status. In other words, status matters to high testosterone people, and consequently affects their performance.

These two experimental procedures provide indirect evidence that higher levels of plasma testosterone influence how people assess both physical and psychological threats to their status, in the form of angry challenging faces, and a psychological threat to an ability important for self-esteem. They complement evidence that testosterone is associated with a personal need to dominate others (Schultheiss et al., 1999, 2003). Taken together with the studies reviewed in this section showing a low (but inconsistent) correlation between measures of aggression and testosterone levels, and a higher and more consistent association with dominance, the evidence is consistent with the following. People with higher existing levels of testosterone are more likely to show higher scores on a variety of different assessments of dominance and also to show higher levels of aggression, although this is a weaker relationship. They also show a more pronounced reaction to situations that challenge their status, whether psychologically or physically.

We introduced this section with the argument that associations between testosterone and measures of aggression, dominance, and status-striving, would reflect the cumulative effect of successful reactions to challenges. This remains one possible explanation for the evidence showing links between these measures. There is, however, an alternative, that these associations represent enduring individual differences reflecting alternative life history strategies. This is explored in the next section.

10. Hypothesis 6: Testosterone is associated with alternative life history strategies

The original challenge hypothesis concentrated on species differences in the allocation of mating versus parental effort in males, and, among monogamous species, temporal changes in the allocation of mating versus parental effort. The general principle of differential allocation of mating versus parental effort may underlie relatively enduring individual differences among males in their relative preference for life history strategies that emphasize either mating or parental effort, differences that will be associated with differences in testosterone levels. Those who show a preference for mating rather than parental effort will show higher levels of testosterone. The evidence reviewed in Section 9, indicating an association between testosterone, aggression, dominance, and status striving among men, can be interpreted in this way. In this section, I assess evidence that individual differences in testosterone levels are associated with a range of other characteristics typical of life histories that emphasize the pursuit of short-term mating opportunities rather than longer-term relationships and paternal care. I also consider evidence that these individual differences are apparent early in life.

There are several lines of evidence relevant to this issue. First, there are studies that have a direct bearing on the association between testosterone and the allocation of mating versus parental effort: these involve the association between testosterone levels and the pursuit of additional (extra-pair) or short-term relationships, as opposed to relationship stability and parental effort. Second, there are studies of the association between testosterone levels and personality characteristics that might predispose individuals to enter such different life courses. Third, there are studies on the association between testosterone and a range of antisocial activities that would tend to be associated with a shorter-term, higher-risk, reproductive strategy. Finally, there are studies relevant to the issue of whether the associations found in adulthood are likely to be in place early in life, and hence represent enduring specialized life history strategies.

10.1. Testosterone and mating versus parental effort

Consistent with the prediction that testosterone is associated with more emphasis on mating versus parental effort is the finding, from a small sample of middle aged men, that low testosterone levels are associated with greater marital satisfaction and better parental relationships (Julian and McHenry, 1989). In a sample of married men without children, Gray et al. (2002) found that the degree of investment in their spouse (measured by a 21-item spousal investment scale) was negatively correlated with testosterone levels ($r=-0.52$), as was the time spent with their spouse on their last day off ($r=-0.65$). A follow-up study (Burnham et al., 2003) reported that young unpaired men

had higher testosterone levels than unmarried men in committed romantic relationships, who had similar levels to those of married men without children ($d = 0.48$). Daitzman and Zuckerman (1980) found positive associations between testosterone, and both an interest in erotica ($r = 0.40$), and a higher number of heterosexual partners ($r = 0.43$). Dabbs et al. (1997) sampled the activities and thoughts of a small group of participants, pre-selected for high and low levels of testosterone. The high testosterone group showed more restless energy, and also mentioned thinking about friends more than they thought about family or partners, compared with the low testosterone group. All of these findings are consistent with the prediction that high testosterone men devote more time and energy to mating than to parental effort.

In a sample of over 4462 military veterans, testosterone levels were positively associated with not marrying and with marital instability, and negatively with measures of marital quality, such as spending less time with their wives, and more extra-marital sex (Dabbs and Morris, 1990). Testosterone was also associated with men's physical aggression to their wives (Booth and Dabbs, 1993). Although these associations are relatively small, they are consistent with the authors' suggestion of a testosterone-induced profile of aggressiveness, dominance and sensation-seeking, which interferes with a wide range of behavior necessary for forming satisfactory relationships. On the other hand, such characteristics would increase the range of sexual partners and render such men more like the polygynous males found in studies of birds.

There is also evidence of more complex interactions between men's and women's testosterone levels and their marital satisfaction. In a study of 92 newly-married couples involved in problem-solving conversations, Cohan et al. (2003) found no overall relationship between testosterone levels and behavior that would be disruptive to the relationship. However, there were a number of more complex associations between testosterone levels and aspects of the conversations. When wives had high testosterone levels, relative to the others in the sample, both partners were less positive in conversations the wives initiated. Husbands were more positive and less negative in their interactions when testosterone levels were concordant between the spouses (i.e. both had similar levels relative to the norm for their own sex in this sample). In observed social support sessions, where one partner selected a personal concern to discuss with the other, there was no association with testosterone levels for the partner seeking support. When giving support, husbands showed more positive and less negative behavior when both spouses had low testosterone levels (relative to their sex in sample). Wives offered more positive and less negative support in cases where they had higher testosterone levels and their husbands had lower levels. Overall, the findings indicated more harmonious interactions when both partners had similar relative levels of testosterone, particularly if they

both had lower levels. There was also some indication that a wife with a relatively high testosterone level had better relations with a lower-testosterone husband. These findings can be explained in terms of the interactions of various personality traits associated with higher or lower testosterone levels, notably dominance and nurturance. Thus there may be greater marital satisfaction if both partners are low in testosterone levels because this profile is associated with being less combative, gentler and more sensitive to the other's needs.

10.2. Antisocial activities

We would also expect a more short-term mating-oriented strategy to involve a range of antisocial activities, all of which can be viewed as putting shorter-term goals before longer-term ones. Using data from the large sample of military veterans, Dabbs et al. (1990) did find an association between testosterone levels and an antisocial personality, alcoholism and drug use (DSM-III criteria), although the magnitude was small ($r = 0.13$–0.18). In an analysis of the same sample, Dabbs and Morris (1990) found that those with the top 10% testosterone levels were higher on antisocial activities including assaults ($r = 0.20$) than the remaining sample. Although the effect size was small, it was greater for men from lower socioeconomic backgrounds. Further analyses of the same sample using regression models (Mazur, 1995) found that combinations of testosterone with social variables such as education and socioeconomic class were better predictors of deviant behavior than was testosterone alone, which was only a weak predictor of violence ($r = 0.10$).

Aromaki et al. (1999) found a higher association ($r = 0.50$) between testosterone and antisocial personality, which included a proneness to reckless driving, frequent change of sex partners, and failure to plan ahead, among a small sample of violent men, but this association was not found in a non-violent control sample. A further study (Booth et al., 2003), of children aged 10–14 and 15–18 years, from 400 families, found a link between testosterone levels and risk taking in boys but not in girls. However, the extent of this association was moderated by the quality of the boy's relationship with his parents. Another large-sample study (van Bokhoven et al., unpublished manuscript) found an association between high or low testosterone levels and delinquency at 21 years of age, but not among the same sample at either 13 or 16 years of age.

Two studies analyzed samples of boys aged 13–16 years using path analysis models that included social and hormonal measures. Udry (1990) found that testosterone and sex hormonal binding globulin predicted problem behavior in a cross-sectional sample of 101 young males, aged 13–16 years ($R^2 = 0.24$). Problem behavior involved activities such as smoking, getting drunk, having sex, using marijuana, and being off school. Again, we find an association with antisocial activities that would be

associated with a polygynous reproductive strategy. Drigotas and Udry (1993) analyzed the longitudinal sample used by Halpern et al. (1994a, section 4). They found that testosterone only contributed to the prediction of problem behaviors at time 1 (13 years), along with the social variables, religiosity and autonomy, but not at times 2 and 3 (6 months and a year later). In a time-lagged model, testosterone at time 1 had a direct influence on problem behavior a year later, and beyond, but testosterone measured at times 2 and 3 did not. This suggests that it is early pubertal maturation, rather than high testosterone as such, that was associated with problem behavior in this sample.

Dabbs et al. (1996) measured saliva testosterone levels among 240 young male students from two universities in the US, from 12 fraternities. They also used a number of sources, such as fraternity officers, yearbooks, photographs, and the researcher's observations, to classify the behavioral style of the fraternities. Overall, fraternities whose members were more unruly in their behavior showed higher testosterone levels than those whose members were characterized as more socially responsible and more successful academically. In the first university, the difference in testosterone levels between individuals from the unruly and the responsible fraternities was modest ($d = 0.28$).

It is not as yet clear what psychological characteristics may mediate the association between testosterone and various forms of antisocial behavior. One characteristic that is often associated with heightened aggression is impulsivity (O'Connor et al., 2001a; Barratt et al., 1999; Stanford et al., 2003). Bjork et al. (2001) used a laboratory measure of impulsivity, involving the failure to withhold responses to a stimulus that is not the target, which had previously been found to correlate with a self-report measure of impulsivity, aggressiveness, and conduct disorders. They found that making such commission errors in a delayed memory task was highly correlated ($r = 0.55$) with testosterone levels in a sample of young women.

There is evidence that men with higher serum levels of testosterone end up in lower-status occupations. Dabbs (1992) reported a large-scale analysis of the relationship between testosterone and occupational achievement among the sample of 4462 military veterans. The findings fitted a model in which the effects of testosterone on occupational achievement were mediated through more antisocial behavior, lower intelligence, and lower education, being associated with a life-path leading away from higher-status white-collar occupations. It is likely that testosterone is associated with uninhibited, risk-taking, behavior that fits men poorly for achievement in higher-status occupations in organizations. In contrast to these findings, among a sample of 55 women, testosterone and other androgens were higher among students, professional and managerial workers than among clerical workers and homemakers (Purifoy and Koopmans, 1979). It seems, therefore, that for women higher levels of androgens are an advantage in gaining occupational status, possibly because higher testosterone women are more assertive and occupationally oriented.

10.3. Personality and behavioral characteristics

Underlying the associations between testosterone and characteristics associated with preferences for shorter-term mating strategies and more uninhibited behavior there should be a comparable link between testosterone and personality profiles, and also with behavior associated with personality characteristics. Daitzman and Zuckerman (1980) found higher testosterone levels among 20 young men with high disinhibition scores than those with low disinhibition scores. They also found a range of other associations between testosterone and personality measures, such as extraversion ($r = 0.41$), sociability ($r = 0.39$) and instrumental traits ($r = 0.29$), as measured by the Bem Sex Role Inventory (BSRI (Archer and Lloyd, 2002). A low positive correlation between testosterone and extraversion ($r = 0.20$) was also found in a sample of men from a pathological gamblers program, and in matched controls (Blanco et al., 2001).

Among a sample of 84 young women, there was also a range of fairly low correlations between testosterone and personality characteristics (Baucom et al., 1985), consistent with Daitzman and Zuckerman's, 1980 findings, in that they included impulsiveness ($r = 0.28$), robustness ($r = 0.28$), resourcefulness ($r = 0.27$), and spontaneity ($r = 0.26$), all of which are associated with extraversion. There were also negative correlations with being civilized ($r = -0.35$), and rational ($r = -0.35$). Udry and Talbert (1988) found associations with a broadly similar set of personality attributes among samples of adolescent boys and girls (ages 12–16 years). They noted that variables forming a coherent factor with testosterone looked like stable extraversion. It included attributes such as show-off, ambitious, dominant, spontaneous, and uninhibited. Although Dabbs and Ruback (1988) found correlations between testosterone and low self-control in a sample of college students, they also noted that it was associated with a lack of exhibition, and having an engaging and attractive personality. In contrast, Dabbs et al. (1990) found inconsistent associations between testosterone levels and personality in four samples of college students.

Other studies have examined the association between testosterone and behavior or facial expressions that are likely to be associated with personality. In a study of young male students from two universities in the US, Dabbs et al. (1996) found a high negative correlation between testosterone levels and the proportion of fraternity members who were smiling in yearbook photographs for seven fraternities ($r = -0.78$). Similarly, Cashdan (1995) found a negative association between testosterone levels and time spent smiling ($r = -0.39$) among co-residential women in a social setting.

In another study by Dabbs and his colleagues (Dabbs, 1997), male and female students were photographed twice,

the first time smiling and the second not smiling, and these photos coded using the Facial Action Coding System, and rated for various characteristics by independent judges. The smiles of higher testosterone men tended to show less wrinkling around the eyes ($r = -0.19$), and to be judged as stronger and more dominant ($r = 0.19$). However, the correlations for non-smiling males were zero, and values were around zero for women.

Dabbs et al. (2001) reported four studies of the association between testosterone levels and behavior in brief social encounters using men and women students. They found modest associations with a number of measures. In the first study, where the instructions were to approach a camera and speak to it, testosterone was correlated with focusing on the camera ($r = 0.25$). In the second, involving knocking on a door, entering and speaking to an older woman, testosterone was correlated with overall forwardness ($r = 0.24$). The third study involved studying the first half minute preceding talking with a younger woman in a more relaxed setting. Testosterone was negatively correlated with the time it took to enter and approach the interviewer ($r = -0.29$). The fourth study involved pairs of high and low testosterone students. From video recordings of their interactions, the researchers concluded that the high testosterone participants were more independent (confident, relaxed and at ease) than were the low testosterone participants (who were characterized as more friendly, attentive and nervous). Thirteen independent judges were then asked to place the pairs of participants into the categories independent or responsive. The majority of the judges placed the high-testosterone individuals into the independent category and the low testosterone individuals into the responsive category.

The studies described in this sub-section provide some evidence of an association between testosterone and a more extraverted, uninhibited, dominant, personality. This is consistent with pursuing a shorter-term reproductive strategy, emphasizing mating rather than parental effort.

10.4. Are these associations present before puberty?

If the associations between testosterone and the characteristics reviewed in Sections 9 and 10 are associated with alternative life history strategies, it is likely that they will be present early in life, before puberty. This is the case for aggression. Table 4 shows the association between testosterone and aggression in studies involving children. Over all the seven samples, the mean weighted r value was 0.15 ($d = 0.29$; CI 0.12/0.47; $p = 0.001$), although this is less meaningful than the separate values for boys and girls. Five samples of boys showed a mean weighted r value of 0.28 ($d = 0.58$; CI 0.37/0.80), whereas two samples of girls showed an r value of -0.08 ($d = -0.41$; CI $-0.74/-0.08$). The sex difference is highly significant ($QB = 24.9$; $p < 0.001$). From this limited analysis, it would

Table 4
Studies measuring the association between testosterone and aggression in children

	N	r	Study coding
Susman et al. (1987): 1	55	0.06	4,2,3,1,1,1,1,4
Susman et al. (1987): 2	52	−0.21	4,2,3,1,1,1,2,4
Constantino et al. (1993)	18/11	0.18	1,1,3,1,2,1,1,2
Scerbo and Kolko (1994)	40	0.47	2,1,1,1,1,1,1,3
[same sample]	[40]	0.45	2,1,2,1,1,1,1,3
[same sample]	[40]	0.14	2,1,3,1,1,1,1,3
Chance et al. (2000)	45	0.36	1,1,3,1,1,1,1,2
Sanchez-Martin et al. (2000): 1	28	0.39	3,1,4,2,1,1,1,1
Sanchez-Martin et al. (2000): 2	20	−0.20	3,1,4,2,1,1,2,1

Study characteristics: 1 = sample (1 = psychiatric center and matched controls; 2 = clinic referrals for disruptive behavior, 3 = preschool; 4 = community sample). 2 = Testosterone measure (1 = saliva; 2 = plasma). 3 = Measure (1 = Child Behavior Check List (CBC): teacher's version; 2 = clinic staff reports; 3 = CBC: parents' version; 4 = observations). 4 = Country (1 = US; 2 = Spain). 5 = Source of r value (1 = correlations from the source; 2 = means and standard deviations for aggressive and control groups). 6 = Time of day sample was collected (1 = morning [6.00 a.m. to 1.00 p.m.]; 2 = afternoon [1–6 p.m.]; 3 = not specified; 4 = throughout the day). 7 = Sex (1 = male or mainly male; 2 = female). 8 = mean age (1 = under 5 years; 2 = 4–10 or 5–11 years; 3 = 10–12; 4 = 9–14 years). All studies are from refereed journal articles.

seem that an association between testosterone and aggression occurs in males, but not in females, during childhood.

Consistent with these findings are a number of studies showing an association with a wider range of antisocial activities. Chance et al. (2000) found that levels were higher in 5–11 year old boys with symptoms of disruptive behavior than they were in a matched control group ($d = 0.49$), and that these differences were considerably greater in children aged 9–11 years ($d = 1.91$). Overall, testosterone was positively associated with aggression ($r = 0.36$), and being withdrawn ($r = 0.41$), correlations that were higher for the lower half of the IQ distribution ($r = 0.50$ for aggression and $r = 0.48$ for withdrawal).

A comparison between boys who had high scores for externalizing behavior (aggression and delinquency) and controls (Maras et al., 2003) found similar results. Testosterone levels were considerably higher among these externalizing boys than they were among the controls ($d = 0.70$), as were DHT (dihydrotestosterone) levels ($d = 0.93$): DHT has a higher affinity with androgen receptors. Again, there were positive correlations between testosterone and delinquent behavior (rho = 0.36), although the correlation with aggression was lower in this study. There were no differences in testosterone or DHT levels between a slightly larger sample of externalizing girls and matched controls. Similarly, van Goozen et al. (1998) found that the levels of dihydroepiandrosterone sulfate (DHEAS),

another androgen found in the brain, were higher in a small sample of conduct disordered boys than they were in controls, although no differences in testosterone were reported. Overall, DHEAS was associated with parents' and teachers' reports of their aggression (rho=0.46 and 0.48) and delinquency (rho=0.33 and 0.39).

All these studies involved boys, and the evidence from the studies of testosterone and aggression in children indicated that the association only applied to boys. In a study of a small sample of unselected children of both sexes aged from 3 to 12 years, and Strong and Dabbs (2000) found that those with higher testosterone levels were rated by their parents as more independent and less attached ($r=0.45$). This applied equally to older and younger children of both sexes. They were also viewed as more often upset, fussy and moody ($r=0.35$), i.e. less agreeable, than lower testosterone children. The correlation between moodiness and testosterone was much more pronounced in the 9–12 year old group than at younger ages ($r=0.68$ vs 0.35). At younger ages higher testosterone children tended to be rated as less sociable ($r=-0.44$).

These findings suggest that high and low testosterone males may tend to set out on different life courses equivalent to alternative life history strategies, and that these differences are apparent from relatively early ages, at least well before puberty. How these individuals progress will of course depend on how their social circumstances interact with their dispositions. Evidence from the large-scale study of US military veterans indicates that associations between testosterone and overt antisocial activity, and with occupational status, are accentuated by living in a low social class environment, and attenuated by living in a higher social class environment. Overall the evidence indicates an association of these life history strategies with testosterone levels and that the association is found before puberty for boys. Whether there is a comparable pattern for girls is unclear at present.

Most of the evidence presented in this section is derived from studies with aims that are unrelated to testing the challenge hypothesis or the concepts of alternative life history strategies. It will in future be possible to link studies of individual differences in testosterone levels directly to hypotheses derived from these evolutionarily-based theories. It would be possible to test more directly whether variations in testosterone levels are related to measures of a preference for short-term mating opportunities (such as sociosexuality) and to an interest in parenting. This would enable a direct link to be made with previous theories of alternative life-history or mating strategies in humans (Archer and Mehdikhani, 2003; Gangestad and Simpson, 2000).

11. Does the Challenge Hypothesis apply to women?

Although the challenge hypothesis is concerned with males, Wingfield et al. (2000) did note that there was considerable variation in testosterone levels between females of different bird species. When sexual dimorphism was less pronounced, as in monogamous species, testosterone levels of females relative to those of males are higher, and it is possible that testosterone may be involved in female competition. Some of the studies covered in this review relate to this possibility. There was only one study involving the impact of competition on women's testosterone levels, and this (Bateup et al., 2002) indicated that they are, like those of men, responsive to competition. The association between testosterone and aggression was found to be higher for female than male samples (Archer et al., 2005). In three studies of women involving measures of dominance, the overall correlation with testosterone was also higher than in male samples, and an association between testosterone and attention to angry faces was found for both men and women (van Honk et al., 1999). When testosterone was administered to young women (van Honk et al., 2001), there were heightened defense reflexes to angry faces, which was attributed to the hormone facilitating dominance behavior. High testosterone women showed the same indications as high testosterone men that they were more sensitive to stereotype-threat than low-testosterone people (Josephs et al., 2003). A further study showed that women with higher androgen levels had higher occupational status, possibly as a result of their being more assertive (Baucom et al., 1985).

All these studies indicate that women may respond with increased testosterone to challenging situations, and that they show similar correlations between testosterone and personality characteristics such as aggressiveness and dominance. These characteristics should generally aid them in competitive situations with other women. However, there are some circumstances when this may be a disadvantage. In Cashdan's (1995) study of co-residential women, ratings by peers of a woman's status was negatively correlated with testosterone levels, whereas the women's own tendency to over-rate themselves relative to peers was positively related to testosterone. It is likely that in such situations, high testosterone levels are associated with an assertive style that hinders forming alliances and engaging in the more subtle forms of competition that occur in such female groups (Archer and Coyne, in press; Björkqvist et al., 1992; Underwood, 2003).

The question of whether high and low testosterone women form consistent life history strategies, as they appear to in men, remains unanswered by the relatively few studies of women. The limited evidence on associations between testosterone and aggression in girls suggests that this does not follow the pattern found in boys, and therefore would not support the life history interpretation. However, the evidence is not sufficient for a definite conclusion on this point.

12. The role of neonatal hormones

The challenge hypothesis addresses the role of circulating testosterone levels during adult life. However, it has

long been known from studies of mammals (and later birds) that androgens influence neural structures at two times in the life history, perinatally and at puberty. The earlier influence, which occurs either prenatally or in early postnatal life, is known as an organizing effect, and typically primes the brain, rather than influencing behavior directly. The pubertal increase typically has a direct influence on behavior. There is, however, increasing evidence that early androgens have direct effects on behavior. For example, it has been known for over 30 years that they influence rough-and-tumble play in mammals such as rhesus monkeys (Rose et al., 1974). In humans, there is evidence that prenatal testosterone influences language development (Finegan et al., 1992), eye contact (Lutchmaya et al., 2002), toy preferences (Berenbaum and Hines, 1992; Hines et al., 2002; Nordenström et al., 2002), and possibly aggression (Berenbaum and Resnick, 1997) in girls. However, these associations have mainly been detected in girls, in some cases those exposed to unusually high levels of androgens. Whether they also occur as a result of variations in prenatal testosterone levels in boys is not clear from the existing evidence.

Thus there is little evidence for early androgenic influences in boys. Yet it is in boys that any association between early androgens and a subsequent pattern of testosterone, personality and antisocial activities before puberty, would be of interest in relation to the hypothesis of different life history strategies. For this to be the case, prenatal testosterone would have to affect both the level of testosterone present throughout childhood, and during adulthood. It may also influence somatic growth and the timing of puberty (Drigotas and Udry, 1993), thus indirectly influencing behavior. We could therefore envisage a life-history pattern beginning with high levels of prenatal testosterone, leading to higher testosterone levels, larger musculature and associated personality attributes during childhood. This would be followed by earlier puberty, higher adult testosterone levels, and associated behavior representing an emphasis on mating rather than paternal effort. Of course, this is at present speculative.

13. Conclusions

Evidence from a range of different studies involving measures of testosterone and behavior indicates a reasonable fit with predictions derived from a modified version of the challenge hypothesis, originally applied to testosterone-behavior relationships in birds. The challenge hypothesis has a sounder basis in evolutionary theory than the alternative 'mouse model', which supposes a straightforward influence of testosterone on aggression in males from puberty onwards. The basis of the challenge hypothesis is a cost-benefit analysis of the physiological and behavioral consequences of high levels of testosterone. As a result, of the costs of high levels of testosterone, it would be adaptive

to avoid maintaining consistently high levels throughout adulthood. Thus, if testosterone can be kept relatively low, and yet still support reproductive physiology and behavior, this will be more adaptive than maintaining consistently high levels. Further, if levels can be raised under conditions of reproductively-related competition, when behavior associated with a rise in testosterone is required, this again would be more adaptive than maintaining consistently high levels. Thus, the challenge hypothesis essentially involves an adaptive mechanism that avoids the high costs of testosterone (Wingfield et al., 2001).

Its specific predictions fitted the human case fairly well. There was little evidence for increased aggression as a function of testosterone at puberty in boys. Five studies, and a meta-analysis of developmental trends in sex differences in direct aggression, showed no sign of increased aggression coinciding with testosterone increases at puberty in boys. One study did report slight increases in aggression among testosterone-treated boys with delayed puberty, although there was a similar increase for girls treated with estrogen, which would not be expected from the challenge hypothesis.

Young adult males showed testosterone increases in situations involving sexual stimuli. Sexual intercourse was associated with increased testosterone, as was watching erotic videos. The only study involving interactions with a potential mate also found increased testosterone levels. Men also showed increased testosterone in response to competition with other young men, although these studies usually involved laboratory tasks or sport-based competitions. The second of these is nearest to the sorts of reproductively-related competitions that the challenge hypothesis involves. The evidence indicated more support for a pre-competition rise in sports competitions, and also greater increases during competitions. This change was higher for winners than for losers. Further, there was some evidence for a vicarious increase in testosterone among supporters of a successful sports team. Mood was unlikely to be a mediator of the higher increase in winners than losers, but making an internal rather than an external attribution for the victory did predict a greater increase in testosterone among winners (whereas an external attribution predicted a higher increase among losers). Additionally, a type of individual assertiveness that involved the need to dominate others in face-to-face encounters, combined with low inhibition, was strongly associated with the extent of testosterone increase among winners. Both these characteristics can therefore be regarded as moderators of the association between competitive outcome and changes in testosterone levels.

There was some, but limited, evidence that higher testosterone levels were associated with measures of aggressiveness in judo competitions, and also in a laboratory aggression measure. However, these associations could reflect longer-term individual differences. There was little indication that injecting testosterone produced changes similar to the heightened competitiveness found in birds. However, studies based more directly on predictions from

the challenge hypothesis have still to be undertaken. These would involve a range of measures related to both mating and parental effort, and involve situations where there was direct competition between young men.

The few studies involving comparing fathers and men who were not fathers did show an association between fatherhood and lower testosterone levels. The single longitudinal study of men preparing for paternal care showed decreased testosterone levels.

Testosterone levels showed a low but positive correlation with measures of aggression and higher correlations with dominance, variously measured by leadership, toughness, personal power, and aggressive dominance. A study of 13-year-old boys found the highest associations with testosterone for being a tough leader, and little sign of an association with measures of fighting. There was also evidence that men with higher testosterone levels were more prone to react in situations that were perceived as challenges, such as an angry face or a more psychologically-induced challenge to their self worth. These studies broadly support the prediction that there would be an association between aggression-based dominance and testosterone levels. They also go beyond this, in indicating that challenges and status matters more to high testosterone people, and influences their behavior.

Long-term variations in testosterone levels between men were associated with a range of measures, consistent with the view that higher testosterone levels are associated with a life-history strategy emphasizing mating effort at the expense of parental effort. This supports extensions of the challenge hypothesis to encompass individual differences in the extent to which different men show tendencies towards one of two life history strategies. These involve either a lower-testosterone adaptive strategy of concentrating on parental effort and reducing the costs of high testosterone levels, or concentrating on mating effort and balancing the costs of high testosterone levels with the advantages of a more polygynous mating strategy. High testosterone men tend to be stable extraverts, and to show a range of characteristics indicating that they tend to prioritize shorter-term goals. For example, high testosterone men show more antisocial behavior, take more risks, and have less stable sexual relationships. There was evidence that high and low testosterone males tend to set out on different life courses from a relatively early age, although it is clear that any initial dispositions interacts with social circumstances. As in the case of other evidence reviewed in this article, there is the need to extend these studies so as to test more precisely the predictions of the challenge hypothesis. For example, tests of individual differences in a range of activities more directly associated with mating versus parental effort could be undertaken.

Wingfield et al. (2000)) found, in species of monogamous birds, that the testosterone levels of females were higher, relative to those of males, in species where sexual dimorphism was less pronounced. They suggested that testosterone may play a part in female competition in such cases. A similar process may occur in humans, with testosterone facilitating female competition for preferred mates and for paternal investment. There was evidence that women respond with increased testosterone levels to competitive situations in a similar way that men do. There was also evidence of a higher association between testosterone and both aggression and dominance among women than among men. This suggests that there are individual differences, possibly the result of the cumulative effects of competition, or representing different life history strategies.

A final point that is important for future research comes from the observation that the challenge hypothesis is based on a mechanism for avoiding the cost of high levels of testosterone. Wingfield et al. (2001) outlined other possible mechanisms for avoiding the costs of high testosterone levels. These included sex-specific steroid binding protein in blood, which would render some of the testosterone inactive, or the use of androgens such as DHEA that are precursors of testosterone, to exert specific effects via aromatization at receptors. Both possibilities may apply to humans. Much of plasma testosterone in humans is in the bound form. Gray et al. (1991) found that measures of aggression and dominance showed a higher association with a variable labeled as "availability of androgens", reflecting availability of free rather than bound androgens, than with levels of plasma testosterone. Meta-analyses of the association between testosterone and aggression have found higher correlations for salivary testosterone, which contains more free testosterone, than for plasma testosterone, where more is in a bound form (Archer et al., 1998, 2005).

Regarding the use of other androgens (precursors of testosterone), which are aromatized at receptors, we noted that a number of studies have found that androgens other than testosterone are associated with behavioral variables. For example, Maras et al. (2003) found that DHT (dihydrotestosterone) levels were considerably higher among externalizing boys than among a control sample, and that this association was stronger than that with testosterone. DHT has a higher affinity with androgen receptors than does testosterone (Maras et al., 2003). van Goozen et al. (1998) found higher dihydroepiandrosterone sulfate (DHEAS), but not testosterone, levels among conduct disordered boys than controls, and that DHEAS was associated with parents' and teachers' reports of aggression and delinquency.

A further point that could be important in future studies concerns individual differences in the sensitivity of receptors to the action of testosterone (Manning et al., 2003). Taking into account receptor sensitivity may yield higher associations between testosterone and behavioral variables than is apparent in existing studies.

References

Albert, D.J., Jonik, R.H., Walsh, M.L., Petrovic, D.M., 1989. Testosterone supports hormone-dependent aggression in female rats. Physiol. Behav. 46, 185–189.

Albert, D.J., Jonik, R.H., Watson, N.V., Gorzalka, B.B., Walsh, M.L., 1990. Hormone-dependent aggression in male rats is proportional to serum testosterone concentration but sexual behavior is not. Physiol. Behav. 48, 409–416.

Albert, D.J., Walsh, M.L., Jonik, R.H., 1993. Aggression in humans: what is its biological foundation. Neurosci. Biobehav. Rev. 405–425.

Alexander, R.D., Hoogland, J.L., Howard, R.D., Noonan, K.M., Sherman, P.W., 1979. Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans, in: Chagnon, N.A., Irons, W. (Eds.), Evolutionary Biology and Human Social Behavior. Duxbury Press, Scituate, MA, pp. 402–435.

Allee, W.C., Collias, N.E., Lutherman, C.Z., 1939. Modification of the social order in flocks of hens by injection of testosterone propionate. Physiol. Zool. 12, 412–440.

Anderson, R.A., Bancroft, J., Wu, F.C.W., 1992. The effects of exogenous testosterone on sexuality and mood of normal men. J Clin. Endocr. Metab. 75, 1503–1507.

Archer, J., 1988. The behavioural biology of aggression. Cambridge University Press, Cambridge, UK.

Archer, J., 1991. The influence of testosterone on human aggression. Br. J. Psychol. 82, 1–28.

Archer, J., 1994. Testosterone and aggression. J. Offender Rehabil. 21, 3–25.

Archer, J., 1998. Problems with the concept of dominance and lack of empirical support for a testosterone-dominance link. Behav. Brain Sci. 21, 363 (commentary on Mazur and Booth 1998).

Archer, J., 2004. Sex differences in aggression in real-world settings: a meta-analytic review. Rev. Gen. Psychol. 8, 291–322.

Archer, J., Coyne, S.M., in press. An integrated review of indirect, relational, and social aggression. Pers. Soc. Psychol. Rev.

Archer, J., Lloyd, B.B., 2002. Sex and Gender, second ed. Cambridge University Press, Cambridge, UK.

Archer, J., Mehdikhani, M., 2003. Variability among males in sexually-selected attributes. Rev. Gen. Psychol. 7, 219–236.

Archer, J., Birring, S.S., Wu, F.C.W., 1998. The association between testosterone and aggression among young men: empirical findings and a meta-analysis. Aggress. Behav. 24, 411–420.

Archer, J., Graham-Kevan, N., Davies, M., 2005. Testosterone and aggression: a re-analysis of Book, Starzyk and Quinsey's (2001) study. Aggress. Viol. Behav. 10, 241–261.

Arnedo, M.T., Salvador, A., Martinez-Sanchis, S., Gonzalez-Bono, E., 2000. Rewarding properties of testosterone in intact male mice: a pilot study. Pharmacol. Biochem. Behav. 65, 327–332.

Aromaki, A.S., Lindman, R.E., Eriksson, C.J.P., 1999. Testosterone, aggressiveness, and antisocial personality. Aggress. Behav. 25, 113–123.

Baron, R.M., Kenny, D.A., 1986. The moderator–mediator variable distinction in social psychological research: conceptual, strategic, and statistical considerations. J. Pers. Soc. Psychol. 51, 1173–1182.

Barratt, E.S., Stanford, M.S., Dowdy, L., Liebman, M.J., Kent, T.A., 1999. Impulsive and premediated aggression: a factor analysis of self-reported acts. Psychiatry Res. 86, 163–173.

Bateup, H.S., Booth, A., Shirtcliff, E.A., Granger, D.A., 2002. Testosterone, cortisol, and women's competition. Evol. Hum. Behav. 23, 181–192.

Baucom, D.H., Besch, P.K., Callahan, S., 1985. Relation between testosterone concentration, sex role identity and personality among females. J. Pers. Soc. Psychol. 48, 1218–1226.

Beeman, A.E., 1947a. The effect of male hormone on aggressive behavior in mice. Physiol. Zool. 20, 373–405.

Beeman, A.E., 1947b. The effect of the interval between castration and first encounter to the aggressive behavior of mice. Anat. Rec. 99, 570–571.

Bem, S.L., 1974. The measurement of psychological androgyny. J. Consult. Clin. Psychol. 42, 155–162.

Berenbaum, S.A., Hines, M., 1992. Early androgens are related to childhood sex-typed toy preferences. Psychol. Sci. 3, 203–206.

Berenbaum, S.A., Resnick, S.M., 1997. Early androgen effects on aggression in children and adults with congenital adrenal hyperplasia. Psychoneuroendocrinology 22, 505–515.

Berg, S., Wynne-Edwards, K.E., 2001. Changes in testosterone, cortisol, and estradiol levels in men becoming fathers. Mayo Clin. Proc. 76, 582–592.

Berman, M., Gladue, B., Taylor, S., 1993. The effects of hormones, Type A behavior pattern, and provocation on aggression in men. Motiv. Emot. 17, 125–138.

Bernhardt, P.C., Dabbs, J.M. Jr, 1997. Testosterone increases in basketball fans. Paper Presented at Meeting of American Psychological Society, Washington, DC.

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. Physiol. Behav. 65, 59–62.

Bjork, J.M., Moeller, F.G., Dougherty, D.M., Swann, A.C., 2001. Endogenous plasma testosterone levels and commission errors in women: a preliminary report. Physiol. Behav. 73, 217–221.

Björkqvist, K., Lagerspetz, K., Kaukiainen, A., 1992. Do girls manipulate and boys fight? Developmental trends in regard to direct and indirect aggression. Aggress. Behav. 18, 117–127.

Blanco, C., Ibáñez, A., Blanco-Jerez, C-R., Baca-Garcia, E., Sáiz-Ruiz, J., 2001. Plasma testosterone and pathological gambling. Psychiatry Res. 105, 117–121.

Book, A.S., Starzyk, K.B., Quinsey, V.L., 2001. The relationship between testosterone and aggression: a meta-analysis. Aggress. Viol. Behav. 6, 579–599.

Booth, A., Dabbs Jr., J.M., 1993. Testosterone and men's marriages. Social Forces 72, 463–477.

Booth, A., Shelley, G., Mazur, A., Tharp, G., Kittok, R., 1989. Testosterone, and winning and losing in human competition. Horm. Behav. 23, 556–571.

Booth, A., Johnson, D.R., Granger, D.A., Crouter, A.C., McHale, S., 2003. Testosterone and child and adolescent adjustment: the moderating role of parent–child relationships. Dev. Psychol. 39, 85–98.

Burnham, T.C., Chapman, J.F., Gray, P.B., McIntyre, M.H., Lipson, S.F., Ellison, P.T., 2003. Men in committed, romantic relationships have lower testosterone levels. Horm. Behav. 44, 119–122.

Buss, A.H., Durkee, A., 1957. An inventory for assessing different types of hostility. J. Consult. Psychol. 21, 343–349.

Buss, A.H., Perry, M., 1992. The aggression questionnaire. J. Pers. Soc. Psychol. 63, 452–459.

Cairns, R.B., Cairns, B.D., Neckerman, H.J., Ferguson, L.L., Gariépy, J.-L., 1989. Growth and aggression: 1. Childhood to early adolescence. Dev. Psychol. 25, 320–330.

Campbell, A., 1995. A few good men: evolutionary psychology and female adolescent aggression. Ethol. Sociobiol. 16, 99–123.

Campbell, A., Muncer, S., Odber, J., 1997. Aggression and testosterone: testing a bio-social model. Aggress. Behav. 23, 229–238.

Cashdan, E., 1995. Hormones, sex, and status in women. Horm. Behav. 29, 354–366.

Cashdan, E., 2003. Hormones and competitive aggression in women. Aggress. Behav. 29, 107–115.

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

Chance, S.E., Brown, R.T., Dabbs Jr., J.M., Casy, R., 2000. Testosterone, intelligence and behavior disorders in young boys. Pers. Individ. Diff. 28, 437–445.

Cherek, D.R., Schnapp, W., Moeller, F.G., Doughterty, D.M., 1996. Laboratory measures of aggressive responding in male parolees with violent and nonviolent histories. Aggress. Behav. 22, 27–36.

Christiansen, K., Knussmann, R., 1987. Androgen levels and components of aggressive behavior in men. Horm. Behav. 21, 170–180.

Cohan, C., Booth, A., Granger, D.A., 2003. Gender moderates the relationship between testosterone and marital satisfaction. J. Fam. Psychol. 17, 29–40.

Cohen, D., Nisbett, R.E., Bowdle, B.F., Schwarz, N., 1996. Insult, aggression, and the Southern culture of honor: An 'experimental ethnology'. J. Pers. Soc. Psychol. 70, 945–960.

Constantino, J.H., Grosz, D., Saenger, P., Chandler, D.W., Nandi, R., Earls, F.J., 1993. Testosterone and aggression in children. J. Am. Acad. Child Adolesc. Psychiatry 32, 1217–1222.

Courtwright, D.T., 1996. Violent Land: Single Men and Social Disorder from the Frontier to the Inner City. Harvard University Press, Cambridge, MA.

Dabbs Jr., J.M., 1992. Testosterone and occupational achievement. Social Forces 70, 813–824.

Dabbs Jr., J.M., 1997. Testosterone, smiling, and facial appearance. J. Nonverbal Behav. 21, 45–55.

Dabbs Jr., J.M., Hargrove, M.F., 1997. Age, testosterone, and behavior among female prisoners. Psychosom. Med. 59, 477–480.

Dabbs Jr., J.M., Mohammed, S., 1992. Male and female salivary testosterone concentrations before and after sexual activity. Physiol. Behav. 52, 195–197.

Dabbs Jr., J.M., Morris, R., 1990. Testosterone, social class, and antisocial behavior in a sample of 4,462 men. Psychol. Sci. 1, 209–211.

Dabbs Jr., J.M., Ruback, R.B., 1988. Saliva testosterone and personality of male college students. Bull. Psychonom. Soc. 26, 244–247.

Dabbs Jr., J.M., Hopper, C.H., Jurkovic, G.J., 1990. Testosterone and personality among college students and military veterans. Pers. Individ. Diff. 11, 1263–1269.

Dabbs Jr., J.M., Hargrove, M.F., Heusel, C., 1996. Testosterone differences among college fraternities: well-behaved vs rambunctious. Pers. Individ. Diff. 20, 157–161.

Dabbs Jr., J.M., Strong, R., Milun, R., 1997. Exploring the mind of testosterone: a bleeper study. J. Res. Pers. 31, 577–587.

Dabbs Jr., J.M., Bernieri, F.J., Strong, R.K., Campo, R., Milun, R., 2001. Going on stage: testosterone in greetings and meetings. J. Res. Pers. 35, 27–40.

Dabbs Jr., J.M., Karpas, A.E., Dyomina, N., Juechter, J., Roberts, A., 2002. Experimental raising or lowering of testosterone level affects mood in normal men and women. Soc. Behav. Personal. 30, 795–806.

Daitzman, R., Zuckerman, M., 1980. Disinhibitory sensation seeking, personality and gonadal hormones. Pers. Individ. Diff. 1, 103–110.

Daly, M., Wilson, M., 1988. Homicide. Aldine de Gruyter, New York.

Davies, N.B., Lundberg, A., 1984. Food distribution and a variable mating system in the dunnock *Prunella modularis*. J. Anim. Ecol. 53, 895–912.

de Ridder, E., Pinxten, R., Eens, M., 2000. Experimental evidence of a testosterone-induced shift from paternal to mating behaviour in a facultatively polygynous songbird. Behav. Ecol. Sociobiol. 49, 24–30.

Drigotas, S.M., Udry, J.R., 1993. Biosocial models of adolescent problem behavior: extension to panel design. Social Biol. 40, 1–7.

Edwards, D.A., 1969. Early androgen stimulation and aggressive behavior in male and female mice. Physiol. Behav. 40, 333–338.

Ehrenkranz, J., Bliss, E., Sheard, M.H., 1974. Plasma testosterone: Correlation with aggressive behavior and social dominance in man. Psychosom. Med. 36, 469–475.

Elias, M., 1981. Serum cortisol, testosterone, and testosterone-binding globulin responses to competitive fighting in human males. Aggress. Behav. 7, 215–224.

Filaire, F., Maso, F., Sagnol, M., Ferrand, C., Lac, G., 2001. Anxiety, hormonal responses, and coping during a judo competition. Aggress. Behav. 27, 55–63.

Finegan, J.-A.K., Niccols, G.A., Sitarenios, G., 1992. Relations between prenatal testosterone levels and cognitive abilities at 4 years. Dev. Psychol. 28, 1075–1089.

Finkelstein, J.W., von Eye, A., Preece, M.A., 1994. The relationship between aggressive behavior and puberty in normal adolescents: a longitudinal study. J. Adolesc. Health 15, 319–326.

Finkelstein, J.W., Susman, E.J., Chinchilli, V.M., Kunselman, S.J., D'Arcangelo, M.R., Schwab, J., Demers, L.M., Liben, L.S., Lookingbill, G., Kulin, H.E., 1997. Estrogen or testosterone increases self-reported aggressive behaviors in hypogonadal adolescents. J. Clin. Endocr. Metab. 82, 2433–2438.

Fleming, A.S., Corter, C., Stallings, J., Steiner, M., 2002. Testosterone and prolactin are associated with emotional responses to infant cries in new fathers. Horm. Behav. 42, 399–413.

Fox, C.A., Ismail, A.A., Love, D.N., Kirkham, K.E., Loraine, J.A., 1971. Studies on the relationship between plasma testosterone levels and human sexual activity. J. Endocrinol. 52, 51–58.

Frank, L.G., Glickman, S.E., Licht, P., 1991. Fetal sibling aggression, precocial development, and androgens in neonatal spotted hyenas. Science 252, 702–704.

Gangestad, S.W., Simpson, J.A., 2000. The evolution of mating: Trade-offs and strategic pluralism. Behav. Brain Sci. 23, 573–644.

Geary, D., 2000. Evolution and proximate expression of human paternal investment. Psychol. Bull. 126, 55–77.

Gerra, G., Avanzini, P., Zaimoviv, A., Fertonani, G., Caccavari, R., Delsignore, R., Gardini, F., Talarico, E., Lecchini, R., Maestri, D., Brambilla, F., 1996. Neurotransmitter and endocrine modulation of aggressive behavior and its components in normal humans. Behav. Brain Res. 81, 19–24.

Gerra, G., Zaimoviv, A., Avanzini, P., Chittolini, B., Giucastro, G., Caccavari, R., Palladino M Maestri, D., Monica, C., Delsignore, R., Brambilla, F., 1997. Neurotransmitter-neuroendocrine responses to experimentally induced aggression in humans: influence of personality variable. Psychiatry Res. 66, 33–43.

Gladue, B.A., Boechler, M., Mccaul, K.D., 1989. Hormonal response to competition in human males. Aggress. Behav. 15, 409–422.

González-Bono, E., Salvador, A., Serrano, M.A., Ricarte, J., 1999. Testosterone, cortisol and mood in a sports team competition. Horm. Behav. 35, 55–62.

González-Bono, E., Salvador, A., Ricarte, J., Serrano, M.A., Arnedo, M., 2000. Testosterone and attribution of successful competition. Aggress. Behav. 26, 235–240.

Grant, V.J., 1992. The measurement of dominance in pregnant women by use of the Simple Adjective Test. Pers. Individ. Diff. 13, 99–102.

Grant, V.J., France, J.T., 2001. Dominance and testosterone in women. Biol. Psychol. 58, 41–47.

Gray Jr., L.E., Whitsett, J.M., Ziesenis, J.S., 1978. Hormonal regulation of aggression towards juveniles in female house mice. Horm. Behav. 11, 310–322.

Gray, A., Jackson, D.N., McKinley, J.B., 1991. The relation between dominance, anger, and hormones in normally aging men: results from the Massachusetts male aging study. Psychosom. Med. 53, 375–385.

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. Evol. Hum. Behav. 23, 193–201.

Greenberg, N., Crews, D., 1990. Endocrine and behavioral responses to aggression and social dominance in the green anole lizard, *Anolis carolinensis*. Gen. Comp. Endocrinol. 77, 246–255.

Gross, M.R., 1985. Disruptive selection for alternative life histories in salmon. Nature 313, 47–48.

Gross, M.R., 1996. Alternative reproductive strategies and tactics: diversity within sexes. TREE 11, 92–98.

Halpern, C.T., Udry, J.R., Campbell, B., Suchindran, C., 1994a. Relationships between aggression and pubertal increases in testosterone: a panel analysis of adolescent males. Social Biol. 40, 8–24.

Halpern, C.T., Udry, J.R., Campbell, B., Suchindran, C., Mason, G.A., 1994b. Testosterone and religiosity as predictors of sexual attitudes and activity among adolescent males: a biosocial model. J. Biosoc. Sci. 26, 217–234.

Halpern, C.T., Udry, J.R., Suchindran, C., 1998. Monthly measures of salivary testosterone predict sexual activity in adolescent males. Arch. Sex Behav. 27, 445–465.

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., Schurmeyer, T., 1985. Changes in saliva testosterone after psychological stimulation in men. Psychoneuroendocrinology 10, 77–81.

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. Biol. Psychiatry 40, 1067–1082.

Hines, M., 1998. Adult testosterone levels have little or no influence on dominance in men. Behav. Brain Sci. 21, 377–378 (commentary on Mazur and Booth 1998).

Hines, M., Golombok, S., Rust, J., Johnston, K.J., Golding, J., et al., 2002. Testosterone during pregnancy and gender role behavior of preschool children: a longitudinal study. Child Dev. 73, 1678–1687.

Hirschenhauser, K., Taborsky, M., Oliveira, T., Canario, A.V.M., Oliveira, R.F., 2004. A test of the 'challenge hypothesis' in cichlid fish: simulated partner and territory intruder experiments. Anim. Behav. 68, 741–750.

Johnson, B.T., 1989. Software for the Meta-analytic Review of Research Literatures. Erlbaum, Hillsdale, NJ.

Josephs, R.A., Newman, M.L., Brown, R.P., Beer, J.M., 2003. Status, testosterone, and human intellectual performance: stereotype threat as status concern. Psychol. Sci. 14, 158–163.

Julian, T., McHenry, P.C., 1989. Relationship of testosterone to men's family functioning at mid-life: a research note. Aggress. Behav. 15, 281–289.

Klein, S.L., Hairston, J.E., Devries, A.C., Nelson, R.J., 1997. Social environmental and steroid hormones affect species and sex differences in immune function among voles. Horm. Behav. 32, 30–39.

Knussmann, R., Christiansen, K., Couwenbergs, C., 1986. Relations between sex hormone levels and sexual behavior in men. Arch. Sex Behav. 15, 429–445.

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. Arch. Sex Behav. 5, 125–132.

Lacourse, E., Côté, S., Nagin, D., Vitaro, F., Brendgen, M., Tremblay, R.E., 2002. A longitudinal-experimental approach to testing theories of antisocial behavior development. Dev. Psychopathol. 14, 909–924.

Lutchmaya, S., Baron-Cohen, S., Raggatt, P., 2002. Foetal testosterone and eye contact in 12-month-old human infants. Inf. Behav. Dev. 25, 327–335.

Manning, J.T., Bundred, P.E., Newton, D.J., Flanagan, B.F., 2003. The second to fourth digit ratio and variation in the androgen receptor gene. Evol. Hum. Behav. 24, 399–405.

Maras, A., Laucht, M., Gerdes, D., Wilhelm, C., Lewicka, S., Haack, D., Malisova, L., Schmidt, M.H., 2003. Association of testosterone and hihydrotestosterone with externalizing behavior in adolescent boys and girls. Psychoneuroendocrinology 28, 932–940.

Mazur, A., 1995. Biosocial models of deviant behavior among army veterans. Biol. Psychol. 41, 171–193.

Mazur, A., Booth, A., 1998. Testosterone and dominance in men. Behav. Brain Sci. 21, 353–397.

Mazur, A., Lamb, T.A., 1980. Testosterone, status and mood in human males. Horm. Behav. 14, 236–246.

Mazur, A., Booth, A., Dabbs Jr., J.M., 1992. Testosterone and chess competition. Soc. Psychol. Q. 55, 70–77.

Mazur, A., Susman, E.J., Edelbrock, S., 1997. Sex differences in testosterone response to a video game contest. Evol. Hum. Behav. 18, 317–326.

McCaul, K.D., Gladue, B.A., Joppa, M., 1992. Winning, losing, mood, and testosterone. Horm. Behav. 26, 486–504.

Moore, M.C., 1986. Circulating steroid hormones during rapid aggressive responses of territorial male mountain spiny lizards, Sceloporus jarrovi. Horm. Behav. 21, 511–521.

Moore, I.T., Wada, H., Perfito, N., Busch, D.S., Hahn, T.P., Wingfield, J.C., 2004. Territoriality and testosterone in an equatorial population of rufous-collared sparrows, Zonotrichia capensis. Anim. Behav. 67, 411–420.

Muller, M.N., Wrangham, R.W., 2004. Dominance, aggression and testosterone in wild chimpanzees: a test of the 'challenge' hypothesis. Anim. Behav. 67, 113–123.

Neave, N., Wolfson, S., 2003. Testosterone, territoriality, and the 'home advantage'. Physiol. Behav. 78, 269–275.

Nisbett, R.E., Cohen, D., 1996. Culture of Honor: The Psychology of Violence in the South. Westview Press, Boulder, CO.

Nordenström, A., Servin, A., Bohlin, G., Larsson, A., Wedell, A., 2002. Sex-typed toy play behavior correlates with the degree of prenatal androgen exposure assessed by CYP21 genotype in girls with congenital adrenal hyperplasia. J. Clin. Endocr. Metab. 87, 5119–5124.

O'Connor, D.B., Archer, J., Hair, W.H., Wu, F.C.W., 2001a. Exogenous testosterone, aggression, and mood in eugonadal and hypogonadal men. Physiol. Behav. 75, 557–566.

O'Connor, D.B., Archer, J., Wu, F.C.W., 2001b. Measuring aggression: self-reports, partner reports and responses to provoking scenarios. Aggress. Behav. 27, 79–101.

O'Connor, D.B., Archer, J., Wu, F.C.W., 2004. Effects of testosterone on mood, aggression and sexual behavior in young men: a double-blind, placebo-controlled, cross-over study. J. Clin. Endocr. Metab. 86, 2837–2845.

Olweus, D., Mattsson, A., Schalling, D., Low, H., 1980. Testosterone, aggression, physical and personality dimensions in normal adolescent males. Psychosom. Med. 42, 253–269.

Pankhurst, N.W., Barnett, C.W., 1993. Relationship of population density, territorial interaction and plasma levels of gonadal steroids in spawning male demoiselles Chromis dispilus (Pisces: Pomacentridae). Gen. Comp. Endocrinol. 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. Int. J. Sports Med. 20, 109–113.

Persky, H., Smith, K.D., Basu, G.K., 1971. Relation of psychologic measures of aggression and hostility to testosterone production in man. Psychosom. Med. 33, 265–277.

Peters, A., 2002. Testosterone and the trade-off between mating and paternal effort in extrapair-superb fairy-wrens. Anim. Behav. 64, 103–112.

Pope Jr., H.G., Kouri, E.M., Hudson, J.I., 2000. Effects of supraphysiological doses of testosterone on mood and aggression in normal men: a randomized controlled trial. Arch. Gen. Psychiatry 57, 133–140.

Purifoy, F.E., Koopmans, L.H., 1979. Androstenedione, testosterone and free testosterone in women of various occupations. Social Biol. 26, 179–188.

Ritter, D., 2003. Effects of menstrual cycle phase on reporting levels of aggression using the Buss and Perry Aggression Questionnaire. Aggress. Behav. 29, 531–538.

Roney, J.R., Maher, S.V., Maestripieri, D., 2003. Behavioral and hormonal responses of men to brief interactions with women. Evol. Hum. Behav. 24, 365–375.

Rose, R.M., Holaday, J.W., Bernstein, I.S., 1971. Plasma testosterone, dominance rank and aggressive behaviour in male rhesus monkeys. Nature 231, 366–368.

Rose, R.M., Gordon, T.P., Bernstein, I.S., 1972. Plasma testosterone levels in the male rhesus: influences of sexual and social stimuli. Science 178, 643–645.

Rose, R.M., Bernstein, I.S., Gordon, T.P., Catlin, S.F., 1974. Androgens and aggression: a review and recent findings in primates, in: Holloway, R.L. (Ed.), Primate Aggression, Territoriality, and Xenophobia. Academic Press, New York, pp. 275–304.

Rose, R.M., Bernstein, I.S., Gordon, T.P., 1975. Consequences of social conflict on plasma testosterone levels in rhesus monkeys. Psychosom. Med. 37, 50–58.

Ruff, J.R., 2001. Violence in Early Modern Europe 1500–1800. Cambridge University Press, Cambridge, UK.

Salvador, A., Simon, V., Suay, F., Llorens, L., 1987. Testosterone and cortisol responses to competitive fighting: a pilot study. Aggress. Behav. 13, 9–13.

Salvador, A., Simon, V., Suay, F. Hormonal measures and behavioral assessment in young male judo competitors. Unpublished manuscript; 1991.

Salvador, A., Suay, F., Martinez-Sanchis, S., Simon, V.M., Brain, P.F., 1999. Correlating testosterone and fighting in male participants in judo contests. Physiol. Behav. 68, 205–209.

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

Sanchez-Martin, J.R., Fano, E., Ahedo, L., Cardas, J., Brain, P.F., Azpiroz, A., 2000. Relating testosterone levels and free play social behavior in male and female preschool children. Psychoneuroendocrinology 25, 773–783.

Sapolsky, R.M., 1991. Testicular function, social rank and personality among wild baboons. Psychoneuroendocrinology 16, 281–293.

Scaramella, T.J., Brown, W.A., 1976. Serum testosterone and aggressiveness in hockey players. Psychosom. Med. 40, 262–265.

Scerbo, A.S.S., Kolko, D.J., 1994. Salivary testosterone and cortisol in disruptive children: relationship to aggressive, hyperactive and internalizing behaviors. J. Am. Acad. Child Adolesc. Psychiatry 33, 1174–1184.

Schaal, N., Tremblay, R.E., Soussignan, R., Susman, E.J., 1996. Male testosterone linked to high social dominance but low physical aggression in early adolescence. J. Am. Acad. Child Adolesc. Psychiatry 34, 1322–1330.

Schultheiss, O.C., Rohde, W., 2002. Implicit power motivation predicts men's testosterone changes and implicit learning in a contest situation. Horm. Behav. 41, 195–202.

Schultheiss, O.C., Campbell, K.L., McClelland, D.C., 1999. Implicit power motivation moderates men's testosterone response to imagined and real dominance success. Horm. Behav. 36, 234–241.

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. Horm. Behav. 43, 293–301.

Schultheiss, O.C., Wirth, M.M., Torges, C.M., Pang, J.S., Villacorta, M.A., Welsh, K.M., 2005. Effects of implicit power motivation on men's and women's implicit learning and testosterone changes after social victory or defeat. J. Pers. Soc. Psychol. 88, 174–188.

Seigel, J.M., 1986. The multi-dimensional anger inventory. J. Pers. Soc. Psychol. 51, 191–200.

Smith, C.P., 1992. Motivation and Personality: Handbook of Thematic Content Analysis. Cambridge University Press, New York.

Smith, E.A., 1998. Is Tibetan polyandry adaptive? Methodological and metatheoretical analyses. Hum. Nat. 9, 225–261.

Stanford, M.S., Houston, R.J., Villemarette-Pittman, N.R., Greve, K.W., 2003. Premeditated aggression: clinical assessment and cognitive psychophysiology. Pers. Individ. Diff. 34, 773–781.

Stoléru, S., Grégoire, M-C., Gérard, D., Decety, J., Lafarge, E., Cinotti, L., Lavenne, F., Le Bars, D., Vernet-Maury, E., Rada, H., Collet, C., Mazoyer, B., Forest, M.G., Magnin, F., Spira, A., Comar, D., 1999. Neuroanatomical correlates of visually evoked sexual arousal in human males. Arch. Sex Behav. 28, 1–21.

Storey, A.E., Walsh, C.J., Quinton, R.L., Wynne-Edwards, K.E., 2000. Hormonal correlates of paternal responsiveness in new and expectant fathers. Evol. Hum. Behav. 21, 79–95.

Strong, R.K., Dabbs, J.R.J.M., 2000. Testosterone and behavior in normal young children. Pers. Individ. Diff. 28, 909–915.

Su, T-P., Pagliaro, M., Schmidt, P.J., Pickar, D., Wolkowitz, O., Rubinow, D.R., 1993. Neuropsychiatric effects of anabolic steroids in male normal volunteers. JAMA 269, 2760–2764.

Suay, F., Salvador, A., González-Bono, E., Sanchis, C., Simon, V.M., Montoro, J.B., 1996. Testosterona y evaluacion de la conducta adresiva en jovenes judokas. Rev. Psicol. Deporte 9/10, 79–91.

Suay, F., Salvador, A., González-Bono, E., Sanchis, C., Martinez, M., Martinez-Sanchis, S., Simon, V.M., Montoro, J.B., 1999. Effects of competition and its outcome on serum testosterone, cortisol and prolactin. Psychoneuroendocrinology 24, 551–566.

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

Thompson, C.W., Moore, M.C., 1992. Behavioral and hormonal correlates of alternative reproductive strategies in a polygynous lizard: tests of the relative plasticity and challenge hypotheses. Horm. Behav. 26, 568–585.

Tricker, R., Casaburi, R., Storer, T.W., Clevenger, B., Berman, N., Shirazi, A., Bhasin, S., 1996. The effects of supraphysiological doses of testosterone on angry behavior in healthy eugonadal men—a clinical research center study. J. Clin. Endocr. Metab. 81, 3754–3758.

Udry, J.R., 1990. Biosocial models of adolescent problem behaviors. Social Biol. 37, 1–10.

Udry, J.R., Talbert, L.M., 1988. Sex hormone effects on personality at puberty. J. Pers. Soc. Psychol. 54, 291–295.

Underwood, M.K., 2003. Social Aggression Among Girls. Guilford Press, New York.

van Bokhoven, I., van Goozen, S.H.M., van Engeland, H., Schaal, B., Arseneault, L., Seguin, J.R., Assaad, J.-M., Nagin, D.S., Vitaro, F., Tremblay, R.E., unpublished manuscript. Salivary testosterone and aggression, delinquency, and social dominance in a population-based sample of adolescent males.

van Duyse, E., Pinxten, R., Eens, M., 2000. Does testosterone affect the trade-off between investment in sexual/territorial behaviour and parental care in male great tits. Behaviour 137, 1503–1515.

van Goozen, S.H.M., Frijda, N.H., van de Poll, N.E., 1994a. Anger and aggression in women: influence of sports choice and testosterone administration. Aggress. Behav. 20, 213–222.

van Goozen, S.H.M., Frijda, N.H., Kindt, M., van de Poll, N.E., 1994b. Anger proneness in women: development and validation of the Anger Situation Questionnaire (ASQ). Aggress. Behav. 20, 79–100.

van Goozen, S.H.M., Matthys, W., Cohen-Kettenis, P.T., Thijssen, J.H.H., van England, H., 1998. Adrenal androgens and aggression in conduct disorder prepubertal boys and normal controls. Biol. Psychiatry 43, 156–158.

van Honk, J., Tuiten, A., Verbaten, R., van den Hout, M., Koppeschaar, H., Thijssen, J., de Haan, E., 1999. Correlations among salivary testosterone, mood and selective attention to threat in humans. Horm. Behav. 36, 17–24.

van Honk, J., Tuiten, A., Hermans, E., Putman, P., Koppeschaar, H., Thijssen, J., Verbaten, R., van Doornen, L., 2001. A single administration of testosterone induces cardiac acceleration response to angry faces in healthy young women. Behav. Neurosci. 115, 238–242.

van Honk, J., Schutter, D.J.L.G., Hermans, E.J., Putman, P., Tuiten, A., Koppeschaar, H., 2004. Testosterone shifts the balance between sensitivity for punishment and reward in healthy young women. Psychoneuroendocrinology 29, 937–943.

Van Rhijn, J.G., 1974. Behavioural dimorphism in male ruffs Philomachus pugnax (L.). Behaviour 47, 153–229.

Vleck, C.M., Brown, J.L., 1999. Testosterone and social and reproductive behaviour in Aphelocoma jays. Anim. Behav. 58, 943–951.

von der Pahlen, B., Lindman, R., Sarkola, T., Mäkisalo, H., Eriksson, C.J.P., 2002. An exploratory study on self-evaluated aggression and androgens in women. Aggress. Behav. 28, 273–280.

Wingfield, J.C., 1984. Androgens and mating systems: testosterone-induced polygyny in normally monogamous birds. The Auk 101, 665–671.

Wingfield, J.C., 1985. Short-term changes in plasma levels of hormones during establishment and defense of a breeding territory in male song sparrows, *Melospiza melodia*. Horm. Behav. 19, 174–187.

Wingfield, J.C., Hegner, R.E., Dufty Jr., A.M., Ball, G.F., 1990. The 'challenge hypothesis': theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. Am. Nat. 136, 829–846.

Wingfield, J.C., Jacobs, J.D., Tramontin, A.D., Perfito, N., Meddle, S., Maney, D.L., Soma, K., 2000. Toward an ecological basis of hormone–behavior interactions in reproduction in birds, in: Wallen, K., Schneider, J.E. (Eds.), Reproduction in Context: Social and Environmental Influences on Reproductive Physiology and Human Behavior. MIT Press, Cambridge, MA, pp. 85–128.

Wingfield, J.C., Lynn, S.E., Soma, K.K., 2001. Avoiding the 'costs' of testosterone: ecological bases of hormone–behavior interactions. Brain Behav. Evol. 57, 239–251.

Wynne Edwards, K.E., 2001. Hormonal changes in mammalian fathers. Horm. Behav. 40, 139–145.

Yates, W.R., Perry, P.J., MacIndoe, J., Holman, T., Ellingrod, V., 1999. Psychosexual effects of three doses of testosterone cycling in normal men. Biol. Psychiatry 45, 254–260.

Zumpe, D., Michael, R.P., 1996. Social factors modulate the effects of hormones on the sexual and aggressive behavior of macaques. Am. J. Primatol. 38, 233–261.